

Grazing effects on soil seed banks: a global synthesis

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Abstract. Livestock grazing is a major disturbance affecting plant diversity and abundance in terrestrial ecosystems. The intermediate disturbance hypothesis (IDH) predicts that moderate-intensity grazing should produce the highest species diversity, while the Milchunas-Sala-Lauenroth (MSL) model posits that the IDH is valid only for mesic areas. However, it remains unclear how grazing affects soil seed bank and whether or not the IDH or MSL models are valid for soil seed bank communities. Here, we presented a global meta-analysis synthesizing 483 observations: we found that grazing had a negative effect on soil seed bank abundance, but did not alter seed bank richness. Further refining the analysis, light-intensity grazing was found to increase seed bank richness, while moderate-intensity grazing had no effect, and heavy-intensity grazing had a negative effect. Additionally, for both arid and mesic areas, soil seed bank richness declined with grazing intensity increased. Overall, grazing effects on soil seed banks differed from expectations set by studies of aboveground vegetation. Our study provides key insights for policy-makers managing livestock grazing and grassland conservation.

Introduction

Grazing is one of the major anthropogenic disturbances affecting on plant community composition (i.e., richness and abundance) (Adler et al., 2001; Diaz et al., 2006). However, most empirical studies to date have focused on the relationship between grazing and the aboveground vegetation, ignoring its impacts on soil seed banks (Plue et al., 2020). Grazing can alter the species composition of soil seed banks by impacting seed inputs and seed outputs (Bakker et al., 1996). According to the intermediate disturbance hypothesis (IDH), moderate-intensity grazing should produce the highest diversity in the aboveground vegetation (Connell, 1978), while the Milchunas-Sala-Lauenroth (MSL) model predicts that the IDH is valid only for mesic areas. Currently, global-scale quantitative and qualitative analyses of grazing effects on soil seed banks remain lacking, not to mention tests of whether the IDH model are applicable to soil seed bank communities. The main objectives of this study were to analyze the spatial and temporal responses of soil seed banks to livestock grazing and to verify whether the IDH model are applicable to soil seed bank communities.

Methods

We conducted a meta-analysis based on 483 paired comparisons from 62 experimental studies (published between 1992 and 2020) to evaluate grazing effects on soil seed banks. The data were limited to two treatments: grazing and grazing exclusion (i.e., we did not include studies that used the distance to a water source as a substitute for grazing intensity). We also excluded studies which combined the grazing and non-grazing treatment with another disturbance, such as moving, fire, fallow and sowing manipulations. The grazing animals were some types of livestock, and we eliminated studies concerning invertebrate grazers. The Web of Science and the China National Knowledge Infrastructure (CNKI) databases were used to collect primary studies in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines. To evaluate the mean grazing effects on soil seed bank and the compositional similarity between the seed bank and aboveground vegetation, the log response ratio (lnRR) was calculated for each data pair. Within and between study variance were considered for effect sizes in our analysis. The inverse of the variance was used to weight observations and residual maximum likelihood (REML) estimation was used to estimate the variance between studies. To test the IDH and MSL model, spatiotemporal variations of soil seed bank responses to grazing was correlated with grazing intensity, grazing duration and regional aridity, among other factors. Trim-and-fill tests showed our results for soil

seed bank richness and abundance were robust, and thus we did not consider publication bias to be an issue for interpretation of the results.

Results and Discussion

Grazing effects on soil seed bank richness

In this study, grazing had no effect on soil seed bank richness at a global scale (Figure 1a), but decreased richness in dry areas (Figure 2c). In mesic areas, light grazing increased soil seed bank richness (Figure 2c), but this was not true for moderate or heavy grazing (Figure 2g). This provides clear evidence that grazing effects on soil seed bank communities may differ from those on aboveground vegetation. Therefore, we cannot extrapolate classical hypotheses on the disturbance-diversity relationship (e.g., the IDH and MSL models) to soil seed bank communities. Our results yield significant insight into the relationship between disturbance and soil seed bank diversity.

Owing to seed dormancy and the generally high diversity of soil seed banks, these have generally been considered to buffer plant communities from the effects of environmental change and anthropogenic disturbance. However, this assumption was not supported by this study, especially for dry areas. While the grazing effects on the soil seed bank are driven by complex mechanisms, a likely explanation for our results is the potential global grassland degradation. Most of the study sites in our analysis had hundreds of years of grazing history; additionally, overgrazing and grassland degradation were not uncommon at these sites. In other words, in degraded ecosystems, light grazing could exceed the local livestock carrying capacity, thereby having negative effects on soil seed bank richness. Therefore, these reasons could contribute to the discrepancy between the IDH and soil seed bank responses in our results.

