

Research

Can the intermediate disturbance hypothesis explain grazing–diversity relations at a global scale?

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In the context of grazing, the intermediate disturbance hypothesis (IDH) predicts that plant diversity peaks under moderate grazing, resulting in a hump-shape pattern for the grazing–diversity relationship. Although this has been debated due to contradictory empirical results, the IDH is still widely accepted among rangeland ecologists. The Milchunas–Sala–Lauenroth (MSL) model predicts that in arid areas grazing affects diversity negatively regardless of grazing intensity, whereas in mesic areas grazing effects on plant diversity are the same as predicted by the IDH. Very few studies have attempted to specifically evaluate the applicability of the IDH and MSL to grazing systems at a global scale, accounting for the possible effects of climate. We conducted a meta-analysis and vote-counting analysis to evaluate these two hypotheses. The results of both analyses show that the IDH cannot be applied globally and that its application largely depends on aridity. The IDH prediction of a hump-shape curve is supported in wet areas, while in dry areas there is a slight decrease in species richness with increasing grazing intensity. Overall, the MSL model correctly predicted grazing–diversity relations in both wet and dry areas. Looking at specific ecosystem types, we found that these results hold in grasslands, but not in woodlands. Differences between livestock types, not considered by the MSL model, were found to be important. Mixed sheep and goat grazing in dry areas resulted in a significant decline of species richness with grazing intensity, while grazing by sheep only had little effect on species richness. Cattle grazing and yak grazing in wet areas yielded a clear hump-shape pattern. Therefore, we conclude that the climate-specific MSL model better predicts the impact of grazing on diversity than the IDH in rangelands, and that the response patterns of plant richness to grazing are dependent on aridity, grazing intensity and grazer type.

Keywords: aridity, grazing intensity, intermediate disturbance hypothesis, meta-analysis, plant diversity, vote-counting

Introduction

The intermediate disturbance hypothesis (IDH) (Grime 1973, Horn 1975, Connell 1978) has been widely used to describe diversity–disturbance relationships. In the context of grazing, it predicts that moderate grazing will result in higher diversity compared to no-, low- and high grazing (Connell 1978, Milchunas et al. 1988). However,

the utility of the IDH has been questioned due to inconsistent empirical results (Mackey and Currie 2001, Kershaw and Mallik 2013). For example, in rangeland, some studies support the IDH (Dupré and Diekmann 2001, McIntyre et al. 2003, Yan et al. 2015, Yuan et al. 2016, Fedrigo et al. 2018), while other studies contradict the IDH, reporting negative effects of grazing intensity on plant richness (Pueyo et al. 2006, Eldridge et al. 2016), or little effect of moderate grazing on plant richness (Fernandez-Gimenez and Allen-Diaz 1999, Ren et al. 2012, Gamoun 2014).

Attempts to explain these inconsistencies have focused on differences in grazing frequency and duration (Shea et al. 2004, Miller et al. 2011, Yeboah and Chen 2016), or differences in the specific diversity metrics examined (species richness, Shannon diversity, evenness) (Svensson et al. 2012), but we are not aware of any study that has tested if, and how, climate (aridity) affects the applicability of the IDH to rangelands at a global scale.

It is clear that aridity, mean annual precipitation, plant productivity and herbivore type influence the impact of grazing on plant diversity (Proulx and Mazumder 1998, Bakker et al. 2006, Lezama et al. 2014, Herrero-Jáuregui and Oesterheld 2018). Bakker et al. (2006) and Lezama et al. (2014) found that grazing, even highly intense grazing, often has a positive effect on plant diversity in mesic (or productive) sites, but a negative effect in arid (or less productive) sites. Bakker et al. (2006) further showed that this conclusion holds only for large herbivores, not for small herbivores. In addition, the IDH may have limited applicability to systems in general (Fox 2013) and is highly context-dependent (e.g. vegetation succession stage, productivity) (Sheil and Burslem 2013, Huston 2014). Thus, there is a need to assess the conditions under which the IDH is a useful predictor of diversity–disturbance relations.

We hypothesize that the applicability of the IDH in rangeland systems depends on climate (aridity) and grazer types. To evaluate this hypothesis, we conducted a global meta-analysis to check whether the hump-shaped grazing–diversity relationship emerges consistently and globally across climates and grazer types using published studies. As an alternative hypothesis, we evaluated the Milchunas–Sala–Lauenroth (MSL) model, which predicts that diversity declines with grazing intensity in arid areas, while in wet areas grazing–diversity relationships are hump-shaped, as predicted by the IDH (Fig. 1) (Milchunas et al. 1988).

