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A global meta-analysis of grazing effects on plant richness

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ABSTRACT

A major challenge in rangeland ecology is understanding diverse responses of diversity to grazing, what factors determine these responses and what their relative importance is. Numerous site-level studies have explored grazing-diversity relations, but meta-analyses of these empirical results at a global scale are scarce. Our goals were to estimate the mean effect of grazing on plant richness and to assess the relative importance of different variables at a global scale. We conducted a global meta-analysis of 259 comparisons of plant richness in grazed vs. ungrazed sites from 96 published studies. Then, we performed analyses of subgroup, meta-regression and correlation for testing the relative roles of regional and local variables (e.g. evolutionary history of grazing, aridity, stocking rate, etc.).

Globally, grazing significantly increased plant richness compared to grazing exclusion, especially in wet grasslands. The effect of evolutionary history of grazing was insignificant, which cannot support the major perception behind Milchunas-Sala-Lauenroth (MSL) model. Aridity, vegetation type, and stocking rate were three important variables that together explained 41 % of the global variation in plant richness. The roles of stocking rate and duration of grazing exclusion were revealed only when aridity and vegetation type were added to the analyses, which showed a stronger effect of stocking rate in wet areas but a stronger effect of the duration of grazing exclusion in dry areas. Changes in plant richness were significantly correlated with changes in soil carbon and nitrogen, both showing hump-shaped patterns.

Our findings substantiate that scholars may improve existing theories (e.g. the MSL model, the intermediate disturbance hypothesis) through further expounding the interactions between grazing variables and aridity and vegetation type. Rangeland managers need to devise local-scale grazing strategies for conserving plant diversity according to site-specific conditions, rather than adopting a one-size-fits-all solution.

1. Introduction

Livestock grazing is the most common anthropogenic disturbance in rangeland ecosystems (Alkemade, 2013). Grazing plays a prominent role in maintaining biodiversity (Mcnaughton, 1983; Yang et al., 2006; Yuan et al., 2016) and productivity (Schönbach et al., 2011; Alkemade et al., 2013), as well as providing livestock production to human beings, through modifications of ecological processes (Mcsherry and Ritchie, 2013; Hautier, 2015; Gao and Carmel, 2015). However, in some areas, grazing may play a negative role by causing vegetation and soil degradation (Wang et al., 2007; Pulido et al., 2016) and further reducing animal production. Therefore, it is essential to understand what factors influence grazing effects on vegetation, and how their mechanisms work.

Over the last several decades, numerous studies on grazing were conducted around the world. Empirical and theoretical studies have concluded that whether the effects of grazing on plant richness are positive, negative, or neutral depends largely on (or can be explained by) regional variables (evolutionary history of grazing, aridity, vegetation type, etc.), local variables (also termed site-specific variables, e.g. grazing intensity, herbivore types, grazing regimes, soil nutrients, species composition, etc.), and temporal and spatial scales and their interactions (Olff and Ritchie, 1998; Bakker et al., 2006). The MSL model (Milchunas et al., 1988) introduced evolutionary history of grazing as a main explanatory variable of the response of plant diversity to grazing, together with grazing intensity and aridity. Later, Cingolani et al. (2005) modified the MSL model by integrating the state-and-transition model with irreversible and non-resilient ecological processes in regions with short evolutionary history of grazing; their rationale was that plant communities with a long evolutionary history of grazing are more resilient than those with a short grazing history. Generally, in wet areas with high productivity, where the Intermediate Disturbance Hypothesis (IDH) tends to be strongly supported (Gao and Carmel In Review), moderate grazing (compared to no-, low- or heavy-grazing) can

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promote at maximal competition release, by reducing the dominance of competitive superior species and thus increasing plant diversity. By contrast, in dry areas with relatively low productivity, interannual precipitation seems to have a stronger effect on plant communities than do grazing variables (Olff and Ritchies, 1998).

Besides evolutionary history of grazing, aridity and grazing intensity, some studies also tested how herbivore types (e.g. cattle grazing, sheep grazing, or mixed grazing, Fensham, 1998; De Bello et al., 2007; Xu et al., 2014), herbivore sizes (large vs. small, Bakker et al., 2006), grazing regimes (seasonal and continuous, Sternberg et al., 2015), and topography (lowland/upland, north/south, Carmel and Kadmon, 1999; Osem et al., 2002) influence grazing effects on plants. However, most of these studies consisted of site-specific grazing experiments or were restricted to specific vegetation types. Surprisingly, very few studies attempted to derive general conclusions from the large volume of grazing research at a global scale (Milchunas and Lauenroth, 1993; Díaz et al., 2007; Herrero-Jáuregui and Oesterheld, 2018). Díaz et al. (2007) focused on plant trait responses to grazing and concluded that the response rules varied with different climate and herbivore history; however, they did not consider grazing intensities. Herrero-Jáuregui and Oesterheld (2018) compared the responses of plant richness and diversity in two grazing-intensity pairs, low vs. moderate and high vs. moderate, and found that more negative effects on richness were observed with increasing stocking rates in arid, low productivity systems than in subhumid and humid systems. However, they treated moderate grazing, rather than grazing exclusion, as a control and they did not consider possible effects of vegetation types (e.g. grasslands, shrublands). Milchunas and Lauenroth (1993) comprehensively explained the variations in changes of species composition using regression models. They found that aboveground net primary productivity (ANPP), evolutionary history of grazing, and level of consumption significantly affected plant community composition, in decreasing order of importance. Another finding was that the effect of grazing on species composition was different in grasslands compared to shrublands (Milchunas and Lauenroth, 1993). Although this research was quantitative, it was not a formal meta-analysis, and its conclusions should be reviewed with caution. Moreover, around 30 years have passed since its publication; many new studies were conducted since. Given the paucity of syntheses and meta-analyses in the domain of grazing impacts on vegetation, it would be valuable to fill this gap.

