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Meta-analysis

Effects of grazing intensity on plant richness and diversity: a meta-analysis

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Most of our knowledge of the effect of grazing on grassland structure is based on grazed–ungrazed contrasts. The effects of grazing in the most common scenario, where grazing intensity varies from low to high grazing intensity, are less known. The objectives of this paper were to 1) quantify the effect of stocking rates on species richness and diversity of grasslands world-wide, and 2) evaluate the response under different environmental and experimental conditions. We conducted a meta-analysis of experiments with at least two levels of controlled stocking rates and evaluated their effect on species richness and diversity. The results showed that the response of richness and diversity to either reducing or increasing stocking rate from a moderate level mostly fell within the range ± 25% or ± 5 species. Mean response of species richness and diversity to increasing stocking rate from moderate to high levels was negative. Mean response to lowering stocking rate from moderate levels was not different from zero. However, overall, species richness significantly decreased as stocking rate increased. The response of richness and diversity to stocking rate was not related to mean precipitation, productivity or aridity. However, the most negative responses of richness to stocking rate were larger in arid, low productivity systems than in subhumid and humid systems. The effects of grazing on richness and diversity found in this review were smaller than the effects on species composition shown by the literature. Thus, grazing drastically changes species composition, but the net change of species and diversity is much smaller.

Keywords: effect size, grassland, precipitation, rangeland, review, shrubland, stocking rate

Synthesis

Based on published studies, we quantified the effect of stocking rates on species richness and diversity of grasslands world-wide under different environmental conditions. Reducing or increasing stocking rate from a moderate level changed species diversity by ± 25% or ± 5 species. Species richness and diversity significantly decreased when increasing stocking rate from a moderate level. Although most responses were consistent across environmental conditions, the most negative impacts occurred in low-productivity systems. The overall relative effects of grazing on richness and diversity were smaller than the effects on species composition often shown by the literature.

Introduction

Grazing is a major control of grassland species composition and diversity (McNaughton 1983, Milchunas et al. 1988, Milchunas and Lauenroth 1993). The most authoritative model of grazing effects proposed that 1) species diversity peaked at intermediate grazing intensity and 2) the impact of grazing on species composition and diversity increased with community productivity across a humidity gradient (Milchunas et al. 1988). Additionally, it stated that the evolutionary history of grazing explained some of the variation. Strong evidence has supported the prediction that the shifts in species composition induced by grazing increase with productivity (Milchunas and Lauenroth 1993, Cingolani et al. 2005, Oesterheld and Semmartin 2011, Lezama et al. 2014). Although the model ultimately aimed at explaining diversity patterns, its quantitative evaluation so far has focused on changes of species composition (Milchunas and Lauenroth 1993). The model also made clear predictions on responses along gradients of grazing intensity, but the quantitative evidence has heavily relied on comparing exclosures and grazed situations.

In fact, most of our knowledge of the effect of grazing on community structure is based on grazed–ungrazed contrasts (i.e. grazing versus exclosures). This makes it difficult to infer the effects of grazing on most plant communities, where exclosures are a rarity. Therefore, the subtle range of variation among actual stocking rates is less known than the drastic effects of exclusion. In addition, several of the few studies that focused on a range of stocking rates did not control them experimentally. They rather inferred stocking rate from indirect evidence such as county records, interviews to local people (Haynes et al. 2013), distance to drinking water (Peter et al. 2012), distance to herder huts (Haynes et al. 2013), density of feces (Gonnet et al. 2003), proportion of bare ground (Jones et al. 2011) or species composition (Li et al. 2008).

The experimental studies that accurately defined and replicated stocking rates and evaluated the effects on species richness and diversity have reported various and often contradictory results. The few reviews on these studies have been restricted to particular ecosystems (O'Connor et al. 2010, Scohier and Dumont 2012, Hanke et al. 2014), plant species (Pakeman 2004) or experimental conditions such as contrasting nutrient richness (Proulx and Mazumder 1998, Borer et al. 2014). Of these, only Pakeman (2004) and Borer et al (2014) provided quantitative measures of effect size (Koricheva and Gurevitch 2014). Thus, a meta-analysis of the effects of stocking rates on species richness and diversity over a climatic gradient could contribute to understanding the effects of grazing on plant communities (Overbeck 2014), test the predictions from current theory (Milchunas et al. 1988), and contrast with empirical studies on the effects of grazing on species composition (Milchunas and Lauenroth 1993). This understanding can provide useful insights for managers when deciding whether to increase or decrease stocking rates.

