INTRODUCTION

Natural grasslands account for 41% of the earth’s surface area and have important ecological functions, such as maintaining biodiversity and stability in terrestrial ecosystems (Firn et al., 2015). Plant community diversity is conducive to maintaining the regional resilience, complexity, ecosystems stability, and ecosystem services (Catano & Stout, 2015; Chen, Ma, Xin, Liu, & Wang, 2017). As an important indicator of community diversity, species richness represents the development status of plant communities, has significant feedback to the interference (Liu, Kan, Yang, & Zhang, 2015).

Plant species richness is regulated by complex interactions of related factors (Lamb, 2008). For example, it is not only closely related to productivity (Bai, Han, Wu, Chen, & Li, 2004; McCann, 2000; Williams, Seabloom, Slayback, Stoms, & Viers, 2005), but also to soil properties and ecosystem microclimate (Ives & Carpenter, 2007; Wang, Zhang, Zhu, Yang, & Li, 2018; Wu et al., 2016). As the main target of land use pattern, plant litter is also one of the main factors regulating plant community richness (Foster & Gross, 1998; Muller, Mesléard, Buisson, & Hölzel, 2014; Wardle, Bonner, & Nicholson, 1997). Studies have shown that moderate litter accumulation contributes to improving plant community species richness (Finegan et al., 2015; Nilsson, Xiong, Johansson, & Vought, 1999; Rajaniemi, 2002), while excessive litter accumulation has a negative effect on plant species richness (Kassen, Buckling, Bell, & Rainey, 2000; Lorrillière, Couvet, & Robert, 2012; Tilman et al., 2001). Furthermore, abandonment or closure significantly increases the accumulation of plant litter (Hosseinzadeh, Jalilvand, & Tamartash, 2010), which had stimulated

Abstract

Plant community diversity is conducive to maintain the regional ecosystems stability and ecosystem services. Seed germination is one of the main ways to regulate plant diversity, owing to seedling recruitment as a basis for plant community renewal. However, the exact mechanism of how plant litter affects seedling recruitment, and species richness is not yet fully understood. Therefore, a litter addition and removal experiment was established in a semiarid grassland to study the effects of plant litter on seedling recruitment and species richness from April to August in 2016 and 2017 in Northern China. The positive correlation between species richness and seedling recruitment indicated that a guarantee of seedling recruitment was the main precondition to protect species richness. Adding rather than removing litter significantly reduced species richness. Litter addition inhibited species richness by directly increasing mechanical damage or indirectly reducing photosynthetically active radiation and seedling recruitment. The results of this study are conducive to understand the evolutionary and regulatory mechanisms of community species richness and seedling recruitment in grassland ecosystems after adding or removing plant litter.

KEYWORDS
light interception, seed bank, seed germination, structural equation model, temperate steppe
Plant litter alters plant growth by affecting seed germination, seedling recruitment, and interspecific interactions (Foster, 2001; Xiong & Nilsson, 1999). Moreover, species composition is also regulated by changes in seedling recruitment, which is selected by the litter layer and size of the seed (Egaw & Tsuyuzaki, 2013). However, a few studies have focused on the effect of plant litter on species richness through seedling recruitment. Plant litter plays an important role in seed bank formation and seedling recruitment (Egaw & Tsuyuzaki, 2013). However, plant litter accumulation had significant positive effects on seedling recruitment, which increased the inconsistency of plant litter effects on plant species richness. In addition, physical conditions (microclimate) indirectly affect species richness due to plant development, which is regulated by light via the phytochrome pigment (Beligni & Lamattina, 2000; Chory et al., 2009). Photosynthetically active radiation (PAR) stimulates or inhibits seedling recruitment and species richness due to plant growth, which is regulated by light via the phytochrome pigment (Beligni & Lamattina, 2000; Chory et al., 1996). Therefore, the inconsistent responses of seedling recruitment to physical conditions may result in an uncertain effect of litter on species richness.

A litter manipulation experiment was conducted to explore the responses of plant community seedling recruitment and species richness to a litter addition and removal treatment in a semiarid grassland in Northern China. This field experiment mainly considered two objectives: (a) identify the factors affecting seedling recruitment and species richness of plant communities; (b) determine whether litter addition and removal affects plant species richness through seedling recruitment.

2  |  MATERIALS AND METHODS

2.1  |  Experiment design

This experiment was performed at the Duolun Restoration Ecology Station of the Institute of Botany, Chinese Academy of Sciences (42°02′N, 116°17′E), Inner Mongolia, China. The station is located in a semiarid temperate steppe, at an altitude of 1,324 m. Mean annual precipitation is 385.5 mm, and mean annual temperature is 2.1°C. The sandy soil of the study site is classified as chestnut accord to the Chinese classification, or as Haplic Calcisol accord to the FAO classification (Song, Niu, & Wan, 2016; Xia & Wan, 2013). The plant species at this experimental site are dominated by Artemisia frigida, Agropyron cristatum, and Stipa krylovii. The growing season is from early May to October.