Thus, the goal of this study is to conduct a formal global meta-analysis to estimate the impact of grazing on plant diversity. Specifically, we use species richness as an index of plant diversity, since other diversity indices mix information on species richness and species evenness (i.e. the relative abundance of species); these indices may be less robust (due to unstable species abundance) than species richness alone. We compared our results with previous findings and asked whether, and if so, how the effects of grazing on plant species richness can be explained by the following factors: regional and local (or site-specific) variables, including evolutionary history of grazing, aridity, vegetation type, stocking rate, duration of grazing exclusion, soil carbon and nitrogen, aboveground biomass, vegetation cover, and species evenness. To this end, we conducted subgroup analyses, meta-regression analyses and correlation analyses, and assessed the relative importance of these factors at a global scale. We believe that the results of this research can broaden our understanding of the effects of grazing on plant richness and their correlations with environmental, ecosystem and grazing variables at a global scale. We hope that these findings may also enhance the scientific basis of decision-making in rangeland management.

2. Methods

2.1. Literature search

We used the Web of Science database (https://webofknowledge.com/) to search for titles, abstracts and author keywords of articles published between 1960 and 2017 that included the following search strings: *grazing* AND (*richness* or *diversity*) AND *plant*. We then eliminated studies that concerned aquatic environments or invertebrate grazers, by searching the collection for the following keywords: *seagrass, aquatic, marine, lake, algae, phytoplankton, insect, nematode, termite, grasshopper, beetle*. This search yielded 5032 articles. We then manually screened these articles and selected only those that satisfied all of the following criteria:

(1) Studies that reported species richness and its standard error or standard deviation, and sample size under both grazing exclusion and grazing. Grazing treatments may include several grazing intensities.
(2) Studies whose grazing animals are livestock, e.g. cattle, goats, sheep, horse, etc.
(3) Studies that were conducted in terrestrial ecosystems, excluding aquatic ecosystems. Salt marshes were included.
(4) Studies that reported geographic location, in order to document their aridity.

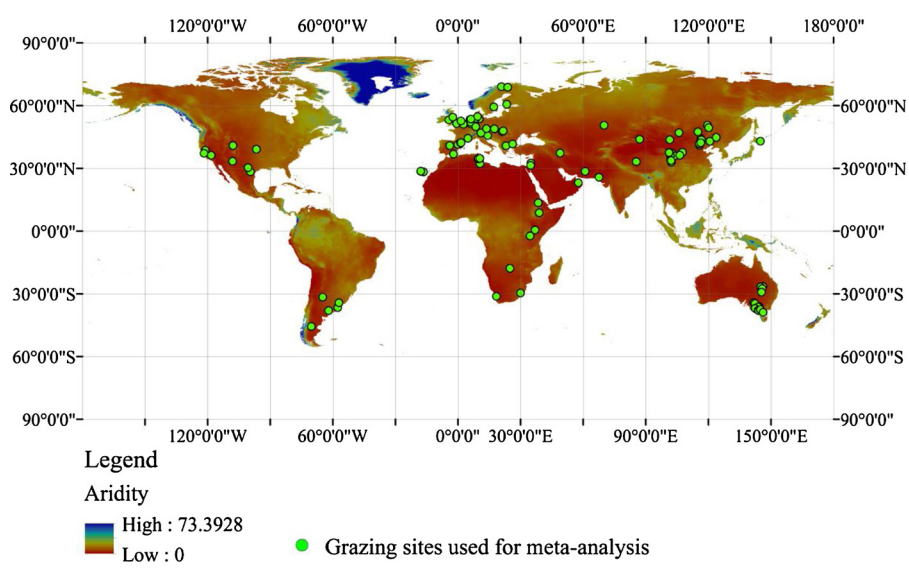

Fig. 1. Map of selected grazing sites for meta-analysis.

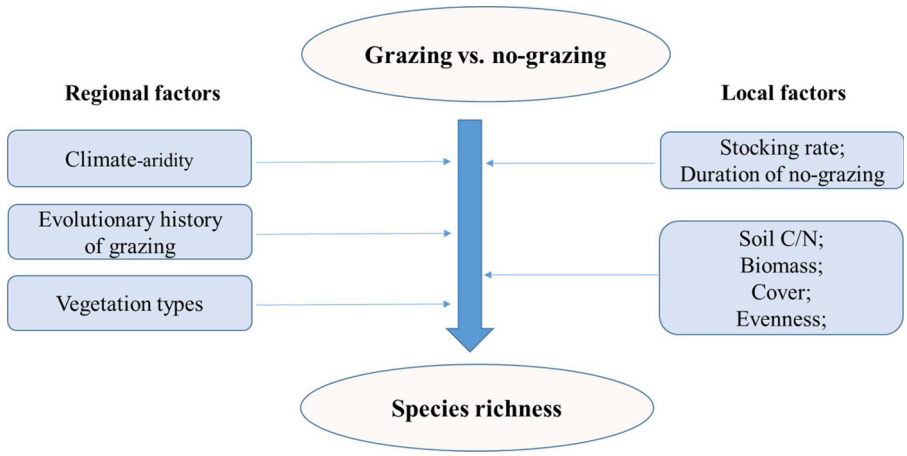

Fig. 2. The possible factors that cause heterogeneity in effect sizes of grazing on species richness.

After searching the literature, we found 98 articles with 268 grazing vs. grazing exclusion comparisons of species richness (Appendix A and Fig. 1). Most (70.4 %) of the studies were from Asia and Europe; 76.8 % of the studies were conducted in grassland areas, and 23.2 % were in shrublands.