Methods

Search strategies and criteria

Using the Scopus database (<https://www.scopus.com/>), we entered “plant” AND (“richness OR diversity”) AND “grazing” as the search strings in ‘Article titles, Abstracts, Keywords’ of articles published between 1960 and October 2017, inclusive. This search yielded 2954 articles (Supplementary material Appendix 2 Fig. A1). Then, we screened these articles

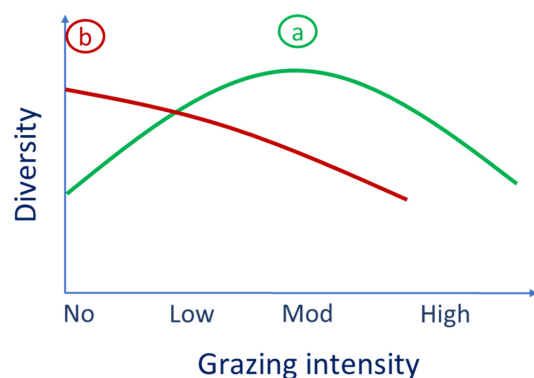


Figure 1. Milchunas–Sala–Lauenroth (MSL) model in (a) wet conditions and (b) dry conditions.

manually, selecting studies that met the following three criteria: 1) studies conducted in grasslands, savannas, shrublands or open forests. 2) Studies that used species richness to measure plant diversity in relation to at least three grazing intensities (e.g. no-, moderate- and high grazing; low-, moderate- and high grazing; or no-, low- and high grazing); hence, studies that investigated only ‘grazing versus no-grazing’ were omitted. 3) Studies whose geographic location was specified (in order to assign an aridity index to each study).

Data extraction

We collected the species richness details reported in each study, including sample size, original observation values and their standard errors (or standard deviations or variances) if reported, regardless of whether species richness had a significant relationship with grazing intensity. For those studies that reported species richness in figures or graphs, we extracted their values manually. Some studies had two or more grazing sites, we included data from all grazing sites, and each site constituted an independent record in the meta-analysis database. For those studies that presented species richness within multiple nested units (quadrat and plot), or in different years, we used only the data of the largest unit and the most recent year. Grazing intensities and coordinates were obtained from the text descriptions. For studies without coordinates, we identified their location using the names of grazing sites. The aridity index for each grazing site was extracted from the Global-Aridity dataset of the Consortium for Spatial Information website (<www.csi.cgiar.org>). World rangelands were classified into four types, according to the aridity index (UNEP 1997): arid, $AI < 0.2$; semiarid, $0.2 < AI < 0.5$; subhumid, $0.5 < AI < 0.65$; and humid, $AI > 0.65$. Only six studies were conducted in arid areas. Therefore, we combined arid and semiarid into a single AI class termed ‘dry areas’; and subhumid and humid areas into a second AI class termed ‘wet areas’.

Analyses

Meta-analysis and vote-counting are two common methods to synthesize published studies on a specific topic. Ecologists

are increasingly criticizing the vote-counting method for focusing solely on statistical significance and ignoring effect sizes. However, when relatively few studies report variation or dispersion of their results, researchers still tend to choose vote-counting (Mackey and Currie 2001, Kershaw and Mallik 2013) or unweighted meta-analysis (Herrero-Jáuregui and Oesterheld 2018). Thus, vote-counting is still valuable as a qualitative method to complement meta-analysis, especially when meta-analysis is not feasible. In our research, 51% of the studies that satisfied the three above-mentioned criteria did not provide measures of data variability (standard error or standard deviation or variance), and thus did not qualify for meta-analysis, but could still be included in a vote-counting procedure. Therefore, we decided to apply both methods independently; each method was conducted using the publications that qualified for that particular method. Supplementary material Appendix 1 documents the list of studies that were used in meta-analysis and vote-counting.

Meta-analysis

More than half of the selected studies estimated grazing intensity in a qualitative manner (e.g. distance from a water point or settlement, plot condition, community structure, forage utilization, etc.), rather than in comparable stocking rate units. Another problem was that the classification of grazing intensities varied among studies. For instance, low grazing intensity in one area could be treated as high grazing intensity in another area. Our approach to solve these problems was to consider each specific study as an independent unit within the meta-analysis. In each study, we can safely assume a coherent ordinal scale. To enable comparisons between different sites and different studies, we followed the original definition and categorization of grazing intensity made by each individual study: no grazing (NO), low grazing intensity (LOW), moderate grazing intensity (MOD) and high grazing intensity (HIGH). If a grazing intensity was classified as LOW in one study, we would refer to it as LOW as well. In any specific study, we presumed that the order of intensities is correct: low is lower than intermediate, etc. Thus, when we pool together all records of low grazing, for example, into a single subgroup LOW, we do not pool absolute grazing intensity and respective richness, but rather effect size relative to other grazing intensities in the same study. Finally, we calculated mean effect size for each class of grazing intensity. For more details on effect size see Eq. 1–4 below. In some cases, slight modifications of the study-specific scheme were applied, in order to adjust it to our scheme. Studies that reported grazing levels beyond HIGH, e.g. ‘very high grazing’ or ‘overgrazing’, were assigned to the class of HIGH-intensity grazing subgroup. For studies in which grazing intensity was represented by more than four stocking rates, we considered zero stocking rate as NO, the highest stocking rate as HIGH, the lowest non-zero stocking rate as LOW and the mean values between LOW and HIGH as MOD. This classification was used also in vote-counting analysis.