This experiment began in April 2016. A randomized block design was established in our experiment. The natural surface soil (10 cm) was collected and mixed after filtering through a 2 mm sieve to ensure that all plots had the same soil seed bank. The mixed surface soil was placed in 36 ceramic pots of 35 cm diameter to observe seedling recruitment of the plant community in the natural state. The base soil without seed bank was placed at the bottom in each pot. Ten centimeters of mixed surface soil was added on the top of base soil to ensure that the soil seed bank in each pot was uniform. All pots were shallowly buried in the field, where soil was taken. Litter treatments were set at three levels: litter left intact (C), litter removal (LR), and litter addition (LA). Plant litter was collected in the surrounding plot in April 2016 with an average amount of 90 g/m². Plant litter was mixed and added directly to the pot without seed inactivation. The longer litter was cut to 30 cm of debris for easy mixing and adding to the pots. The mixed plant litter (8.66 g) was added to the control plots, and the litter addition plots received 17.32 g of mixed plant litter. There was no plant litter in the litter removal plots. Finally, 5-cm mesh nylon net was used to cover all plots to fix the litter and eliminate experimental errors. Each treatment was replicated 12 times. This study was implemented during the growing seasons of 2016 and 2017, and the experiment in 2017 was completely repeated the treatments in 2016.

2.2  |  Measurement factors

We set up plots at the end of April of each year and monitored the plots in the subsequent spring and Autumn (April to September). All seedlings were counted and identified to species level until the time of peak emergence, that is, 20 August. The number of seedlings was also counted simultaneously to determine species richness. The census interval was 2–5 days for this experiment. Physical variables were measured simultaneously with seedling recruitment. Soil temperature and moisture were measured in the 5-cm soil layer. Photosynthetically active radiation was determined at the soil surface in the litter removal plots, but PAR in the litter addition and control plot was determined as the average PAR at canopy height (PARc) and underplant litter (PARl). Light interception (ΔPAR) was defined as the difference between PARc and PARl.

2.3  |  Statistical analysis

Repeated-measures analysis of variance (ANOVA) with a random block design was performed to test the main and interactive effects of the plant litter manipulation and year on physical values,
TABLE 1  Effects of litter addition and removal on microclimate, seedling recruitment, and species richness with time

|            | SM (%) | ST (°C) | PAR (µmol m⁻² s⁻¹) | PAR_c (µmol m⁻² s⁻¹) | PAR_s (µmol m⁻² s⁻¹) | ΔPAR (µmol m⁻² s⁻¹) | Seedling recruitment | Species richness |
|------------|--------|---------|--------------------|-----------------------|-----------------------|----------------------|----------------------|-------------------|
| L         | 7.09** | 11.8*** | 128***             | 0.66                  | 80.0***               | 64.8***              | 25.1***              | 6.43**            |
| years     | 3.6*   | 111***  | 8.7**              | 65.1***               | 5.48*                 | 0.23                 | 9.65**              | 9.08**            |
| L × years | 1.28   | 2.48†   | 0.26               | 0.23                  | 0.55                  | 0.70                 | 1.47                 | 0.21              |

Note: Linear mixed-effects model of the effects of the number of treatment years and the number of litter manipulations (litter addition and removal) on microclimate, seedling recruitment, and species richness, with plot nested in year, nested in site, as random effects, using all 30 sites. Abbreviation: L, litter addition and removal treatments. Significant level: *p < .1, **p < .05, ***p < .01, ****p < .001.

seedling recruitment, and species richness. Between-subject effects were evaluated as a block, by litter manipulation, and their interactions, and the within-subject effect was year. The effect of block was tested together with the treatment in all analyses, but they were not discussed in this study. One-way ANOVA and the least significant difference test were used to analyze the differences in the physical values, seedling recruitment, and species richness among litter treatments. A regression analysis was conducted to test the relationship between physical values, seedling recruitment, and species richness. All data were tested for normality and homogeneity of variance prior to ANOVA. All results were analyzed with SAS V8 software (SAS Institute).

The structural equation model (SEM) was used to examine the relationships among physical variables, seedling recruitment, and species richness (Gaitán et al., 2014; Grace, Anderson, Olff, & Scheiner, 2010). The initial model was based on the conceptual model of litter effect on species richness. The species richness and physical variables, seedling recruitment, and species richness among litter treatments. A regression analysis was conducted to test the relationship between physical values, seedling recruitment, and species richness. All data were tested for normality and homogeneity of variance prior to ANOVA. All results were analyzed with SAS V8 software (SAS Institute).

The chi-square test of model fit was used to determine whether the fit between the model and data was adequate ($p > .05$). Each path coefficient was divided by its standard error to assess significance. The resulting value followed a t distribution, allowing $p$ values to be calculated. Given the exploratory nature of these analyses, coefficients with $p < .1$ were considered significant. A thicker line represents a stronger correlation, and the nonsignificant paths were retained as dotted lines in the final model (Lamb, 2008).