2.2. Effect size and random-effects model

We extracted species richness information from each study, including their raw observation values, standard deviations (or standard errors), sample sizes and sampling unit sizes. If studies had two or more grazing sites, we included data from all grazing sites as independent records in the meta-analysis database. For those studies that presented species richness within multiple nested units (e.g. quadrat, subplot and plot), or in different years, we used only the data of the largest unit and the most recent year. Standard mean difference (SMD, Eq. 1) was used to calculate the effect size of grazing on species richness within each study.

$$ES_{ij} = SMD = \frac{\mu_g - \mu_c}{s},\ s = V_{ES_{ij}} = \sqrt{\frac{(N_g - 1)^* s_g^2 + (N_c - 1)^* s_c^2}{N_g + N_c - 2}} \quad (1)$$

ES_{ij} : the effect size of grazing treatment j in study i; μ_g: the mean value of richness for grazing treatment; μ_c: the mean value of richness for grazing exclusion treatment; $V_{ES_{ij}}$: the variance of ES_{ij} within a study; s_g: the standard deviation of richness for grazing treatment; s_c: the standard deviation of richness for grazing exclusion treatment; N_g: the sample size for grazing treatment; N_c: the sample size for grazing exclusion treatment;

Standard mean difference is adequate for comparing between studies using different richness matrices (e.g. the average number of species, accumulative number of species) and for comparing between species-rich and species-poor sites.

We considered two sources of variance of effect sizes, within-study variance ($V_{ES_{ij}}$) and between-study variance (τ^2). We chose a random-effects model and used Residual maximum likelihood (REML) estimation to estimate the variance between studies. Then, we weighted each single effect size by the inverse of its total variance ($V_{ES_{ij}} + \tau^2$) (Borenstein et al., 2009).

$$\tau^2 = \frac{Q - df}{C} \quad (2)$$

$$Q = \sum w_{ij}{}^*ES_{ij}{}^2 - \frac{(\sum w_{ij}{}^*ES_{ij})^2}{\sum w_{ij}};\ C = \sum w_{ij} - \frac{\sum w_{ij}^2}{\sum w_{ij}};\ W_{ij} = \frac{1}{V_{ES_{ij}}};\ df = k - 1 \quad (3)$$

In Eqs. 2 and 3, τ^2 is the variance between studies; Q is a statistic to test true variance between studies; W_{ij} is the weight of each effect size; C is a scaling factor; df is the degree of freedom; k is the number of studies.

I^2 was used to estimate the proportion of total variation caused by real differences between studies and to measure the heterogeneity among effect sizes (Higgins et al., 2003; Borenstein et al., 2009). I^2 can be calculated as the ratio of between-studies variance to total variation in species richness (Eq. 4).

$$I^2 = \frac{\tau^2}{\tau^2 + V_{ES_{ij}}} \quad (4)$$

We conducted regression deletion diagnostics (Belsley et al., 1980; Baujat et al., 2002; Fox and Weisberg, 2011) to evaluate the influence of each data point and detect possible outliers (Fig. B.1, Appendix B). Finally, we included 259 comparisons of species richness between grazing and grazing exclusion from 98 published studies. To detect possible skewness in effect sizes from publication bias, we checked the funnel plot of standard errors on effect sizes and found the funnel plot was symmetric, indicating no publication bias (Fig. B.2, Appendix B). In addition, we found no correlations between effect sizes and sampling unit sizes (Fig. B.3, Appendix B).

2.3. Heterogeneity analysis

In order to estimate heterogeneity in effect size of grazing on species richness, and stratify the source of heterogeneity, we conducted subgroup and meta-regression analyses (Borenstein et al., 2009).

Following the results of previous research (Dyksterhuis, 1949; Noy-Meir, 1975; Milchunas et al., 1988; Milchunas and Lauenroth, 1993; Proulx and Mazumder, 1998), we listed the potential factors that may lead to heterogeneity in effect size: climate, evolutionary history of grazing, vegetation type, stocking rate, duration of grazing exclusion, soil carbon (C) and nitrogen (N), biomass, vegetation cover and species evenness (Fig. 2). We quantified these factors using the following indices and surrogates.

Aridity (AI) was used as an indicator of climate. The aridity of each grazing site was extracted from the Global-Aridity data set of the Consortium for Spatial Information website (http://www.csi.cgiar.org) based on its geographical coordinates. When AI is smaller than 0.5, it belongs to arid and semi-arid areas (here we termed them as 'dry areas'); when AI is larger than 0.5, it belongs to subhumid and humid areas (here we termed them as 'wet areas') (UNEP, 1997).

In this paper, we used Old world (Asia, Europe and Africa) and New world (Americas and Australia) to represent long- and short evolutionary history of grazing, respectively. Perhaps, this way is general and simplistic. However, attempts to define the length of evolutionary history of grazing in more detail may be speculative (Milchunas et al.,

Table 1
Animal unit equivalents for various herbivores.
Source: Vallentine, 1990, p 279.

Animals	Animal unit (AU)	Note
cow-calf pair	1	
cattle	1.4	usually refers to large cow
sheep/goat	0.25	the average of non-lactating mature sheep and ewe or lamb pair
yak	0.75	
horse	1.083	the average among one-, two- and three-year old and over
pony	0.75	the same with one-year old
bison	1.25	the average of bison cow and bison bull

1988 and 1993; Cingolani et al., 2005; Díaz et al., 2007). Therefore, a more precise classification of long- vs. short evolutionary history of livestock grazing would probably still conform to the old- vs. new world classification.

Following the original description of vegetation in each study, we distinguished between two vegetation types, grasslands and shrublands, and between several ecosystem types (Appendix A). We selected six major and typical ecosystem types for subgroup analysis: steppe, prairie (i.e. tallgrass prairie), alpine meadow, Mediterranean (Mediterranean open shrublands and montane grasslands), savanna and salt marsh and riparian.

Different studies quantified grazing intensities differently, e.g. stocking rate, distance from water point or paddock, degradation degree, species composition, etc. Only stocking rate enables quantitative comparisons across studies, and therefore, only 42 studies that reported stocking rates were included in the heterogeneity analysis. In order to make different units of stocking rate comparable among studies, we normalized the raw values of stocking rates to standardized animal units by using the criteria shown in Table 1 (Vallentine, 1990).