Hedges’ g , Cohen’s d and the log response ratio are metrics commonly used to calculate effect size in ecology (Gurevitch et al. 2001). However, in our sample, some studies did not have NO grazing as control treatment. Also, grazing intensity is an ordinal variable. For these two reasons, the above effect size metrics could not be used in our study. We therefore applied the method used by Yeboah and Chen (2016) to calculate effect size (Eq. 1) for each grazing intensity in each study. This method helped us address the inconsistency between species-rich and species-poor sites. Here we treated the grand mean species richness under all grazing treatments as a control within each study (or each grazing site).

$$ES_{ij} = \frac{D_{ij}}{U_i} \quad (1)$$

where ES_{ij} is the effect size of grazing treatment j in study i ; D_{ij} is the mean value of richness of the j th treatment in the i th study; U_i is the grand mean of all treatments within study i .

Effect size > 1 means that species richness under this grazing intensity is larger than the calculated value of grand mean species richness (the mean value of species richness from all grazing intensities) and therefore this grazing intensity has a positive effect on species richness. Effect size < 1 means species richness is lower than the grand mean species richness and hence the respective grazing intensity has a negative effect on species richness. The variance of each effect size ($V_{ES_{ij}}$) was estimated using the second moment of Taylor expansion (Benaroya et al. 2005) (Eq. 2).

We assumed that the variance in effect sizes comes from two sources: within-study variance (sampling error) and between-studies variance (heterogeneity). Thus, we chose the random-effects model. We used the REML method (restricted maximum-likelihood) to estimate between-studies variance τ^2 (Eq. 3, 4, Borenstein et al. 2009) and then weighted each effect size with the inverse of $\left[V_{ES_{ij}} + \tau^2 \right]$ (Borenstein et al. 2009). The proportion of true variance (τ^2) in species richness explained by grazing intensities is denoted as I^2 (Eq. 5, Borenstein et al. 2009).

$$V_{ES_{ij}} = \text{var} \left(\frac{D_{ij}}{U_i} \right) \approx \frac{\text{var}(D_{ij})}{E(U_i)^2} - \frac{2E(D_{ij})}{E(U_i)^3} \text{cov}(D_{ij}, U_i) + \frac{E(D_{ij})^2}{E(U_i)^4} \text{var}(U_i) \quad (2)$$

$$\tau^2 = \frac{Q - df}{C} \quad (3)$$

$$Q = \sum w_{ij} \times ES_{ij}^2 - \frac{(\sum w_{ij} \times ES_{ij})^2}{\sum w_{ij}}; C = \sum w_{ij} - \frac{\sum w_{ij}^2}{\sum w_{ij}};$$

$$W_{ij} = \frac{1}{V_{ES_{ij}}}; df = k - 1$$
(4)

$$I^2 = \frac{\tau^2}{\tau^2 + V_{ES_{ij}}}$$
(5)

Where $V_{ES_{ij}}$ is the variance of ES_{ij} ; $E(D_{ij})$ and $\text{var}(D_{ij})$ are the mean and variance of D_{ij} , respectively; $E(U_{ij})$ and $\text{var}(U_{ij})$ are the mean and variance of U_{ij} , respectively; 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; and I^2 is the ratio of between-studies variance to total variation in species richness.

To evaluate the IDH and MSL models (Fig. 1), we conducted subgroup analysis for NO, LOW, MOD and HIGH grazing intensities, respectively. We compared the summary effect size between subgroups using Z-test (Borenstein et al. 2009) at a global scale, as well as in dry areas and in wet areas. Next, we checked how ecosystem types (grasslands and woodlands) and types of livestock grazing (cattle, sheep, goats and yak) influence our results. The MSL model also predicts differences in the response of diversity to grazing between regions with short- and long evolutionary history of livestock grazing. Yet, our literature survey yielded very few relevant studies from areas with a short evolutionary history of grazing (Supplementary material Appendix 1). Therefore, we did not evaluate the evolutionary history aspect of the MSL model. Similarly, due to a lack of available data on species evenness and on grazing frequency, these two indicators were not considered in our study.

To test for possible publication bias, we used funnel plot and rank correlation to test for asymmetry (Sterne and Egger 2001). The Kendall's correlation showed no significant relationship between effect sizes and standard errors, indicating that funnel plots were symmetric for all subgroups and there was no publication bias in effect sizes (Supplementary material Appendix 2 Fig. A2–A4).

Statistical analyses were performed with R ver. 3.4.0 (<www.r-project.org>), using the package metafor 2.0 (Viechtbauer 2010).