### Results

#### 3.1 Microclimate

Repeated-measures ANOVA revealed significant effect of litter manipulation on SM ($F = 7.09$, $p < .01$), ST ($F = 11.8$, $p < .001$), PAR ($F = 128$, $p < .001$), PAR_c ($F = 80.0$, $p < .001$), and ΔPAR ($F = 64.8$, $p < .001$). There was a substantial interannual variation of SM ($F = 3.60$, $p < .05$), ST ($F = 111$, $p < .001$), PAR ($F = 8.70$, $p < .01$), PAR_c ($F = 65.1$, $p < .001$), and PAR_s ($F = 5.48$, $p < .05$) under experimental periods 2 years, but there was no interaction between litter manipulation and year on each microclimate index (Table 1). Litter addition and removal significantly increased and reduced soil moisture

| Microclimate | LR (%) | C (%) | LA (%) | F-value |
|--------------|--------|-------|--------|---------|
| SM (%)       | 18.4 ± 0.25 c | 19.1 ± 0.24 b | 20.1 ± 0.18 a | 13.6*** |
| ST (°C)      | 25.8 ± 0.49 a | 24.9 ± 0.37 ab | 24.4 ± 0.38 b | 2.88*  |
| PAR (µmol m⁻² s⁻¹) | 1.844 ± 12.8 a | 1.706 ± 17.8 b | 1.512 ± 17.8 c | 105*** |
| PAR_c (µmol m⁻² s⁻¹) | 1.990 ± 11.0 a | 1.960 ± 12.5 a | 1.903 ± 20.1 b | 8.68*** |
| PAR_s (µmol m⁻² s⁻¹) | 1.700 ± 20.8 a | 1.526 ± 39.3 b | 1.134 ± 45.8 c | 61.8*** |
| ΔPAR (µmol m⁻² s⁻¹) | 330 ± 23.6 c | 492 ± 38.2 b | 877 ± 51.8 a | 50.5*** |

Note: Different letter superscripts indicate a significant difference ($p < .05$). Abbreviations: C, control; LA, litter addition; LR, litter removal; PAR, Average photosynthetically active radiation; PAR_c, photosynthetically active radiation in the canopy height; PAR_s, photosynthetically active radiation in soil surface; SM, soil moisture; ST, soil temperature; ΔPAR, radiation interception.

*p < .1, **p < .05, ***p < .01, ****p < .001: significant level of F-value.
by 4.99% and 3.64%, respectively (V/V%, p < .05, Table 2). Neither litter addition nor removal affected soil temperature (Table 2). Litter addition significantly inhibited PAR by 11.43% (p < .001) via decreasing PARc by 2.9% (p < .001) and PARs by 25.67% (p < .001, Table 2). However, litter removal significantly stimulated PAR by 8.09% (p < .001) via increasing PARc by 11.41% (p < .001, Table 2). Litter addition and removal significantly increased and reduced the radiation interception of the ecosystems (ΔPAR) by 78.26% and 33.00%, respectively (p < .001, Table 2).

### 3.2 Effects of litter addition and removal on seedling recruitment and species richness

Repeated-measures ANOVA revealed significant effects of litter manipulation on seedling recruitment (F = 25.13, p < .001). A substantial interannual variation in seedling recruitment was observed (F = 9.65, p < .01, Table 1) under the litter-manipulated treatments across the experimental period of 2 years, but there was no interaction between litter manipulation and year on seedling recruitment. Litter removal significantly inhibited seedling recruitment by 37.25% (p < .001), whereas litter addition did not affect seedling recruitment, despite that adding litter inhibited seedling recruitment by 17.46% (p < .11, Figure 1a and Table 1).

### 3.3 Relationship between species richness and seedling recruitment

The annual mean data in all plots were used in the correlation analysis of seedling recruitment and species richness. A significant linear positive correlation was observed between seedling recruitment and species richness (R² = .23, p < .01, Figure 2). Furthermore, a significant positive correlation was detected between species richness and seedling recruitment in our SEM, whether it was the litter addition model or litter removal model (Figure 4a,b).

### 3.4 Factors influencing seedling recruitment and species richness

The response of species richness to soil temperature was a single peak curve (R² = .19, p < .05, Figure 3a). Photosynthetically active radiation was linearly and positively correlated with species richness (R² = .19, p < .01, Figure 3c), but soil moisture was not correlated with species richness (Figure 3b). Photosynthetically active radiation and seedling recruitment were the main drivers of species richness. Radiation interception (ΔPAR) was defined as the difference between PARc and PARs in this experiment. A significant linear negative correlation was observed between ΔPAR and species richness (R² = .24, p < .01, Figure 3d).