The period of grazing is a complicated issue. Some areas may have been grazed for thousands of years, yet the reported experimental period may be just three or five years. Thus, instead of using the period of grazing, we used the duration of grazing exclusion and evaluated its influence on effect size (in richness). If a paper reported a range of durations of grazing exclusion, we used the mean value.

The effects of soil C and N, aboveground biomass, vegetation cover and species evenness were calculated as the difference in these parameters between grazing and grazing exclusion as follows:

$$X_{Diff} = \frac{X_G - X_{NG}}{X_{NG}} \quad (5)$$

Where X_G and X_{NG} are the values of factor X (i.e. soil C and N, aboveground biomass, vegetation cover and species evenness) under grazing, and grazing exclusion treatments, respectively.

We conducted subgroup analyses for categorical variables (evolutionary history of grazing, continent, vegetation- and ecosystem type), in order to estimate their mean effect sizes and to test for significant differences between subgroups. Then, we used meta-regression in order to quantify the proportion of variation in effect size that can be explained by evolutionary history of grazing, aridity, vegetation type (grasslands and shrublands), stocking rate and duration of grazing exclusion. In this procedure, effect size was the dependent variable; evolutionary history of grazing, aridity, vegetation type, stocking rate and duration of grazing exclusion were the independent variables. We added categorical variables into the meta-regression as dummy variables. Given the importance of aridity in meta-regression analysis for all data (see results section below), we decided to add two meta-regression analyses, conducted separately for wet areas and for dry areas. We did not have enough data to use meta-regression to evaluate the five following variables: soil C/N, aboveground biomass, vegetation cover and species evenness. Instead, we only looked for possible correlations between these variables and the effect sizes of grazing on plant richness.

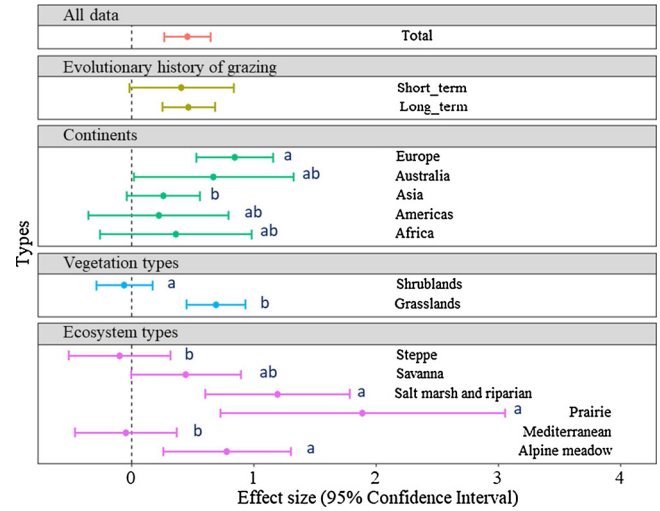

Fig. 3. The summary effect size (standard mean difference) (± 95 % confidence intervals) in species richness for all grazing sites (n = 259), sites with long- and short evolutionary history of grazing (n_{short} = 45, n_{long} = 214), and sites in different continents (n_{Europe} = 71, $n_{Australia}$ = 17, n_{Asia} = 109, $n_{Americas}$ = 28, n_{Africa} = 34), vegetation types ($n_{shrublands}$ = 73, $n_{grasslands}$ = 186), and ecosystem types (n_{steppe} = 74, $n_{savanna}$ = 25, $n_{salt\ marsh\ and\ riparian}$ = 17, $n_{prairie}$ = 8, $n_{mediterranean}$ = 35, $n_{alpine\ meadow}$ = 35). n is the sample size, the same as follows. Black bars indicate confidence intervals of effect sizes. Bars not sharing the same letters are significantly different at $P < 0.05$.

All statistical analyses and plots were performed in R packages "metafor" (Viechtbauer, 2010), multcomp (Hothorn et al., 2008) and "ggplot2" (Wickham, 2016).

3. Results

3.1. Overall effects of grazing on species richness

Across all experiments at a global scale, grazing significantly increased species richness (Fig. 3). I^2 was larger than 90 %, indicating a high heterogeneity among studies. Our sensitivity analyses demonstrated that the effects of grazing on species richness were robust to the inclusion and removal of outlier studies (Fig. B.1, Appendix B).

3.2. Evolutionary history of grazing

Grazing with long evolutionary history had a significant positive effect on species richness ($P < 0.0001$). In contrast, grazing with short evolutionary history had a similar mean effect size but there was large variability between studies ($P = 0.0561$, Fig. 3). The small difference in mean effect sizes between grazing with long- and short history was insignificant, and the same trend was observed also at a continental level. The Americas and Australia (both with a short history of grazing) had a similar mean effect size of grazing as Asia, Europe and Africa (all with a long history of grazing, Fig. 3). Asia and Europe, both with a long history of grazing, differed from each other in their mean effect sizes, with Europe showing a significantly larger positive effect of grazing (Fig. 3).