Vote-counting

All studies that met the selection criteria could be used for vote-counting. In this analysis we used the same grazing intensity classification that was employed in meta-analysis. We first summarized the main diversity-grazing relationship shapes observed in real rangelands. Then we proposed a new evaluation scheme for vote-counting, by comparing species richness in the following pairs of increasing grazing intensities:

NO-LOW, NO-MOD, LOW-MOD and MOD-HIGH. Therefore, in each study, we labeled the difference in richness for each pair: if richness was higher with the higher grazing intensity, we labeled it as a positive (+); if richness was higher with the lower grazing intensity, a negative (–); and if no difference was found, we marked it as an equal (=). According to the IDH, differences in richness between the following pairs of grazing treatments should be positive: NO-LOW, LOW-MOD and NO-MOD. In contrast, the difference in richness for the grazing intensity pair MOD-HIGH should be negative. Whenever a study reported a grazing treatment as high intensity, we assigned it as HIGH, even in cases in which it was not high enough to cause a negative effect on richness compared to moderate grazing. Thus, we might not observe a negative relationship between MOD-HIGH even if one exists at theoretical very high grazing intensities outside traditional management or stocking rates, etc. The IDH does not have a specific prediction of the differences between LOW and HIGH, and therefore this pair was not included in this analysis. In contrast, based on the expectations derived from the MSL model, in dry areas, differences in richness between all pairs of grazing treatments should be negative; in wet areas, differences should follow the IDH predictions. We counted the frequency of positive differences, negative differences and no differences in richness between pairs that represent an increase in grazing intensity. The χ^2 frequency test was used to check whether the frequency distribution is significantly different from a random model. If it is not significantly different from a random model, then the IDH and MSL models cannot be supported.

Results

Systematic review of selected studies

Altogether, 63 studies met our selection criteria, of which 51 studies and 12 studies, were from the old world, and the new world, respectively. Roughly five-sixths of the studies examined grasslands, and the other one-sixth concerned shrublands and open forests (commonly referred to as 'woodlands' hereafter) (Fig. 2). These studies included 83 different grazing sites, all of which were used for the vote-counting analysis. Standard error, standard deviation or variance of species richness were only reported in 31 of the studies, encompassing 48 grazing sites. Therefore, the meta-analysis was conducted using these 48 different grazing sites.

Meta-analysis

For all studies combined, a weak hump-shape pattern was observed, with moderate grazing having slightly but significantly higher species richness than other grazing intensities (Fig. 3a). Accounting for aridity, studies from dry areas revealed a notable, yet insignificant decline in species richness with increasing grazing intensity; no-grazing had a significant positive effect on richness (Fig. 3b). In contrast,

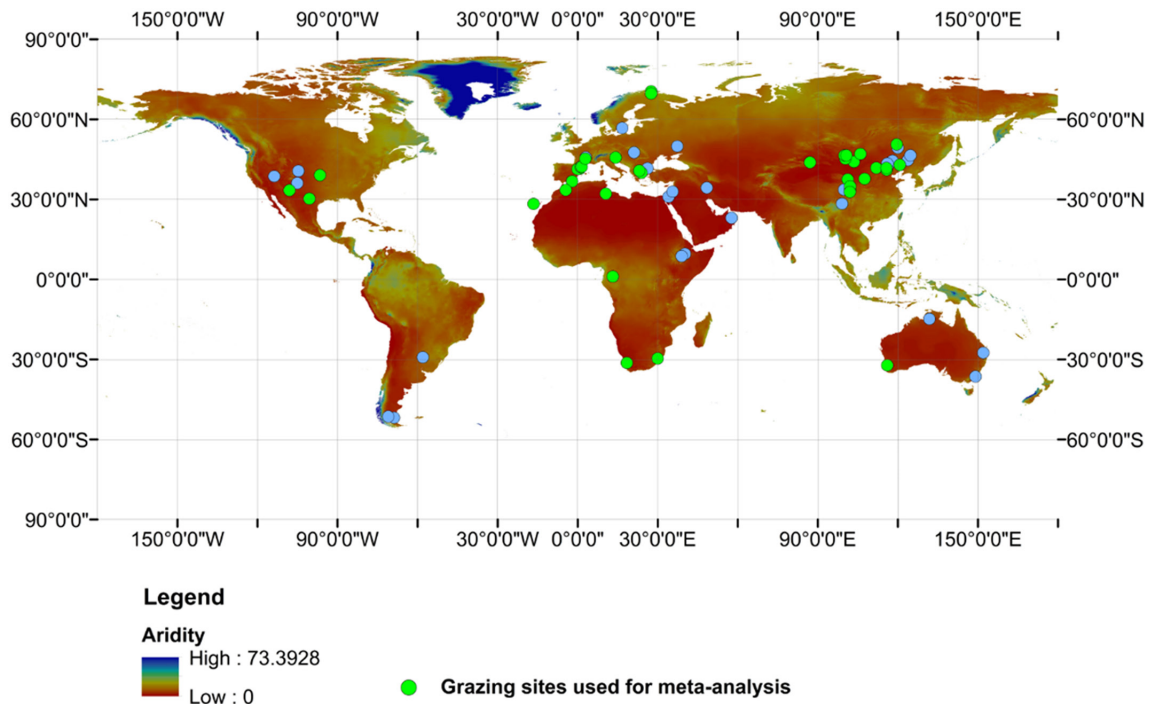


Figure 2. The global distribution of the 63 studies that met our criteria. Studies in green dots could be used for meta-analysis (reported either standard error, or standard deviation). All studies were used for vote-counting. The world aridity map was downloaded from <www.cg iar-csi.org/>.

when only studies from wet areas were considered, a significant negative effect of no-grazing, and a significant positive effect of moderate grazing on species richness were found, wherein a significant and stronger hump-shape emerged (Fig. 3c), indicating a good fit to the MSL model. In addition, a relatively large proportion of variability in species richness was explained by grazing intensities, with I^2 ranging from 40% to 88%, except in the case of MOD grazing in dry areas (see detailed results in Supplementary material Appendix 3).