We provide here such a meta-analysis. Our objective is to assess how variation across low, moderate, and high stocking rates of domestic herbivores affects species richness and diversity of grasslands worldwide. Our predictions, based on Milchunas et al. (1988) and Cingolani et al. (2005) models were: 1) species diversity will peak at intermediate stocking rates; 2) grazing-induced changes of species diversity will be larger in more productive than in less productive ecosystems. To our knowledge, this is the first world-wide meta-analysis that quantifies the effect size of different controlled stocking rates on species richness and diversity.

Methods

Data collection

We searched published articles, reports and congress proceedings tabulated in Scopus and Google Scholar until July 2016. We used 'grazing intensity', 'grazing gradient' or 'stocking rate' as keywords, together with variables describing plant community structure such as 'species richness' or 'species diversity'. We also reviewed all volumes of Grassland Science in Europe (Proceedings of the European Grassland Federation), Journal of Range Management (currently Rangeland Ecology and Management) and references cited by the selected papers.

To be selected, the articles had to fulfill the following requirements. 1) At least two stocking rates other than grazing exclusion had been experimentally manipulated. 2) Plant species richness or a species diversity index was used as response variable. 3) Vegetation physiognomy was either grassland or shrubland that had not been sown in the past. 4) Grazers had to be domestic herbivores, thus excluding small rodents and other non-comparable grazers. As a result, the study included natural grasslands and shrublands conditioned by climate, altitude or edaphology, and semi-natural grasslands, whose physiognomy is maintained by some form of human intervention, such as grazing by livestock or mowing for hay, but have not been substantially modified by intensive agriculture. For example, semi-natural grasslands have existed in Europe for over 6000 years, since the beginning of pastoral agriculture, and occur where the potential vegetation is a forest (King 2010). Two studies were on burnt grasslands as it was the traditional management system of the region (Ash and McIvor 1998, Hickman et al. 2004). Some redundant data, such as the same experiment being published twice, were excluded to avoid duplication bias. In these cases, the most recent study was selected. When stocking rate was combined in a factorial experiment with other treatments (e.g. grazing season, grazing period, site, ratio between species of grazers), we treated each level of the other treatment as an independent contrast of stocking rates. We transformed stocking rates into three categories: low, moderate and high, based on the description given by the authors. In most cases the moderate stocking rate was the traditional stocking rate in the region, and thus, it was taken as the reference to which stocking rate increased (high versus moderate) or decreased (low versus moderate). Therefore, stocking rate levels within a study represented a range of variation considered locally by the authors of the study and cannot be compared across sites. For example, a high level in dry steppes may be much lower

than a low level in humid grasslands. For species diversity, we only considered the antilog of the Shannon–Wiener index or indices that could be transformed to it (i.e. Pielou index). We did not include studies from which we could not obtain the original data of richness or diversity from the publications, even though they were used as response variables but in a processed manner (i.e. multivariate analysis plots, change rate, etc.). An exception to this was the study by Pizzio et al. (2016) because we had direct access to the original data.

From each study, we extracted data on species richness and/or species diversity indexes, stocking rate, type of domestic grazer, number of replicates, duration of the experiment, and whether the system was a natural grassland or shrubland, or a semi-natural grassland on a site with a different potential vegetation type. Additionally, we gathered information based on the geographical coordinates of each study site: ecoregion (< www.worldwildlife.org >), mean annual precipitation (MAP) from 1950–2000 (< www.worldclim.org >), mean annual real evapotranspiration (ET) from 2000–2006 and an index of aridity calculated as MAP/Potential evapotranspiration (PET), which decreases with aridity (< www.ntsg.umt.edu/ >, Trabucco and Zomer 2009).

Our search and selection resulted in 48 studies that included 63 comparisons of species richness or diversity for at least two stocking rates (Table 1). The number of specific comparisons was: for high versus moderate stocking rates, 39 comparisons for species richness and 32 for species diversity; for low versus moderate stocking rates, 35 comparisons for species richness and 32 for species diversity. The 48 studies were published from 1995 to 2016 in eighteen different countries covering a range between 50ºE and 55ºW latitude and 117ºS to 144ºN longitude (Supplementary material Appendix 1). Sheep were involved as grazers in 28 experiments, cattle in 19, goats in 3, yaks in 3 and horses in 1 (Table 1). Common problems within the literature included the lack of true replication (i.e. in 13 studies there was one paddock per treatment) and the lack of data on variability among plots.

Data analysis

Because many of the selected studies did not report a measure of variability among plots, we performed an unweighted meta-analysis. In this way, we included as many studies as possible and minimized publication bias (Koricheva et al. 2013). We used a typical effect size metric, the response ratio: the log proportional change in the means of a treatment and control group, $\ln (r) = \ln (X_t/X_c)$.