3.3. Vegetation- and ecosystem type

The effect of grazing differed significantly between grasslands and shrublands worldwide. In grasslands, effect size was significantly positive, while in shrublands it was insignificantly negative (Fig. 3). We found a significantly positive effect of grazing on richness in tallgrass prairie, salt marsh, riparian, alpine meadow, and savanna, and an

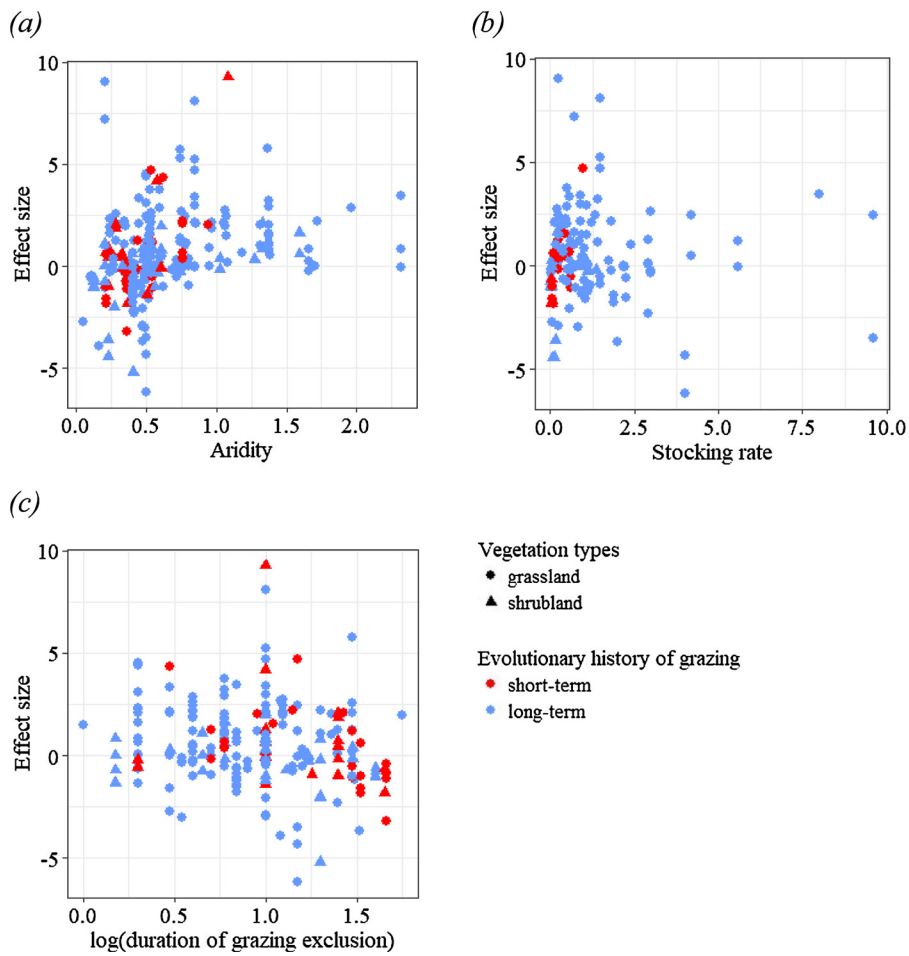

Fig. 4. Scatter plots between effect sizes and aridity (n = 257) (a), stocking rate (n = 133) (b), and duration of grazing exclusion (n = 228) (c).

insignificant effect in steppe and in Mediterranean vegetation (Fig. 3).

3.4. The relative roles of aridity, vegetation type, stocking rate, and duration of grazing exclusion

The scatter plot of effect sizes of grazing on richness against aridity (Fig. 4a) showed that in arid regions (AI ≤ 0.51), the mean effect size was negative, on average, and highly variable ($effect\ size_{AI \leq 0.51}$ = -0.2453, P = 0.0712); while in wet regions (AI > 0.51), grazing effects were significantly positive ($effect\ size_{AI > 0.51}$ = 1.0789, P < 0.0001). The scatter plots revealed no obvious correlations between effect sizes for either stocking rate or duration of grazing exclusion (Fig. 4 b and c).

At a global scale, aridity showed a hump-shaped relationship with grazing effects, and explained 24.21 % of the variation in effect sizes, while vegetation type, as a dummy variable including two classes of grasslands and shrublands, explained only 7.16 % of the variation (models I and II, Table 2). However, in wet areas, vegetation type explained a greater percentage of the variation in effect sizes than did aridity (models I and II, Table 3). By contrast, in dry areas, vegetation type was insignificant in any model we tested. Neither at a global scale nor in wet or dry areas did evolutionary history of grazing explain the variation in effect sizes.

At a global scale, stocking rate alone did not explain any of the variation in effect sizes. However, stocking rate together with aridity and vegetation type explained 41.21 % of the variation in effect sizes (model IV, Table 2), much higher than the proportion explained by aridity, vegetation type, and duration of grazing exclusion together (15.62 %, model VI, Table 2). In wet areas, the effect of stocking rate alone was insignificant, but stocking rates together with aridity and vegetation type explained 39.88 % of the variation in effect sizes (model III, Table 3). By contrast, the effect of duration of grazing exclusion was not significant, either alone, or combined with aridity and vegetation type; its interactions with other variables were also insignificant. In dry areas, duration of grazing exclusion did not explain the variation of effect sizes at all, while duration of grazing exclusion and aridity together explained 14.42 % of variation of effect sizes (model VI, Table 3). Neither alone nor together with other variables did stocking rate have a significant influence on effect size in dry areas.

3.5. Correlation analyses and the possible roles of soil C/N, aboveground biomass, vegetation cover and species evenness

Effect sizes (i.e. standard mean differences) in richness were significantly and positively correlated with differences in soil C and N ($P_{soil\ C}$ = 0.0012, $P_{soil\ N}$ = 0.0038, Table 4, Fig. 5a, b). No significant correlation was found between effect sizes and aboveground biomass, vegetation cover or species evenness.

4. Discussion

As we have seen, species richness responds differently to grazing in different sites, and the range of different responses is wide. A major challenge in rangeland ecology is understanding these diverse responses, what factors determine these responses and what their relative importance is. Numerous site-level studies have been conducted to explore grazing-richness relationships, but very few meta-analyses of these empirical results at regional or global scales have been conducted (Milchunas and Lauenroth, 1993; Díaz et al., 2007; Herrero-Jáuregui

Table 2
Meta-regression models for effect size of grazing on species richness across all studies, and the proportion (R^2) of variation in effect size that can be explained by aridity (AI), vegetation type, stocking rate (SR) and duration of grazing exclusion (enclo_yr). Only significant models were presented here.