Similar response patterns of species richness to grazing intensity were observed between all areas and all grasslands, as well as between wet areas and wet grasslands (Supplementary

material Appendix 2 Fig. A5a, c). No clear pattern of grazing intensity–plant richness relationship was found in dry grasslands and all woodlands (Supplementary material Appendix 2 Fig. A5b, d). The small sample size of available studies in woodlands prevented us from comparing between dry and wet woodlands.

Sheep grazing studies were conducted in both dry areas and wet areas, in similar proportions (Table 1). However, the results from sheep grazing supported neither the IDH nor the MSL model (Fig. 4a–c). In dry areas, mixed sheep and goat grazing showed a significant decline in species richness (Fig. 4d), whereas mixed grazing by cattle, sheep, goats, etc. across all studies revealed a slight hump-shape pattern along

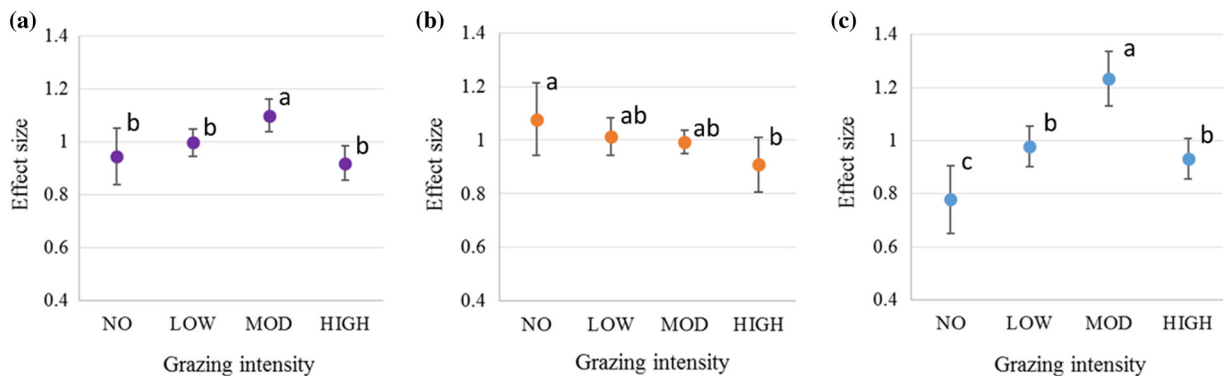


Figure 3. Effect sizes (\pm 95% confidence intervals) of each grazing intensity on species richness. (a) Across all studies, $n_{NO} = 32$, $n_{LOW} = 39$, $n_{MOD} = 42$, $n_{HIGH} = 47$. (b) In dry areas, $n_{NO} = 17$, $n_{LOW} = 18$, $n_{MOD} = 21$, $n_{HIGH} = 23$. (c) In wet areas, $n_{NO} = 15$, $n_{LOW} = 21$, $n_{MOD} = 21$, $n_{HIGH} = 24$. Black bars indicate confidence intervals of effect sizes. Values not sharing the same letters are significantly different at $p < 0.05$.

Table 1. Number of records of studies and sites with different types of livestock.

Types of livestock	Dry areas		Wet areas		Total	
	No. of studies	No. of sites	No. of studies	No. of sites	No. of studies	No. of sites
Cattle	1	1	5	8	6	9
Sheep	5	7	5	6	9	13
Goat	0	0	1	1	1	1
Sheep, goats	4	7	0	0	4	7
Cattle, sheep, goats, etc.	5	7	1	2	6	9
Yaks	0	0	2	4	2	4
Sheep, yaks	0	0	1	1	1	1
Reindeer	0	0	1	2	1	2
Not clear	1	2	0	0	1	2
Total	16	24	16	24	31	48

grazing intensity (Fig. 4e). Cattle grazing and yak grazing studies conducted mainly in wet areas revealed a clear hump-shape pattern (Fig. 4f), fitting the IDH, as well as the prediction of the MSL model in wet areas.

Vote-counting

A visual representation of the relationship between species richness and grazing intensities across studies revealed diverse responses to increased grazing intensities, from NO to LOW, MOD and HIGH (Table 2). The most frequent shapes of these responses across all studies were a hump-shape, and a monotonic decrease (row 1–2 and column 3 in Table 2), which together accounted for 60% of all observed relationships in species richness. These two shapes correspond to the IDH as well as to the MSL model. Interestingly, the percentage of other responses that do not easily fit any ecological theory was relatively higher in dry areas (around 52%), than in wet areas (about 27%) (Table 2). A hump-shape response curve was more common in grasslands than in woodlands (row 1 in Table 2).