We performed three types of analysis. First, we analyzed the distribution and net result of the high versus moderate and low versus moderate stocking rates. In this case, X_t was the richness or diversity of high or low stocking rates and X_c was the richness or diversity of moderate stocking rates (high versus moderate and low versus moderate comparisons). Mean response ratio for each treatment was calculated using fixed effects models with bias-corrected 95% confidence intervals (CI) generated by a bootstrapping procedure (5000 iterations) using Meta-Win software (Rosenberg et al. 2000). Grazing treatments were considered to have a significant

overall influence on a variable if the bootstrap CI of their mean effect size did not overlap zero. Second, we regressed the response ratio of the two most extreme stocking rates (high versus low) against the log ratio of the corresponding stocking rates. In this case, X_t and X_c were the richness or diversity of the highest and lowest stocking rate of each site. This analysis provided a quantitative assessment of the effect of relative changes of stocking rate on richness and diversity. Third, we regressed the response ratios of the first analysis against continuous variables (precipitation, evapotranspiration, aridity and length of the experiment), by means of simple regressions and quantile regressions. This analysis informed how the responses, varied across environmental gradients or experimental conditions. Statistical analyses were carried out with R (< www.r-project.org/ >), using the R package 'quantreg' for quantile regressions (Koenker 2017).

We performed separate analyses for each response variable (species richness and diversity) considering all studies and discriminating between natural and seminatural systems.

Data deposition

Results

Overall, stocking rate had little effect on species richness and diversity: most studies that compared high versus moderate or low versus moderate stocking rates reported small positive and negative effects around zero (Fig. 1). Most studies had a response ratio between –0.25 and +0.25, which correspond to percent changes within the range –22% to +28%. More specifically, the response ratio for species richness was between –0.25 and +0.25 in 72% of the high versus moderate contrasts and in 77% of the low versus moderate contrasts. For species diversity, the ± 0.25 range was observed in 78% of the high versus moderate contrasts and in 94% of the low versus moderate contrasts.

Within this limited response, high stocking rate more often decreased than increased species richness and diversity (Fig. 1): the mean response ratio was significantly lower than zero, and there were 54% negative responses for richness and 72% negative responses for diversity. In contrast, mean response ratio of lowering stocking rate was not significantly different from zero. In terms of absolute number of species, less than five species were gained or lost in 59% of the high versus moderate contrasts and in 74% of the low versus moderate contrasts (Fig. 2).

When instead of using categorical classes of stocking rate, we used a quantitative measure of stocking rate change, the response ratio of richness became more negative as the relative change in stocking rate increased (Fig. 3, $y = 0.177 – 0.292\ x$, $t = -3.102$, $p = 0.0034$). Overall, this model indicates that two-fold, three-fold and ten-fold increases of stocking rate reduced species richness by 3, 14 and 40%

Table 1. Characteristics of selected studies. Domestic grazers are cattle (C), sheep (S), goats (G), horses (H) and yaks (Y). Studies are sorted by year of publication.