Model		Coefficients		R^2 (%)	P-value	AIC	NO. of records	NO. of studies
All data	I	intercept ***	−1.1308	24.21	< 0.0001	980	257	95
		AI ***	3.5567					
		(AI)^2 ***	−1.1533					
	II	Grasslands ***	0.6868	7.16	0.0002	1020	259	96
		Shrublands ***	−0.7767					
	III	Grasslands **	−0.8851	25.55	< 0.0001	975	257	95
		AI ***	3.2962					
		(AI)^2 **	−1.0793					
		Shrublands *	−0.4176					
	IV	Grasslands ***	−1.5975	41.21	< 0.0001	437	123	38
		AI ***	5.3046					
		(AI)^2 ***	−1.9953					
		AI × SR	0.2199					
		SR *	−0.5518					
		(SR)^2.	0.0442					
		Shrublands.	−0.7245					
	V	intercept ***	1.0302	1.04	0.0252	888	230	86
		log(enclo_yr) *	−0.5984					
	VI	Grasslands	−0.0137	15.62 %	< 0.0001	860	230	86
		AI × log(enclo_yr) ***	1.0242					
		Shrublands *	−0.4514					

Significant codes: *** < 0.001; ** < 0.01; * < 0.05;. < 0.1. AIC: the Akaike information criterion. The same as follows.

and Oesterheld, 2018). Here, we used a global meta-analysis to estimate the mean effect sizes of grazing on species richness for different subgroups and assessed the relative importance of regional and local variables, including evolutionary history of grazing, aridity, vegetation type, stocking rate, duration of grazing exclusion, soil carbon (C) and nitrogen (N), biomass, vegetation cover and species evenness.

4.1. Evolutionary history of grazing

The MSL model (Milchunas et al., 1988; Cingolani et al., 2005) maintains that evolutionary history of grazing strongly affects grazing-diversity relations through influencing vegetation resilience. However, we found no significant difference in effect sizes of grazing on species richness between sites with long- and short evolutionary history in the

Table 4
Pearson's correlations for differences in soil C/N, aboveground biomass, vegetation cover, specie evenness between grazed and ungrazed sites with corresponding effect sizes.

	Effect size	n
Soil C	0.4888**	41
Soil N	0.4143**	47
Aboveground biomass	0.0922	82
Vegetation cover	0.1499	81
Species evenness	0.1397	78

Note: **: correlation is significant at the 0.01 level (2-tailed); n: sample size.

Table 3
Meta-regression models for effect size of grazing on species richness from wet and dry areas, separately, and the proportion (R^2) of variation in effect size that can be explained by aridity (AI), vegetation type, stocking rate (SR) and duration of grazing exclusion (enclo_yr). Only significant models were presented here.

Model		Coefficients		R^2 (%)	P-value	AIC	NO. of records	NO. of studies
Wet areas	I	intercept	−0.5906	8.16	0.0198	489	135	52
		AI *	2.8849					
		(AI)^2.	−0.9722					
	II	Grasslands ***	1.2215	11.47	0.0028	489	135	52
		Shrublands **	−0.8378					
	III	Grasslands	−1.0027	39.88	< 0.0001	250	76	25
		AI **	4.4804					
		(AI)^2 **	−1.5523					
		AI × SR	−0.2806					
		SR	−0.402					
		(SR)^2 *	0.1601					
		Shrublands **	−1.3357					
	IV	Grasslands	−0.4938	19.41	0.0021	421	121	47
		AI.	2.6454					
		(AI)^2 *	−1.0179					
		AI × log(enclo_yr)	0.3437					
		Shrublands *	−0.7646					
Dry areas	V	intercept *	−2.2224	8.17	< 0.0001	475	122	46
		AI *	14.856					
		(AI)^2 *	−23.8413					
	VI	intercept **	−2.7791	14.42	< 0.0001	389	107	41
		AI ***	23.698					
		(AI)^2 ***	−35.0817					
		AI × log(enclo_yr) **	−2.8092					

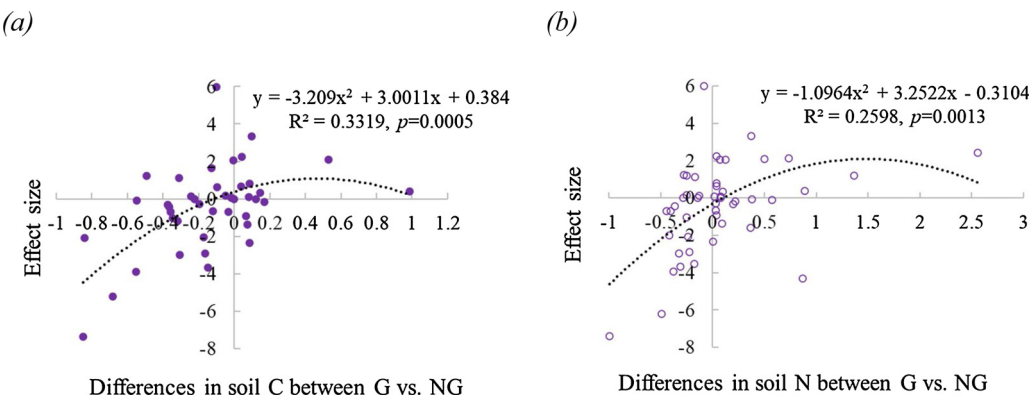

Fig. 5. Relations between differences in soil C (a) and soil N (b) in grazed and ungrazed sites and corresponding effect sizes in species richness.

subgroup analysis (Fig. 3), suggesting that evolutionary history of grazing may not be a major player in affecting vegetation responses to grazing. Variability in effect size in the sites with a short evolutionary history of grazing was much larger than in the sites with a long evolutionary history, which may be caused by a relatively small sample size ($n_{short} = 45$, $n_{long} = 214$). Another indication of the minor role of evolutionary history stems from the significant difference between effect sizes of grazing in Europe and Asia (Fig. 3), both continents with a similarly long evolutionary history of livestock grazing. Yet, the higher positive effect size in Europe than in Asia may be related to aridity, since most grazing sites in Europe are from wet areas, while most sites in Asia are from dry areas (Appendix A). Therefore, the major theme of the MSL model cannot be supported by our results. Other factors (e.g. aridity) may play a stronger role in grazing effects on plant richness than the evolutionary history of grazing. Similarly, the meta-regression analysis shows that evolutionary history of grazing does not explain the variation of grazing effect sizes on species richness, again, contradicting the finding of Milchunas and Lauenroth (1993). Several explanations of these inconsistencies may be proposed.