### 3.5 Effects of litter addition and removal on seedling recruitment and species richness

The fit between the species richness model and data was adequate for litter addition (R² = 3.70, p = .16, Figure 4a). We chose to accept this model, as it explained 64.0% of the variation in species richness. Litter addition did not directly affect ST, but it had a direct negative effect and a positive effect on PAR and SM, respectively. Litter addition and ST had a direct negative effect on seedling recruitment, whereas SM had a direct positive effect on seedling recruitment. Litter addition synthetically had a negative effect on seedling recruitment, as the direct negative effect of litter addition transcended the positive effect indirectly by increasing SM. Both SM and PAR had a significant positive effect on species richness, but litter addition and ST directly inhibited species richness. Thus, litter addition inhibiting species richness by significantly and indirectly reducing PAR and seedling recruitment, despite that the increase in SM had an indirectly positive effect on species richness. Moreover,
Litter addition did not affect seedling recruitment by regulating ST, although ST had a significant positive effect on seedling recruitment in our SEM (Figure 4a). The fit between the species richness model and data was adequate for litter removal ($\chi^2 = 10.47$, $p = .11$, Figure 4b). We chose to accept this model because it explained 47.0% of the variation in species richness. Litter removal significantly and directly inhibited and stimulated SM and PAR, respectively, but did not affect ST. Soil temperature and PAR had significant negative effects on seedling recruitment, while SM significantly stimulated seedling recruitment. Litter removal did not directly affect species richness. Litter removal indirectly stimulated species richness by increasing PAR, whereas removing litter indirectly inhibited species richness by decreasing seedling recruitment. However, litter removal did not affect species richness, as the positive effect of increasing PAR offset the negative effect by inhibiting seedling recruitment.

4 | DISCUSSION

4.1 | Different regulatory mechanisms of litter addition and removal on seedling recruitment

Litter addition could indirectly affect seedling recruitment by regulating microclimate factors. For example, seedling recruitment occurs immediately after soil moisture increases in summer (Giménez-benavides, Escudero, & Iriondo, 2007), and adding litter plays a positive role in seedling recruitment by preventing seedling death due to improved soil water content (Patane & Gresta, 2006; Warren, Bahn, & Bradford, 2013). However, soil temperature and radiation were not the major factors regulating seedling recruitment in this study. Furthermore, study has evident that plant litter addition had direct negative effects on seedling recruitment by allelopathy (Ruprecht et al., 2010; Zhang et al., 2015) and mechanical interference (Li & Ma, 2003; Li, Jia, Long, & Zerbe, 2005; Mitschunas, Fisler, & Wagner, 2009). These effects may be the main reason for litter addition can directly and significantly inhibit seedling recruitment.

![Figure 2](image1.png) Dependence of the seedling recruitment number on species richness across all 36 plots in the three litter treatments

![Figure 3](image2.png) Dependence of soil temperature (ST, a), soil moisture (SM, b), photosynthetically active radiation (PAR, c), and radiation interception (ΔPAR, d) on species richness across all 36 plots in the three litter treatments.
in this study (Figure 4a). In general, the direct inhibition of litter addition was much greater than that indirect stimulation of increasing water stimulation on seedling recruitment (Figure 4a); Litter addition had a decreasing trend in seedling recruitment (Figure 2a). Litter removal indirectly inhibited seedling recruitment by increasing PAR because strong radiation prolongs seed dormancy as radiation is a stimulus signal that breaks seed dormancy and increases seedling mortality due to loss of water (Aynehb & Afsharin, 2012; Jiao, Lau, & Deng, 2007; Valladares et al., 2008). Therefore, removing litter significantly reduces seedling recruitment by stimulating PAR. Moreover, litter removal can indirectly inhibit seedling recruitment by reducing soil moisture (Figure 4b). Moreover, the increase in soil temperature inhibits seedling recruitment by sharply decreasing seed vigor (Auld & Ooi, 2009; Avhad & Marchetti, 2015; Lombraña, Porceddu, Dettori, & Bacchetta, 2016), or accelerating seedlings death at early stage (Binder & Fielder, 1995; Harper & O’Reilly, 2000). Litter removal does not regulate seedling recruitment by affecting ST because ST did not increase in litter removal treatment.

4.2 The relationship between seedling recruitment and species richness

Species richness is not only depending on the magnitude and of abiotic factors but also restricted by species regeneration and interactions (Gross, Mittelbach, & Reynolds, 2005). As the basis of plant community richness regeneration, seedling recruitment number is closely related to species richness (Houseman, 2014). Species richness decreased as seedling recruitment increased (Figures 2 and 4a,b), indicating that the number of seedlings recruitment is the main condition regulating species richness. However, litter addition significantly reduced species richness rather than seedling recruitment, whereas litter removal significantly reduced seedling recruitment rather than species richness in our experiment (Figure 1a,b), indicating that manipulating litter may affect the relationship between seedling recruitment and species richness. Plant litter regulates species richness by selectively affecting seedling recruitment of some species. For example, litter inhibits small seeds more than large seeds at the early stage of seedling growth, because seedlings of small species often do not have sufficient energy to break through the soil and litter layer (Paz, Mazer, & Martinez-Ramos, 2005; Seiwa, Watanabe, Saitoh, Kannu, & Akasaka, 2002). However, a large number of recruit seedlings is an important basis for ensuring species richness, regardless of how litter regulates the seed germination process.