Study	Comparison	Reference	Country	Ecoregion	Duration (year)	Grazer
1	2[a]	Hartnett 1995	USA	Flint Hills tall grasslands	3	C
2	2[b]	Grant et al. 1996	UK	Celtic broadleaf forests	6	S
3	1	Oliva et al. 1998	Argentina	Patagonian steppe	10	S
4	1	Ash and McIvor 1998[†]	Australia	Kimberly tropical savanna	3	C
5	3[a,c]	Sternberg et al. 2000	Israel	eastern Mediterranean conifer-sclerophyllous-broadleaf forests	4	C
6	1	Wang et al. 2001	China	Mongolian-Manchurian grassland	8	S
7	1	Hart 2001	USA	western short grasslands	55	C
8	1	Lucas et al. 2004	USA	Arizona mountains forests	2	C
9	1	Zhang et al. 2004	China	Mongolian-Manchurian grassland	5	S
10	1	Hickman et al. 2004	USA	Flint Hills tall grasslands	6	C
11	1	Zhao et al. 2004	China	northeast China plain deciduous forests	5	S
12	1	Louault et al. 2005	France	western European broadleaf forests	12	S
13	1	del Pozo et al. 2006	Chile	Valdivian temperate forests	4	S
14	1	Zhou et al. 2006	China	southeast Tibet shrublands and meadows	17	S
15	1	Liu et al. 2006	China	Mongolian-Manchurian grassland	13	S
16	1	Yang et al. 2006	China	Mongolian-Manchurian grassland	–	S
17	4[b]	Scimone et al. 2007	UK, Germany, France, Italy	Celtic broadleaf forests, western European broadleaf forests, Po Basin mixed forests	3	C
18	1	Dumont et al. 2009	France	western European broadleaf forests	5	C
19	1	Wu et al. 2009	China	southeast Tibet shrublands and meadows	10	S,Y
20	1	Duan et al. 2010	Tibet	central Tibetan Plateau alpine steppe	–	S
21	1	Celaya et al. 2010	Spain	Cantabrian mixed forests	4	G
22	1	Škornik et al. 2010	Slovenia	Illyrian deciduous forests	10	S
23	2[c]	Campbell et al. 2010	USA	Great Basin shrub steppe	73	S
24	1	Kobes et al. 2010	Czech Republic	western European broadleaf forests	8	C
25	1	Dumont et al. 2011	France	western European broadleaf forests	5	C,S
26	5[d]	O'Connor et al. 2011	South Africa	Drakensberg montane grasslands, woodlands and forests	16	C,S
27	1	Shoji et al. 2011	Japan	Hokkaido montane conifer forests	5	H
28	2[c]	Dong et al. 2011	China	Tibetan Plateau alpine shrublands and meadows	2	Y
29	1	Golodets et al. 2011	Israel	eastern Mediterranean conifer-sclerophyllous-broadleaf forests	10	C
30	2[e]	Rigueiro-Rodríguez et al. 2011	Spain	Cantabrian mixed forests	0.6	S
31	1	Wrage et al. 2011	Germany	western European broadleaf forests	9	C
32	1	Zhao et al. 2011	China	Mongolian-Manchurian grassland	4	S
33	1	Allred et al. 2012*	USA	Edwards Plateau savanna	45	C,S,G
34	1	Ren et al. 2012	China	Mongolian-Manchurian grassland	6	S
35	1	Zhu et al. 2012	China	southeast Tibet shrublands and meadows	16	S
36	1	Campbell et al. 2013	Mexico	Veracruz moist forests	5	C
37	1	Zhou et al. 2013	China	Mongolian-Manchurian grassland	14	S
38	1	Xun et al. 2013	China	Tian Shan montane steppe and meadows	–	S
39	1	Gamoun 2014	Tunisia	north Saharan steppe and woodlands	4	S,G
40	1	Jerrentrup et al. 2014	Germany	western European broadleaf forests	10	C
41	1	Yan et al. 2014	China	Mongolian-Manchurian grassland	3	C
42	1	Zou et al. 2015	China	southeast Tibet shrublands and meadows	3	Y
43	1	Wan et al. 2015	China	Mongolian-Manchurian grassland	5	S
44	1	Ganjurjav et al. 2015	China	Tibetan Plateau alpine shrublands and meadows	5	S
45	1	Wang et al. 2016	China	central China loess plateau mixed forests	3	S
46	1	Pizzio et al. 2016	Argentina	Espinal	7	C
47	2[b]	Li et al. 2016	China	Mongolian-Manchurian grassland	7	S
48	1	Porensky et al. 2017	USA	western short grasslands	75	C

[a]grazing system (rotational, continuous); [b]different locations; [c]grazing period; [d]cattle to sheep ratio; [e]influence of tree cover; [†]richness and diversity were measured 25 months after treatment.*richness and diversity were measured 10 years after treatment finished and high stocking rate equaled moderate at 0.105 AUY ha^{-1}

respectively. In contrast, the response ratio of diversity was not significantly related with the relative change in stocking rate (Fig. 3).