Across all studies, the frequency of negative effects was significantly higher than positive effects when grazing intensity was increased from MOD to HIGH, while differences in frequencies between positive and negative effects for all other pairs (NO-LOW, NO-MOD, LOW-MOD) were smaller and insignificant (Table 3). In dry areas, negative responses were more common than positive responses in all comparison

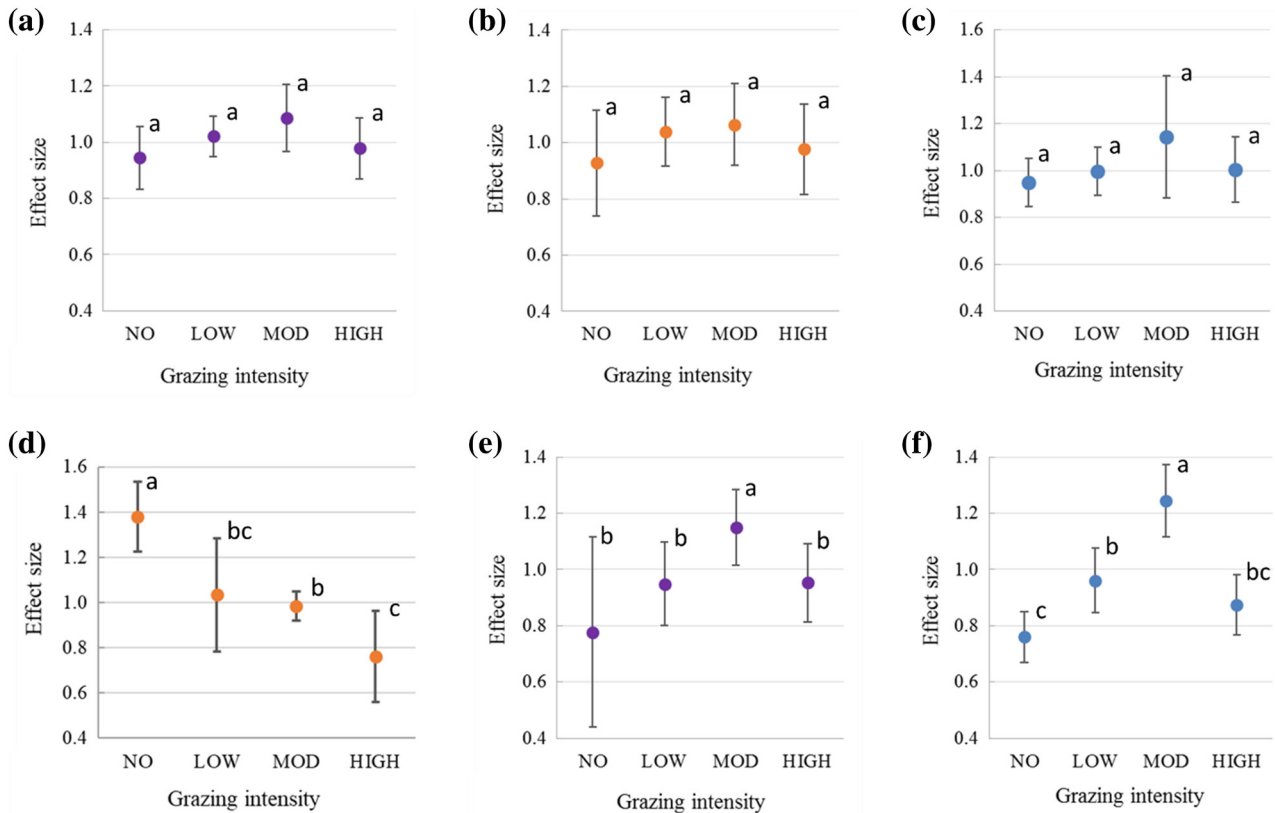




Figure 4. Effect sizes ($\pm 95\%$ confidence intervals) of each grazing intensity on species richness for sheep grazing in all areas (a) ($n_{\text{NO}} = 11$, $n_{\text{LOW}} = 13$, $n_{\text{MOD}} = 8$, $n_{\text{HIGH}} = 13$), in dry areas (b) ($n_{\text{NO}} = 6$, $n_{\text{LOW}} = 7$, $n_{\text{MOD}} = 4$, $n_{\text{HIGH}} = 7$), and in wet areas (c) ($n_{\text{NO}} = 5$, $n_{\text{LOW}} = 6$, $n_{\text{MOD}} = 4$, $n_{\text{HIGH}} = 6$), for mixed grazing with sheep and goats in dry areas (d) ($n_{\text{NO}} = 5$, $n_{\text{LOW}} = 3$, $n_{\text{MOD}} = 7$, $n_{\text{HIGH}} = 7$), for mixed grazing with cattle, sheep, goats, etc. in all areas (e) ($n_{\text{NO}} = 6$, $n_{\text{LOW}} = 5$, $n_{\text{MOD}} = 9$, $n_{\text{HIGH}} = 9$), and for cattle grazing and yak grazing in wet areas (f) ($n_{\text{NO}} = 6$, $n_{\text{LOW}} = 12$, $n_{\text{MOD}} = 12$, $n_{\text{HIGH}} = 12$). Black bars indicate confidence intervals of effect sizes. Values not sharing the same letters are significantly different at $p < 0.05$.