4.3 Effects of litter addition and removal on species richness

Previous studies have shown that species richness is inhibited by litter accumulation in high productivity areas (Fang, Xun, Bai, Zhang, & Li, 2012; Nilsson et al., 1999; Sagar, Li, Singh, & Wan, 2019; Su et al., 2018; Xiong & Nilsson, 1999). On the one hand, litter addition inhibits species richness by directly inhibiting seedling recruitment of some species. Litter addition may cause an increase in allelopathy, as some plant litter may inhibit various species by producing a high concentration of toxins (Zhang et al., 2015). On the other hand, litter addition can reduce species richness by maintaining the absolute superiority of dominant species, whose litter prevents recruitment by other species. Therefore, litter addition directly inhibited species richness by maintaining the absolute superiority of dominant species, whose litter prevents recruitment by other species. Therefore, litter addition directly inhibited species richness in our experiments. Furthermore, litter addition indirectly influences species richness by regulating microclimate factors. For example, litter addition indirectly stimulates species richness by increasing soil moisture, as photosynthesis of seedlings is highly and positively correlated with available soil water in an infertile grassland (Davis et al., 1999). Studies have suggested that shading is not conducive to recruitment of seedling populations in communities (Craine & Dybzinski, 2013). The radiation interception of the vegetation canopy and standing litter was the main reason for the significant decrease in species richness (Figure 3e), which further verified that PAR was the main regulator of species richness in the litter-added plots. The increase in photosynthesis was benefited by the increased PAR, and indirectly increased the growth of underlying or
adjacent plants (Davis et al., 1999). Therefore, litter addition indirectly inhibited species richness by reducing PAR.

Litter removal indirectly and significantly stimulated species richness by increasing PAR in our SEM, because increased PAR stimulates species richness by stimulating photosynthesis in most species (Craine & Dybzinski, 2013; Davis et al., 1999), despite some other studies reporting that radiation has no effect on species richness (Dorji, Moe, Klein, & Totland, 2014; Zhou et al., 2019). However, the decrease of SM and the increase of PAR indirectly inhibited species richness by inhibiting seedling recruitment rather than directly affecting species richness in the litter removal plots. Therefore, litter removal has a neutral effect on species richness.

There is a 2-year short-term experiment, and the long-term effects of seedling recruitment and species richness on litter addition and removal need to be further studied. Long-term overgrazing and mowing reduce seedling recruitment by reducing litter accumulation without affecting diversity. However, long-term enclosure is harmful to species diversity rather than seedling recruitment owing to litter accumulation. The number of seedlings that colonize is not the only basis for judging the protection of species richness. Soil seed bank, plant phenology, and vegetation growth information should be comprehensively investigated to guide grassland management and biodiversity conservation scientifically.

5 | CONCLUSIONS

Litter addition inhibited species richness, whereas had no effect on seedling recruitment. Litter removal inhibited seedling recruitment rather than species richness in this study. The number of seedlings that colonize is a major prerequisite for protecting species richness. However, litter addition and removal can regulate species richness by affecting ecosystem resources and microclimate. The negative effect of litter addition on species richness due to the inhibition of allelopathy, mechanical interference, and seedling recruitment exceeded the stimulating effect of soil moisture on species richness. Litter removal did not affect species richness, mainly because the stimulatory effect of photosynthetically active radiation on species richness was offset by the inhibited seedling recruitment on species richness. An enclosure is not conducive to protect species diversity through litter accumulation.

ACKNOWLEDGMENTS

Thanks to Duolun Restoration Ecology Station of the Institute of Botany of the Chinese Academy of Sciences for providing the research sites and the support and technical assistance from the people who work there. This research was funded by the National Natural Science Foundation of China (31430015 and 31830012).

CONFLICT OF INTEREST

None declared.

AUTHORS’ CONTRIBUTION

Ang Zhang designed the research, collected data, performed the analysis, and wrote the article. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

A copy of the data will be archived using the DRYAD international repository (https://doi.org/10.5061/dryad.5dj3jg5).

ORCID

Ang Zhang https://orcid.org/0000-0002-1196-8960
Dong Wang https://orcid.org/0000-0003-4533-1615

OPEN RESEARCH BADGES

This article has been awarded Open Data, Open Materials and Preregistered research design Badges. All materials and data are publicly accessible via the Open Science Framework at https://doi.org/10.5061/dryad.5dj3jg5 and http://doi:10.5061/dryad.13gj03s