The effects of stocking rate on richness differed across the environmental gradient. Although there was not an overall relationship between the response ratio of richness and three
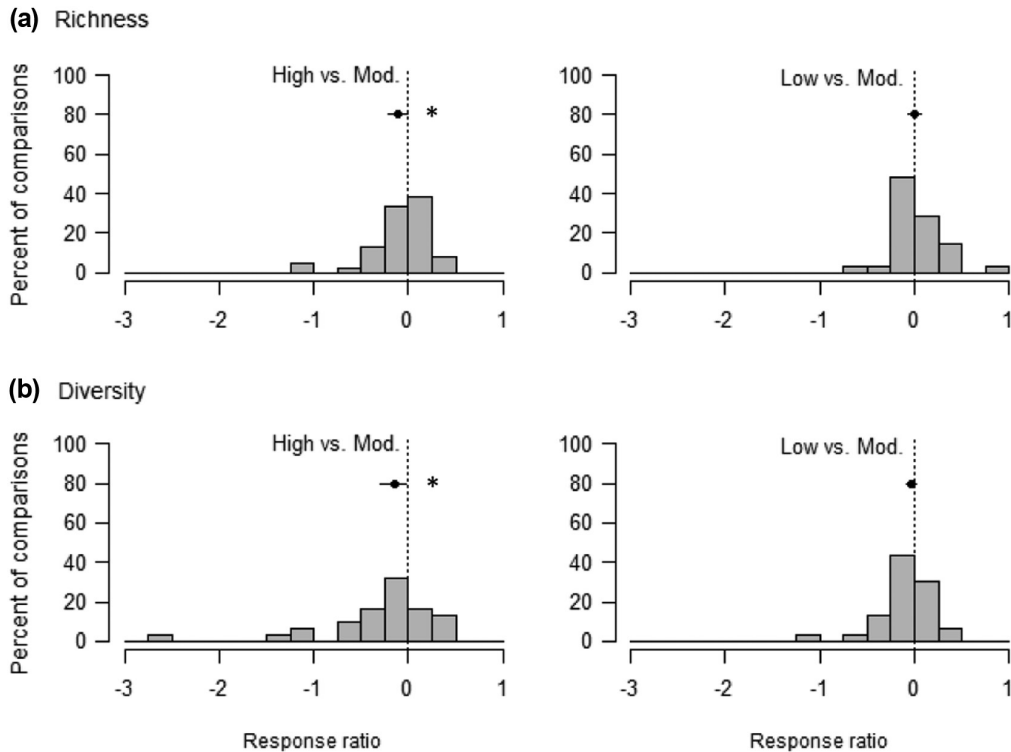
Figure 1. Frequency distribution of response ratio (ln (Xt / Xc)) of species richness and diversity to high and low stocking rate. Xt is the value under either high or low stocking rate and Xc is the value under moderate stocking rate. Vertical dashed line indicates zero, no response. Data point and dispersion bars represent the mean response ratio and its bias-corrected 95% confidence interval. An asterisk indicates significant differences of mean response ratio, when confidence intervals do not overlap zero.

variables describing water availability and productivity, there were more extreme negative effects of high versus moderate stocking rate in drier, less productive ecosystems than in more humid and productive ones (Fig. 4a–c, significant nonlinear quantile regressions at the 10% quantile). In contrast, the effect of low versus moderate stocking rates was similar across the gradient (p > 0.05; Fig. 4a–c). When considered with their positive or negative sign, the response ratios of richness to stocking rate did not change significantly as experiments became longer (Fig. 4 d). However, the absolute response
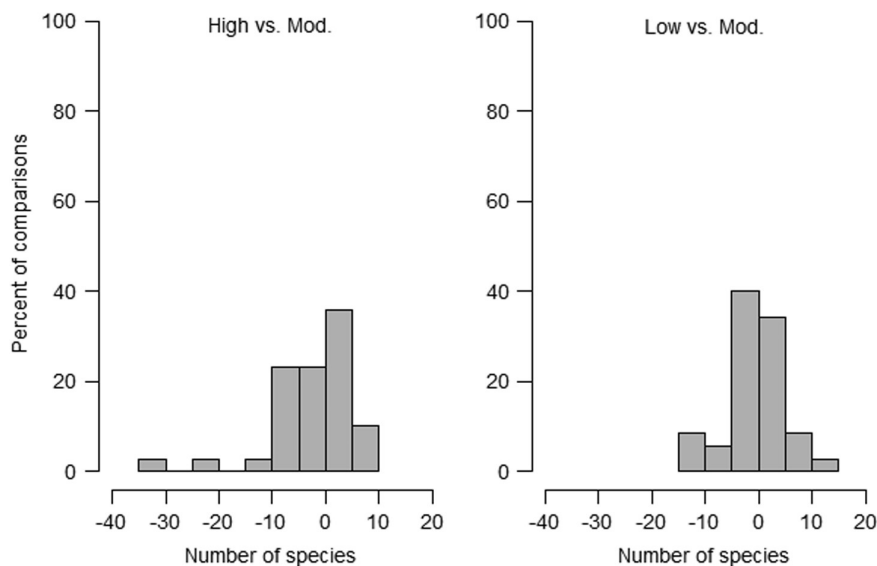