Firstly, the notion that livestock grazing history determines vegetation responses is widely accepted today. However, to define the evolutionary history of grazing of a site has difficulties, e.g. lack of information on historical population of herbivores (Oesterheld and Semmartin, 2011). Presumably, vegetation that has only recently experienced livestock grazing did not have enough time to adapt. However, even where livestock was introduced recently (e.g. Australia), wild animals have roamed the land for eons, making the vegetation in such areas preadapted to livestock grazing. If this proposition is correct, the difference in responses to grazing between areas with long and short evolutionary history will tend to be small and insignificant. An alternative explanation may be that the recent decades of very intensive livestock grazing all over the world may have brought about large degradation in plant communities, blurring the role of evolutionary history of grazing. Many policies and regulations were implemented to recover degraded vegetation and to achieve sustainable use of rangelands, such as the "*Public Rangelands Improvement Act of 1978*" in US, "*3-North Shelter Forest Program of* 1979" *and* "*Returning farmland to forestland and grassland of* 1999" in China, and "*National Principles and Guidelines for Rangeland management of* 1999" in Australia, etc. These programs, where applied, consist of a special type of human interference, and may also conceal the effects of evolutionary history of grazing. Other regional factors, such as vegetation type, stocking rate, soil nutrients, and regional species pools, may exert stronger impacts on species richness than evolutionary history of grazing. In fact, the definitions of long- and short evolutionary history of grazing are inconsistent between studies (Milchunas et al., 1988, 1993; Cingolani et al., 2005; Díaz et al., 2007), and except for the general notion of 'long- vs. short evolutionary history', very few studies have been published about the role of evolutionary history of grazing and how it interacts with regional or local factors.

An alternative explanation of the disparity between our results and those of Milchunas and Lauenroth (1993) is the differences between these two studies in terms of the datasets and the variables of interest. Milchunas and Lauenroth (1993) used grazing data from studies published before the year 1988 and personal communications. In contrast, our dataset included studies published after 1990. The explained variable in Milchunas and Lauenroth (1993) was species composition; they used different methods to quantify changes in species composition, including density, frequency, basal cover, canopy cover, biomass and others; they ignored data variability within- and between-studies, and treated each study equally. Here, we addressed this shortcoming by calculating the weighted standard mean difference (i.e. effect size) in species richness and used it as the explained variable. Compared to species composition, the use of richness as an indicator of the community is perhaps more robust, given that community composition is more erratic and may readily change, compared to species richness (Cingolani et al., 2005).

4.2. Aridity, vegetation- and ecosystem type

Our results showed that aridity played a significant role in the responses of plants to grazing globally, explaining a much higher proportion of variation in species richness than other variables (Table 2). This finding is in line with previous studies (Milchunas et al., 1988; Olff and Ritchie, 1998; De Bello et al., 2007; Gao and Carmel, 2020), but inconsistent with Herrero-Jáuregui and Oesterheld (2018) who found insignificant correlation between aridity and grazing effects on richness. Here are two possible reasons for this inconsistency, (i) Herrero-Jáuregui and Oesterheld (2018) compared low/high grazing to moderate grazing, rather than to grazing exclusion; (ii) their sample size is relatively small ($n < 40$). However, they did observe that increasing grazing levels tend to positively affect richness in wet areas. This is similar to our finding that for $AI > 0.51$, most grazing effects on richness were positive, while for $AI < 0.51$, effects were more variable (Fig. 6). The threshold of $AI = 0.51$, identified in our study as separating negative- and positive mean effect sizes of grazing, resembles the general climate classification for semi-arid ($AI < 0.5$) and subhumid ($AI > 0.5$) climates (UNEP, 1997). In view of these findings, we separated all data into two groups, wet- and dry areas, according to the boundary point $AI = 0.5$, in order to stratify the relative importance of other variables.

Vegetation type explained more of the variation in species richness in wet areas than in dry areas (Table 3). Ecosystem types are closely related to aridity. In our dataset, more diverse types of grasslands occurred in wet areas (Appendix A), including tallgrass prairie, salt marsh and riparian and alpine meadow. Grazing in these wet grassland ecosystems significantly increased species richness (Fig. 4). Such ecosystems are often characterized by higher productivity and moisture

compared to other grassland types. Grazing may increase species richness by reducing plant height, cover, dominance and litter, increasing the availability of light, and opening niche gaps for less competitive species (Milchunas et al., 1988; Olff and Ritchie, 1998; Segre et al., 2016). For instance, grazing could change growth form of plant communities by decreasing tall, erect, palatable or perennial grasses, and favoring small, prostrate, rosette, less palatable or annual species (Noy-Meir et al., 1989; Díaz et al., 2007). Spatial and temporal heterogeneity caused by direct grazing or indirect non-grazing activities (e.g. dung, urine deposition, trampling and wallowing) encourages species coexistence and further increase species richness (Veen et al., 2008), for example by generating patchy communities and increasing heterogeneous redistribution of soil N (Manning et al., 2017).