REFERENCES

Auld, T. D., & Ooi, M. K. J. (2009). Heat increases germination of water-permeable seeds of obligate-seeding darwinia species (Myrtaceae). Plant Ecology, 200, 117–127. https://doi.org/10.1007/s11258-008-9437-7
Avhad, M. R., & Marchetti, J. M. (2015). Temperature and pretreatment effects on the drying of Hass avocado seeds. Biomass & Bioenergy, 83, 467–473. https://doi.org/10.1016/j.biombioe.2015.10.028
Aynehb, A., & Afsharinafar, K. (2012). Effect of gamma irradiation on germination characters of amaranth seeds. European Journal of Experimental Biology, 2, 995–999.
Bai, Y., Han, X., Wu, J., Chen, Z., & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature, 431, 181–184. https://doi.org/10.1038/nature02850
Beligni, M. V., & Lamattina, L. (2000). Nitric oxide stimulates seed germination and de-etiolation, and inhibits hypocotyl elongation, three light-inducible responses in plants. Planta, 210, 215–221. https://doi.org/10.1007/PL00008128
Binder, W. D., & Fielder, P. (1995). Heat damage in boxed white spruce (Picea glauca [Moench.] Voss) seedlings: Its pre-planting detection and effect on field performance. New Forests, 9, 237–259. https://doi.org/10.1007/BF00035490
Bonanomi, G., Incerti, G., Antignani, V., Capodilupo, M., & Mazzoleni, S. (2010). Decomposition and nutrient dynamics in mixed litter of Mediterranean species. Plant and Soil, 331, 481–496. https://doi.org/10.1007/s11104-009-0269-6
Catano, C. P., & Stout, I. J. (2015). Functional relationships reveal keystone effects of the gopher tortoise on vertebrate diversity in a long-leaf pine Savanna. Biodiversity Conservation, 24, 1957–1974. https://doi.org/10.1007/s10531-015-0920-x
Chen, H., Ma, L. N., Xin, X., Liu, J., & Wang, R. (2017). Plant community responses to increased precipitation and belowground litter addition: Evidence from a 5-year semi-arid grassland experiment. Ecology and Evolution, 8, 4587–4597. https://doi.org/10.1002/ece3.4012
Chory, J., Chatterjee, M., Cook, R. K., Elch, T. D., Fankhauser, C., Li, J., … Vitart, V. (1996). From seed germination to flowering, light controls plant development via the pigment phytochrome. Proceedings of the National Academy of Sciences of the United States of America, 93, 12066–12071. https://doi.org/10.1073/pnas.93.22.12066

Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. Functional Ecology, 27, 833–840. https://doi.org/10.1111/1365-2435.12081

Davidson, K. E., Fowler, M. S., Skov, M. W., Doerr, S. H., Beaumont, N., & Griffin, J. N. (2017). Livestock grazing alters multiple ecosystem properties and services in salt marshes: A meta-analysis. Journal of Applied Ecology, 54, 1395–1405. https://doi.org/10.1111/1365-2644.12892

Davis, M. A., Wrage, K. J., Reich, P. B., Tjoelker, M. G., Schaeffer, T., & Muermann, C. (1999). Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecology, 145, 341–350. https://doi.org/10.1023/A:1009802211896

Dorji, T., Moe, S. R., Klein, J. A., & Totland, Ø. (2014). Plant species richness, evenness, and composition along environmental gradients in an alpine meadow grazing ecosystem in central Tibet, China. Arctic, Antarctic, and Alpine Research, 46, 308–326. https://doi.org/10.1657/1938-4246-46.2.308

Dovčiak, M., Reich, P. B., & Frelich, L. E. (1998). Temperature response in wild oat (Avena fatua L.) generations segregating for seed. Heredity, 81, 674–682. https://doi.org/10.1046/j.1365-2644.1998.00431.x

Finegan, B., Penacho, M., Oliveira, A. D., Ascarrunz, N., Bretharte, M. S., Carrenorocabado, G., … Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. Journal of Ecology, 103, 191–201. https://doi.org/10.1111/1365-2745.12346

Finn, J., Maggini, R., Chadé, I., Nicol, S., Walters, B., Reeson, A., … Carwardine, J. (2015). Priority threat management of invasive animals to protect biodiversity under climate change. Global Change Biology, 21, 3917–3930. https://doi.org/10.1111/gcb.12034

Foster, B. L. (2001). Constraints on recruitment and species richness along a grassland productivity gradient: The role of propagule availability. Ecology Letters, 4, 530–535. https://doi.org/10.1046/j.1461-0248.2001.00266.x

Foster, B. L., & Gross, K. L. (1998). Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. Ecology, 79, 2593–2602. https://doi.org/10.2307/176503

Gaitán, J. J., Oliva, G. E., Bran, D. E., Maestre, F. T., Aguilar, M. R., Jobbágy, E. G., … Massara, V. (2014). Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. Journal of Ecology, 102, 1419–1428. https://doi.org/10.1111/1365-2745.12273

Giménez-benavides, L., Escudero, A., & Iriondo, J. M. (2007). Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. Annals of Botany, 99, 723–734. https://doi.org/10.1093/aob/mcm007

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. Ecological Monographs, 80, 67–87. https://doi.org/10.1890/09-0464.1