Figure 2. Frequency distribution of the number of species gained (positive x-axis values) or lost (negative x-axis values) in response to increasing (left) or decreasing (right) stocking rate compared to a moderate level.
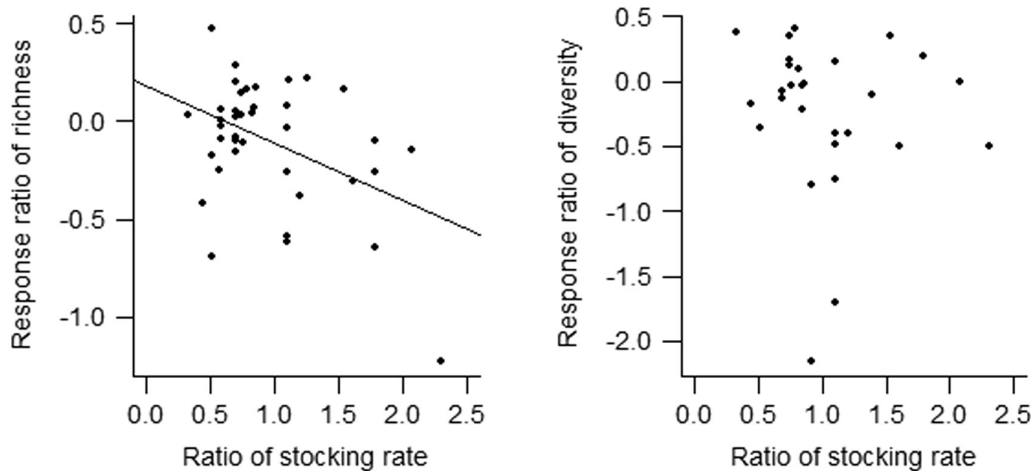
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Figure 3. Linear relationships between response ratio (ln (Xt / Xc)) of species richness (a) and diversity (b) and relative change in stocking rate (ln (max. stocking rate / min. stocking rate)) . Significant regression at $p < 0.05$ is represented.

ratio (i.e. the magnitude of the response, either positive or negative) increased with the duration of the experiment ($y = 0.155 + 0.003$ x, $t = 2.209$, $p < 0.03$).

Response ratios of species diversity were also more dispersed in drier, less productive ecosystems, but the pattern was weaker than for richness, with no significant relationships (Fig. 5). When data were analyzed separately by the type of system (i.e. natural rangeland or semi-natural grasslands) the results were essentially similar to those describe above (Supplementary material Appendix 1–5). However, they showed that, as expected, most of the systems to the right of Fig. 4a–c and Fig. 5a–c were semi-natural.

Discussion

We highlight the following findings. First, stocking rate generally had little effect on richness and diversity. The response to either reducing or increasing stocking rate from a moderate level mostly fell within the range ±25%. Second, mean response of species richness and diversity to increasing stocking rate from moderate levels was negative. Third, there was a negative relationship between the ratio of stocking rate and the response ratio of richness. Fourth, the most negative responses of richness to stocking rate were larger in arid, low productivity systems than in subhumid and humid systems.
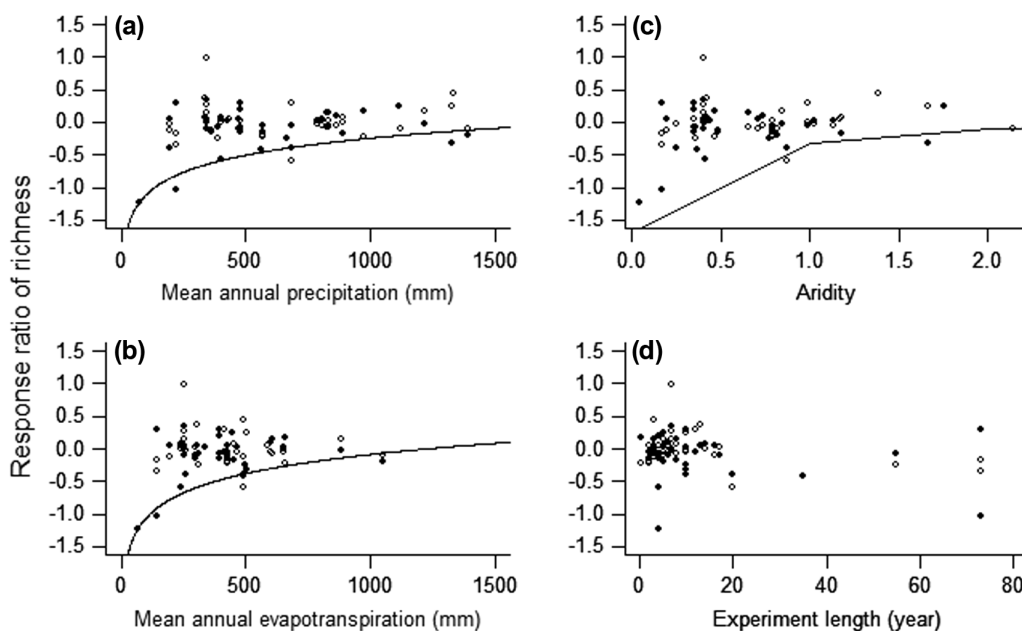

Figure 4. Response ratio (ln (Xt / Xc)) of species richness to high (black dots) and low (white dots) stocking rate as a function of: (a) mean annual precipitation, (b) mean annual evapotranspiration, (c) aridity index (more arid at low values), (d) duration of experiment. Xt is the value under either high or low stocking rate and Xc is the value under moderate stocking rate. Significant 0.1 quantile regression lines are shown.