In contrast, grazing in shrublands had a low and insignificant effect on species richness (Fig. 4), consistent with the finding of Milchunas and Lauenroth (1993). One possible reason is that dominant shrubland species are harder for grazers to reduce than dominant grass species in grasslands (Milchunas and Lauenroth, 1993). Thus, grazing in shrublands may cause changes in species abundance or composition, rather than in species richness (Cingolani et al., 2005; Jones et al., 2017). This may also explain the small effects of grazing in Mediterranean ecosystems, as 87.5 % of these studies were conducted in shrublands (Appendix A).

4.3. Stocking rate and duration of grazing exclusion

Stocking rate and duration of grazing exclusion are two important grazing variables and are often used to manage rangeland systems. Their effects on species richness have been studied for decades. Inconsistent results of grazing effects on species richness were reported in individual studies, with positive (Hickman et al., 2004; Cao et al., 2016), negative (Pueyo et al., 2006; Gamoun, 2014), or insignificant (Ren et al., 2012; Deng et al., 2013) effects. We found an overall significant positive effect of grazing treatment on species richness compared to grazing exclusion treatment at a global scale (Fig. 3). Yet, no obvious correlations between effect sizes and stocking rates or duration of grazing exclusion were observed across grazing sites. Our results cannot support any of the well-known theories that explain the relationship between grazing intensity and species diversity, the Intermediate Disturbance Hypothesis (Grime, 1973; Horn, 1975; Connell, 1976), Huston model (Huston, 1976) and MSL model (Milchunas et al., 1988). By contrast, Herrero-Jáuregui and Oesterheld (2018) found a significant decrease in the response ratio of richness to the relative change in stocking rate. One main possible reason is that they compared relative value of change in stocking rate, whereas we compared standardized absolute value of stocking rates.

At a global scale, stocking rate and duration of grazing exclusion alone did not explain much of the variation in plant richness, compared to aridity and vegetation type. This finding is consistent with the conclusion of Milchunas and Lauenroth (1993), suggesting that environmental- and ecosystem variables are more influential on species richness than grazing variables at regional and global scales. Interestingly, the role of stocking rate and duration of grazing exclusion in affecting species responses to grazing varied with aridity, which is in line with the finding of Herrero-Jáuregui and Oesterheld (2018). In some areas, short-term (annual weather) fluctuations and long-term climatic cycles may mask grazing effects (Hyder et al., 1975; Milchunas and Lauenroth, 1993). Here, we found that in wet areas, stocking rate, together with aridity and vegetation type, explained more variation in effect size than did duration of grazing exclusion (Table 3); however, in dry areas, duration of grazing exclusion together with aridity explained a higher proportion of variation in effect size than other models did, demonstrating a negative interaction between aridity and duration of grazing exclusion (Table 3). One possible reason is that increasing the duration of grazing exclusion in dry areas may contribute to an increase in species richness and thus decrease the difference in species richness between grazing and grazing exclusion, suggesting that duration of grazing exclusion plays a positive role in maintaining species richness in dry areas. Based on these results, we speculate that at the site level, grazing variables are more important for maintaining species richness than environment and ecosystem variables, because the environment is quite homogeneous at a small scale. At the continental and global levels, aridity and ecosystem variables become important. Presumably, this is why there is a discrepancy in findings between any single study, and data syntheses at regional and global levels, highlighting the importance of meta-analyses in ecology.

4.4. Soil C and N

We found that changes in soil C and N between grazing and grazing exclusion treatments significantly correlated with corresponding effect sizes in species richness (Table 4), with revealing hump-shaped patterns (Fig. 5). Our results contrast with the results from Milchunas and Lauenroth (1993) in terms of changes in species composition. Previous studies reveal that Plant communities should interact with soil C and N in some way (Burke and Lauenroth, 1998). Grazing may affect soil C and N indirectly, by changing species richness, species composition, vegetation cover, little biomass, root distribution, etc. (Pineiro et al., 2010; Mcsherry and Ritchie, 2013; Xu et al., 2014). In turn, the concentrations and spatial distribution of soil nutrients may also influence plant communities (Burke and Lauenroth, 1998). For example, the low level of soil C and N may not support plant growth and further promote species extinction under moderate to high grazing. Heterogeneous distribution of soil C and N may cause community patches and thus increase species richness. Even though our results cannot tell whether species richness affects soil nutrients (Tilman et al., 1996) or vice versa (Grime, 1973; Tilman and Pacala, 1993), our results still provide some support to the diversity-sustainability of soil hypothesis by showing a significant correlation between both (Tilman et al., 1996).

5. Conclusions

The meta-analysis presented here enabled us to conduct a quantitative and objective summary of how local and regional variables (i.e. evolutionary history of grazing, aridity, vegetation type; stocking rate, duration of grazing exclusion, soil carbon and nitrogen, aboveground biomass, vegetation cover, species evenness) affect the impact of grazing on species richness at large scale, and the magnitude and direction of these effects. This gave us a full picture of grazing effects on species richness, at the site level, the regional level and the global level. Globally, evolutionary history of grazing and grazing intensity alone had no significant effect on species richness, suggesting that well-known theories in rangeland ecology, such as MSL model and intermediate disturbance hypothesis, cannot be supported. This conclusion does not constitute a full rejection of these theories, but it indeed reveals that these theories have limitations and we need to use them properly. The role of grazing variables (stocking rate and duration of grazing exclusion) closely relates to aridity and vegetation types. Possibly, scholars may improve existing theories by expounding the interactions between grazing variables and aridity and vegetation type. At the same time, our findings substantiate the need of rangeland managers to devise local-scale grazing strategies for maintaining plant diversity and achieving rangeland sustainable development according to site-specific conditions, rather than adopting a one-size-fits-all solution.

Data accessibility

We confirm that the data supporting the findings of this study are available within the article and its supplementary material. More details about the data are available from the corresponding author on request. Once this manuscript gets published, we will share our data in

GitHub.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.107072.

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