Table 2. The frequency of observed relationships that show the responses of species richness to increasing grazing intensity (NO, LOW, MOD, HIGH) in 83 grazing sites from the 63 collected studies.

Row number	Shapes	All areas	Dry areas	Wet areas	Grasslands	Woodlands
1.		31	7	24	26	5
2.		19	13	6	13	6
3.	Others	33	22	11	23	10
4.	Total	83	42	41	62	21

Others include the shapes of , , ,  and .

pairs, yet these results were insignificant. By contrast, in wet areas, negative effects were more frequent than positive effects between MOD-HIGH, while positive effects were more frequent in all other pairs (NO-LOW, NO-MOD and LOW-MOD), supporting IDH expectations (Table 3).

Discussion

The predictive power of the IDH and MSL models across an aridity gradient

The interaction of aridity and grazing intensity

We found that the IDH was weakly supported by the meta-analysis and not supported by vote-counting, when evaluated across all ecosystem types and grazing intensities. However, when only studies from wet areas were considered, results of both meta-analysis and vote counting showed that moderate grazing clearly had the highest positive effect on richness compared to no-, low- and high-grazing treatments, with a good overall fit to the predictions of the IDH and MSL models. In dry areas, the meta-analysis showed an overall decrease in diversity with increased grazing intensity, which contradicts the predictions of the IDH while supporting the MSL model. The results of vote-counting from dry areas did not differ from random expectations and therefore cannot support either the IDH or the MSL model.

These results suggest that aridity influences the relationship between grazing intensity and plant richness at the global scale and the more nuanced predictions of the MSL model were upheld by this study overall. This finding is inconsistent with recent work by Herrero-Jáuregui and Oesterheld (2018), who found that species richness was significantly

reduced with increasing stocking rate, but these responses did not change across environmental conditions. Yet, most of the negative responses occurred in arid, low productivity systems. In contrast, we found clear trends of decreasing species richness in dry areas, and a hump-shape pattern in wet areas. There are two possible reasons for this inconsistency. One is a difference in the data. Herrero-Jáuregui and Oesterheld (2018) included studies with at least two grazing levels (LOW versus MOD, or HIGH versus MOD), and excluded no grazing. However, we included only studies with at least three of four grazing levels, NO, LOW, MOD and HIGH. This difference resulted in a small overlap of studies (17) between the two datasets. Another difference is in the methods. Herrero-Jáuregui and Oesterheld (2018) used unweighted meta-analysis, while we used a weighted meta-analysis.

Further, we found that ‘no grazing’ in dry areas significantly increased plant richness, but had an opposite effect in wet areas. This suggests that ‘no grazing’ is a good strategy to conserve biodiversity in dry areas. By contrast, moderate grazing in wet areas had a significant positive effect on richness, revealing that moderate grazing is required for maintaining higher plant diversity in wet areas. Plus, the mean effect size of high grazing in both dry and wet areas were similar, so was that of low grazing. We therefore conclude that in wet areas the strong hump-shaped pattern of grazing intensity–plant richness relationship was mainly due to the significant negative effect of no-grazing and significant positive effect of moderate grazing.

The interaction of aridity and vegetation type

Aridity, which is closely related to productivity, largely determines vegetation types and attributes, and thus determines

Table 3. χ^2 test for evaluation of the IDH and MSL models. All null hypotheses mean the frequency of positive and negative differences should distribute randomly and evenly within each pair of treatments.

	Grazing effect	M-H (+)	M-H (-)	N-L (+)	N-L (-)	N-M (+)	N-M (-)	L-M (+)	L-M (-)
All areas	Obs.	23	51	26	17	26	19	36	29
	Exp.	37	37	21.5	21.5	22.5	22.5	32.5	32.5
	p-value	0.001		0.170		0.297		0.385	
Dry areas	Obs.	15	21	10	13	11	15	13	17
	Exp.	18	18	11.5	11.5	13	13	15	15
	p-value	0.317		0.532		0.433		0.465	
Wet areas	Obs.	8	29	15	4	14	4	22	12
	Exp.	18.5	18.5	9.5	9.5	9	9	17	17
	p-value	0.001		0.012		0.018		0.086	

N, L, M and H: no-, low-, moderate- and high-grazing; Obs.: observation frequency; Exp.: expected frequency from null (random) model.