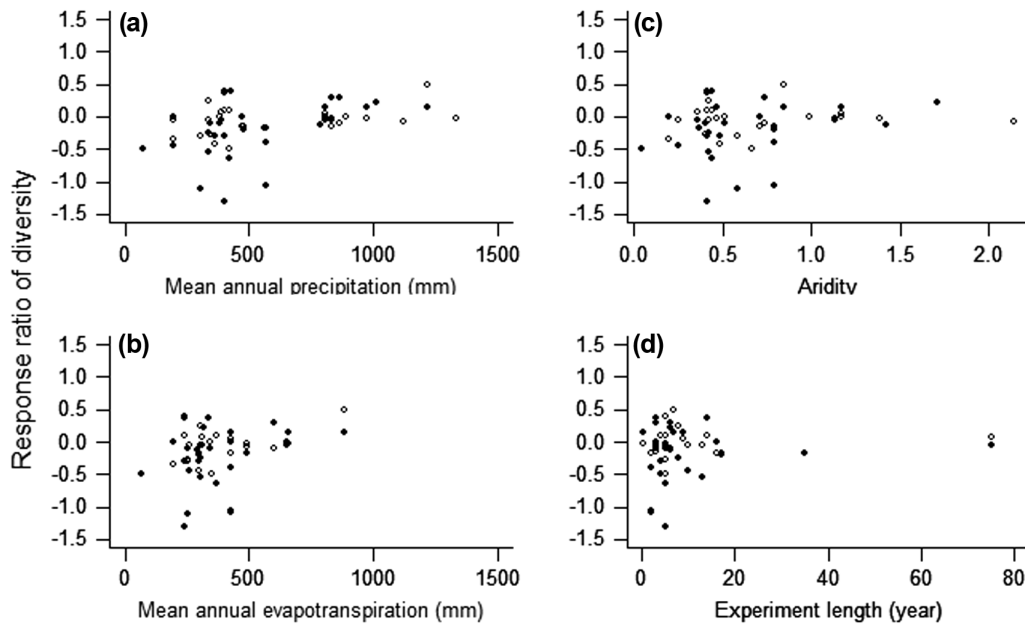Figure 5. Response ratio (ln (Xt / Xc)) of species diversity to high (black dots) and low (white dots) stocking rate as a function of: (a) mean annual precipitation, (b) mean annual evapotranspiration, (c) aridity index (more arid at low values), (d) duration of experiment. Xt is the value under either high or low stocking rate and Xc is the value under moderate stocking rate.

Regarding the general minor effect of reducing or increasing stocking rate on species richness and diversity, Mackey and Currie (2001) also concluded from their meta-analysis of diversity–disturbance relationships that nonsignificant diversity–disturbance relationships were the most common response, particularly for anthropogenic disturbances. When compared to exclosures, grazed plots usually have higher species richness, particularly in more humid, productive ecosystems (Lezama et al. 2014). This response is explained by competitive exclusion acting in exclosures, particularly in humid environments where competition for light is exacerbated (Milchunas and Lauenroth 1993). Our study, which focused on more subtle changes of disturbance regime given by realistic ranges of stocking rates, showed a different pattern: the effects were small on average and became predominantly negative when disturbance increased. The variety of responses of diversity to disturbance depends on the intensity and frequency of the disturbance regime (Miller et al. 2011). In the particular case of grazing, different stocking rates change both the intensity (the amount of plant tissue removed) and frequency (the number of times a plant is grazed) of disturbance. In this study we have pooled the effect of stocking rate of different domestic herbivores, such as cows, sheep, yaks and horses. Although grazing or browsing by different species may have different effects on vegetation structure (Sanson 2006, Liu et al. 2015, Veblen et al. 2015), our dataset did not allow for a proper testing of this difference; sheep and cattle were over-represented in the dataset (Table 1) and unevenly distributed across the gradient (sheep are more frequent in dryer systems and cattle in subhumid systems).