Gross, K. L., Mittelbach, G. G., & Reynolds, H. L. (2005). Grassland invasibility and diversity: Responses to nutrients, seed input, and disturbance. Ecology, 86, 476–486. https://doi.org/10.1890/04-0122

Harper, C. P., & O’Reilly, C. (2000). Effect of warm storage and date of lifting on the quality of Douglas-fir seedlings. New Forests, 20, 1–13. https://doi.org/10.1023/A:1006716046347

Hattenschwiler, S., Tiong, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics, 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hosseinzadeh, G., Jalivand, H., & Tamartash, R. (2010). Short time impact of enclosure on vegetation cover, productivity and some physical and chemical soil properties. Journal of Applied Sciences, 10, 2001–2009. https://doi.org/10.3923/jas.2010.2001.2009

Housman, G. R. (2014). Aggregated seed arrival alters plant diversity in grassland communities. Journal of Plant Ecology, 7, 51–58. https://doi.org/10.1093/jpe/rtt044

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., … Birnbaum, P. (2018). Regional forcing explains local species diversity and turnover on tropical islands. Global Ecology and Biogeography, 27, 474–486. https://doi.org/10.1111/geb.12712

Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystem science. Science, 317, 58–62. https://doi.org/10.1126/science.1133258

Jensen, L. S., Salo, T., Palmason, F., Breland, T. A., Henriksen, T. M., Stenberg, B., … Esala, M. (2005). Influence of biochemical quality on C and N mineralisation from a broad variety of plant materials in soil. Plant and Soil, 273, 307–326. https://doi.org/10.1007/s11104-004-8128-y

Jiao, Y., Lau, O. S., & Deng, X. W. (2007). Light-regularized transcriptional networks in higher plants. Nature Reviews Genetics, 8, 217–230. https://doi.org/10.1038/nrg2049

Kassen, R., Buckling, A., Bell, G., & Rainey, P. B. (2000). Diversity peaks at intermediate productivity in a laboratory microcosm. Nature, 406, 508–512. https://doi.org/10.1038/35020060

Lamb, E. G. (2008). Direct and indirect control of grassland community structure by litter, resources, and biomass. Ecology, 89, 216–225. https://doi.org/10.1890/07-0393.1

Larreguy, C., Carrera, A. L., & Bertiller, M. B. (2017). Reductions of plant cover induced by sheep grazing change the above-belowground partition and chemistry of organic C stocks in arid rangelands of Patagonian Monte, Argentina. Journal of Environmental Management, 199, 139–147. https://doi.org/10.1016/j.jenvman.2017.04.086

Li, Q., & Ma, K. P. (2003). Factors affecting establishment of Quercus liotungensis Koidz. under mature mixed oak forest overstory and in shrubland. Forest Ecology and Management, 176, 133–146. https://doi.org/10.1016/S0378-1127(02)00274-8

Li, X. R., Jia, X. H., Long, L. Q., & Zerbe, S. (2005). Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert (N China). Plant and Soil, 277, 375–385. https://doi.org/10.1007/s11104-005-8162-4

Liu, N., Kan, H. M., Yang, G., & Zhang, Y. J. (2015). Changes in plant, soil, and microbes in a typical steppe from simulated grazing: Explaining potential change in soil C. Ecological Monographs, 85, 269–286. https://doi.org/10.1890/14-1368.1