the ways in which grazing intensity affects plant richness (Milchunas et al. 1988, Milchunas and Lauenroth 1993, Cingolani et al. 2005). The vegetation types in dry areas included desert steppe, sandy grasslands, steppe, succulent Karoo and semi-arid savanna (Supplementary material Appendix 1), with sparse or degraded vegetation, dominated by less palatable species (Milchunas et al. 1988, Olff and Ritchie 1998, Wan et al. 2015). Borer et al. (2014) concluded that herbivores affect plant diversity via light limitation, irrespective of climate and site productivity. However, competition release through increasing light availability by grazing is relatively small in most dry areas compared to wet areas (Olff and Ritchie 1998, Eldridge et al. 2016). Thus, grazing may not affect plant richness by increasing light availability in dry areas. Instead, grazing may reduce species richness by decreasing the palatable-subdominant species, further increasing the dominance of less palatable species, and thus increasing competitive exclusion and decreasing plant richness (Fox 2013, Papanastasis et al. 2017, Koerner et al. 2018). We observed a small decline in species richness with increasing grazing intensity in dry areas, which is consistent with other findings from low productivity areas (Bakker et al. 2006, Lezama et al. 2014).

In our dataset, there were more woodlands in dry areas than in wet areas. The responses of plant richness to grazing intensity in woodlands are inconsistent, showing an increase (Fernández-Lugo et al. 2013, Verwijmeren et al. 2014), a decrease (Papanastasis et al. 2017), or no change in richness (Alados et al. 2004). Unfortunately, the few records for woodlands do not allow a firm conclusion.

By contrast, in wet areas vegetation types were alpine meadow, meadow steppe, Mediterranean grasslands and tall-grass prairie, where vegetation is relatively dense and with high growth rate, dominated by tall or intermediate grasses. Unlike in dry areas, light competition is relatively intense in wet areas. Compared to no grazing, grazing in wet areas may decrease light limitation and thus reduce the dominance of intermediate and tall grasses, opening niches for less competitive species, such as short grasses, forbs or exotics (Milchunas et al. 1988, Proulx and Mazumder 1998, Roxburgh et al. 2004, Díaz et al. 2007, Segre et al. 2016). These effects are stronger under moderate grazing than under low grazing, resulting in increased plant richness (Huston 1979, Milchunas et al. 1988, Bakker et al. 2006, Lezama et al. 2014).

The interaction of aridity and livestock type

Accounting for livestock types, our results revealed a significant decrease in richness under mixed grazing of sheep and goats in dry areas (Fig. 4d), while grazing by sheep-only in dry areas resulted in no difference between grazing intensity classes (Fig. 4b). In wet areas, a strong hump-shaped pattern was found for cattle- and yak grazing (Fig. 4f), and still no difference between grazing intensities for sheep-grazing (Fig. 4c). Mixed grazing of cattle, sheep, goat, etc. yielded a slight humped shape across all aridity (Fig. 4e). The observed differences between livestock types may be because of species-specific dietary preferences (Walker 1994, Gamoun 2014,

Tóth et al. 2016). These results support the conclusion of Wan et al. (2015) and Tóth et al. (2016) that livestock type plays an important role in shaping diversity–grazing relationships and in conserving biodiversity in rangelands.

Overall, the response patterns of plant richness to grazing may vary with different combinations of grazing intensity, aridity and livestock types. Therefore, adjustments of the IDH and MSL models that account for specific combinations of these factors will help us to better use these models to guide biodiversity conservation and rangeland management. For instance, in dry areas the decrease in plant richness predicted by the MSL model is greater when mixed grazing of sheep and goats is included, suggesting that this kind of grazing regime is not good for maintaining diversity in dry areas. Thus, climatic conditions, especially aridity and grazer type should be considered in prescribing grazing regimes.

Future prospects

Our study revealed that the predictions of the IDH in rangelands are conditional on climate and that the climate-specific MSL model better reflects the impact of grazing on diversity. In addition, a promising topic for future studies is the effect of specific grazers, and the interaction between aridity and grazer type in diversity–grazing relationships.

However, most livestock grazing studies do not use a standard measure of grazing intensity, and do not report species richness variability. In addition, most studies are limited to grazing versus no-grazing or low versus high grazing comparisons, which greatly reduces the predictive power of grazing–diversity models. Our initial search yielded around 2900 papers, but only 63 studies (including 83 grazing sites) were more than just ‘grazing versus no grazing’ studies, and only 31 studies (48 grazing sites) quantified the variation of species richness, which is essential for meta-analysis. Here, we only included studies that observed at least three grazing intensities (including no grazing) and sampled species richness. This significantly reduced the number of available studies, but also gave our study a unique focus on the relationship between grazing intensity and species richness. Standardized measures of multiple grazing intensities in future studies have the potential to enhance our understanding of the effects of grazers on plant community diversity.

Data availability statement

Data are available from the Github Digital Repository: <<http://github.com/Junjing2019/data-for-Gao-and-Carmel-2019-1>> (Gao and Carmel 2019).

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Supplementary material (available online as Appendix oik-06338 at <www.oikosjournal.org/appendix/oik-06338>). Appendix 1–2.