We estimated that the range of variation of richness and diversity induced by experimental manipulations of stocking rate was largely 0 ± 25%. Cases outside the 0 ± 25% range were rare, usually negative, and mainly observed because of high stocking rates. Our range of variation contrasts with the strong variations in species composition observed by Milchunas and Lauenroth (1993). The average dissimilarity of species composition in 152 ungrazed–grazed contrasts around the world was 46%, with individual values encompassing a 5–95% range (Milchunas and Lauenroth 1993). Thus, grazing changes act mainly on species composition through a turnover of species (Milchunas and Lauenroth 1993) with a much smaller net change in species richness and diversity indices (Fig. 1). Therefore, changes in ecosystem functioning driven by grazing would be related to the replacement of some species by others with different functional traits (Tilman and Downing 1994, Chapin III et al. 2000, Tilman et al. 1997, Grime 1997, Díaz and Cabido 2001) rather than to the number of species. More precisely, increasing grazing intensity will often favour species with a ruderal strategy, an annual life history, seasonal regeneration by seed, flowering and seed dispersal early in the season, higher requirement for light and a lower minimum height with stoloniferous and rosette architecture (Pakeman 2004, De Bello et al. 2005, Díaz et al. 2007).

Our results show a lack of overall relationship between the effect of stocking rate and environmental variables describing the humidity gradient considered by the generalized model of grazing effects (Milchunas et al. 1988). Interestingly, however, the most extreme negative effects of stocking rate on richness were in the driest end of the gradient (Fig. 4–5). This was evidenced by a positive 10% quantile regression between the effect on richness and mean annual precipitation, mean annual evapotranspiration and the

inverse of aridity. This pattern brings three interesting contrasts to the patterns previously proposed and observed for diversity and species composition (Milchunas and Lauenroth 1993). First, the lack of overall pattern of the response across the humidity gradient is not consistent with the prediction by the generalized model, which expected greater changes as humidity increases. Second, the most negative responses of richness at the dry end of the gradient are opposite to predictions by the model. Third, the patterns of the response of richness and diversity differ from observations on species dissimilarity between contrasting grazing regimes, which strongly increased across a productivity–moisture gradient (Milchunas and Lauenroth 1993) (Fig. 4–5). The size of regional species pools increases with precipitation and productivity (Oesterheld and Semmartin 2011). Therefore, the response to grazing in arid systems involves little species turnover (Milchunas et al. 1988, Milchunas and Lauenroth 1993) and strong changes in richness (Fig. 4–5). In more humid ecosystems there are more species with diverse adaptive traits. Consequently, grazing induces strong changes of species composition (Milchunas et al. 1988, Milchunas and Lauenroth 1993) with little change of species richness and diversity (Fig. 4–5). The wide variation of richness responses at the dry end of the gradient poses a question about its causes. Probably certain unmeasured characteristics of these dry locations confer different resistance in terms of richness responses. The evolutionary history of grazing is a candidate variable to account for that difference, as proposed by Milchunas et al. (1988). However, we were not able to assign values to that variable in our dataset because of general limitations of the data (Oesterheld and Semmartin 2011) and because many of our grasslands were not climatically determined. Exploring this wide variation at the dry end of the continuum is a fertile area for future research. Our results show that the effect of stocking rate, either positive or negative, increased as time elapsed. The experiments included here had an average length of 6 years, with only four lasting more than 20 years. Therefore, our knowledge is constrained by the lack of long-term experiments on stocking rate, which contrasts with the availability of exclosures expanding several decades. As it is widely acknowledged, controlled stocking rate experiments are expensive and difficult to implement, which results in not many manipulative experiments worldwide, most of which last for a few years (but see Porensky et al. 2017 for an exception). Given that networking in ecology has become common practice, it could be interesting to design a set of long-term, worldwide controlled experiments with the range of stocking rates most commonly explored in each region.

Our study included a broad range of annual precipitation (76–1991 mm) and potential vegetation types (desert steppe through forests), but the current vegetation type of each study site was either shrubland, grassland or savanna. Several of the grassland sites were located in the temperate forest biome in Europe, and one was located in a tropical forest in Mexico (Campbell et al. 2013; Table 1.). Although, we cannot assess with certainty when forests were cleared for grasslands (except in Campbell et al. 2013), most

semi-natural grasslands in Europe have co-evolved with pastoralism and presumably they are old enough to have a stable pool of species. The similar responses obtained when considering the type of system is a further argument to support the validity of our results, which do not appear to be conditioned by the origin of the grassland. We did not try to determine the evolutionary history of grazing at each site, as we believe there are several limitations to do so at meaningful temporal and spatial scales. The lack of information on the historical population and distribution of herbivores with an adequate spatial and temporal resolution, and the lack of agreement on the size of the relevant evolutionary time window, difficult the assignation of a given evolutionary grazing history to a site (Oesterheld and Semmartin 2011).

In summary, this study demonstrates that the overall effect of increasing stocking rate was small and negative in the case of species richness and null on diversity. This response did not change across environmental conditions, but the most negative responses of richness to stocking rate were in arid, low-productivity systems. The effects of grazing on richness and diversity were smaller than the effects on species composition shown by the literature. Thus, grazing drastically changes species composition, but the net change of species richness and diversity is much smaller.

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