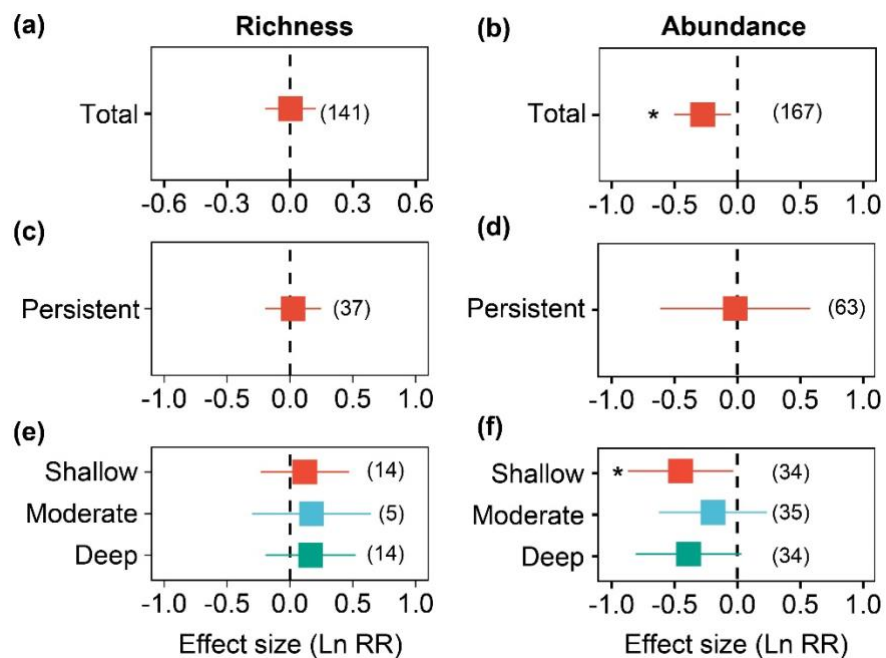


Figure 1. Grazing effects (mean and 95% confidence interval) on species richness and abundance for all grazing sites (a, b), the persistent soil seed bank (c, d) and different soil depths (e, f). Sample sizes are provided in parentheses. * represents significant effect size at $p = 0.05$ level.

Grazing-induced decrease in soil seed bank abundance

Grazing decreased soil seed bank abundance (Figure 1b), another important metric of the composition of the soil seed bank. This reduction may be associated with vegetation damage and removal by livestock

foraging and trampling (Marquez et al., 2002), thus indirectly reducing seed production. Direct livestock consumption of seeds further reduces the number of seeds entering the soil seed bank (Zhao, et al., 2008).

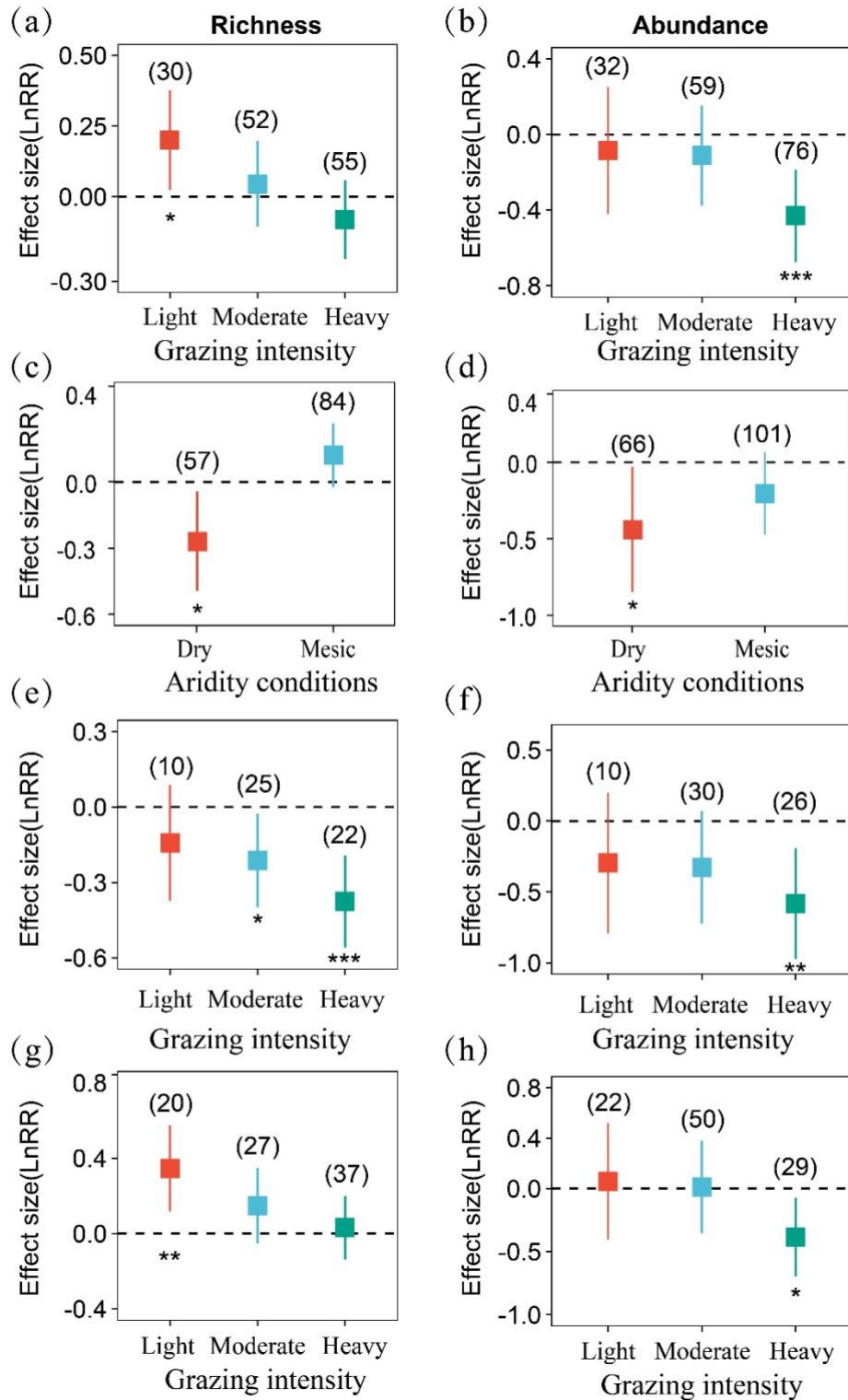


Figure 2. Grazing effects (mean and 95% confidence interval) on species richness and abundance for different grazing intensities (a, b) and aridity conditions (c, d), as well as for arid (e, f) and mesic areas (g, h). Sample sizes are provided in parentheses. *, **, and * represent significant effect size at $p = 0.05$, 0.01 , and 0.001 level, respectively.**

Uncertainties and implications for future research and grassland management

Our results provide insights into how soil seed bank composition responds to grazing at a global scale. In order to better understand our findings, we suggest careful consideration of the following aspects. First, most studies included in the meta-analysis were from temperature climates in Asia and Europe. Given that the effects of grazing may differ with the climate (especially in Africa, America and Australia), future studies should be conducted at a larger spatial scale. Second, although the impacts of grazing on the seed bank occurred over long timespans, recent global change trends are accelerating this process; for example, global warming, changes to precipitation regimes, nitrogen deposition and other factors might promote the degradation of terrestrial ecosystems. Hence, future research should take into the consideration that the combination of grazing effects and global change factors. Finally, to formulate a sustainable grazing system, policy-makers should take both the aboveground vegetation and soil seed bank into account.

Conclusions

First, grazing effects on soil seed banks differed from expectations set by studies of aboveground vegetation. Light-intensity grazing increases soil seed bank richness, while moderate- and heavy-intensity grazing has no effect and decreases soil seed bank richness, respectively. As grazing intensity increased, soil seed bank richness decreases in both arid and mesic areas. Therefore, we cannot extrapolate classical hypotheses on the disturbance-diversity relationship (e.g., the IDH and MSL models) to soil seed bank communities. Second, our results indicate that some global change factors, such as increasing aridity, may accelerate the grazing impacts on soil seed banks. Third, our results suggest the potential grassland degradation across the world and highlight the importance of taking both aboveground vegetation and soil seed bank into account in grassland conservation and livestock grazing management.

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