Lombrana, A., Porceddu, M., Dettori, C. A., & Bacchetta, G. (2016). Gentiana lutea L. subsp. lutea seed germination: Natural versus controlled conditions. Botany-botanique, 94, 32–39. https://doi.org/10.1139/cjbb-2016-0030
Lorillièrè, R., Couvet, D., & Robert, A. (2012). The effects of direct and indirect constraints on biological communities. Ecological Modelling, 224, 103–110. https://doi.org/10.1016/j.ecolmodel.2011.10.015
McCann, K. S. (2000). The diversity-stability debate. Nature, 405, 228–233. https://doi.org/10.1038/35012234
Mitschunas, N., Filser, J., & Wagner, M. (2009). On the use of fungicides in ecological seed burial studies. Seed Science Research, 19, 51–60. https://doi.org/10.1017/S0960258508018727
Muhl, Q. E., Du-Toit, E. S., & Robbertse, P. J. (2009). Temperature effect on seed germination and seedling growth of Moringa oleifera Lam. Seed Science and Technology, 39, 208–213. https://doi.org/10.15258/sst.2011.39.1.19
Muller, I., Mesléard, F., Buisson, E., & Hölzel, N. (2014). Effect of top ‐ soil removal and plant material transfer on vegetation development in created Mediterranean meso ‐ xeric grasslands. Applied Vegetation Science, 17, 246–261. https://doi.org/10.1111/aavsc.12059
Nilsson, C., Xiong, S., Johansson, M. E., & Vought, L. B. M. (1999). Effects of leaf ‐ litter accumulation on riparian plant diversity across Europe. Ecology, 80, 1770–1775. https://doi.org/10.2307/176567
Paz, H., Mazer, S. J., & Martinez‐Ramos, M. (2005). Comparative ecology of seed mass in Paychotria (Rubiaceae): Within ‐ and between ‐ species effects of seed mass on early performance. Functional Ecology, 19, 707–718. https://doi.org/10.1111/j.1365‐244X.2005.00984.x
Rajaniemi, T. K. (2002). Why does fertilization reduce plant species diversity? Testing three competition ‐ based hypotheses. Journal of Ecology, 90, 316–324. https://doi.org/10.1046/j.1365‐2745.2001.00662.x
Rotundo, J. L., & Aguilar, M. R. (2005). Litter effects on plant regeneration in arid lands: A complex balance between seed retention, seed longevity and soil ‐ seed contact. Journal of Ecology, 93, 829–838. https://doi.org/10.1111/j.1365‐244X.2005.01022.x
Rotundo, J. L., Aguilar, M. R., & Benech‐Arnold, R. (2015). Understanding erratic seedling emergence in perennial grasses using physiological models and field experimentation. Plant Ecology, 216, 143–156. https://doi.org/10.1007/s11258‐014‐0423‐y
Ruprecht, E., Enyedi, M. Z., Eckstein, R. L., & Donath, T. W. (2010). Restorative removal of plant litter and vegetation 40 years after abandonment enhances re ‐ emergence of steppe grassland vegetation. Biological Conservation, 143, 449–456. https://doi.org/10.1016/j.biocon.2009.11.012
Sagar, R., Li, G. Y., Singh, J. S., & Wan, S. Q. (2019). Carbon fluxes and species diversity in grazed and fenced typical steppe grassland of Inner Mongolia, China. Journal of Plant Ecology, 12, 10–22. https://doi.org/10.1093/jpe/rtx052
Seiwa, K., Watanabe, A., Saitoh, T., Kannu, H., & Akasaka, S. (2002). Effects of burying depth and seed size on seedling establishment of Japanese chestnuts, Castanea crenata. Forest Ecology and Management, 164, 149–156. https://doi.org/10.1016/S0378‐7758(01)00607‐7
Song, B., Niu, S. L., & Wan, S. (2016). Precipitation regulates plant gas exchange and its long ‐ term response to climate change in a temperate grassland. Journal of Plant Ecology, 9, 531–541. https://doi.org/10.1093/jpe/rtw010
Su, L., Yang, Y., Li, X., Wang, D., Liu, Y., Liu, Y., ... Li, M. (2018). Increasing plant diversity and forb ratio during the revegetation processes of trampled areas and trails enhances soil infiltration. Land Degradation and Development, 29, 4025–4034. https://doi.org/10.1002/ldr.3173
Tilman, D., Reich, P. B., Knops, J. M. H., Wedin, D. A., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long ‐ term grassland experiment. Science, 294, 843‐845. https://doi.org/10.1126/science.1060391
Trammell, T. L. E., Rhoades, C. C., & Bukaveckas, P. A. (2004). Effects of prescribed fire on nutrient pools and losses from glades occurring within oak ‐ hickory forests of central Kentucky. Restoration Ecology, 12, 597–604. https://doi.org/10.1111/j.1526‐2987.2003.00027.x
Valladares, F., Zaragoza‐Castells, J., Sánchez‐Gómez, D., Mat漾anz, S., Alonso, B., Portsmouth, A., ... Atkin, O. K. (2008). Is shade beneficial for mediterranean shrubs experiencing periods of extreme drought and late ‐ winter frosts? Annals of Botany, 102, 923–933. https://doi.org/10.1093/aob/mcn182
Wang, D., Zhang, B., Zhu, L., Yang, Y., & Li, M. (2018). Soil and vegetation development along a 10 ‐ year restoration chronosequence in tailing dams in the Xiaojinling gold region of Central China. Catena, 167, 250–256. https://doi.org/10.1016/j.catena.2018.05.007
Wang, X., Yang, X., Wang, L., Chen, L., Song, N., Gu, J., & Xue, Y. (2018). A six ‐ year grazing exclusion changed plant species diversity of a Stipa breviflora desert steppe community, northern China. Peerj, 6, e4359. https://doi.org/10.7717/peerj.4359
Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos, 79, 247–258. https://doi.org/10.2307/3546010
Warren, R. J. I., Bahn, V., & Bradford, M. A. (2013). Decoupling litter barrier and soil moisture influences on the establishment of an invasive grass. Plant and Soil, 367, 339–346. https://doi.org/10.1007/s11104‐012‐1477‐z
Williams, J. W., Seabloom, E. W., Slabyback, D., Stoms, D. M., & Viers, J. H. (2005). Anthropogenic impacts upon plant species richness and net primary productivity in California. Ecology Letters, 8, 127–137. https://doi.org/10.1111/j.1461‐0248.2004.00706.x
Wu, G.‐L., Wang, D., Liu, Y. U., Hao, H.‐M., Fang, N.‐F., & Shi, Z.‐H. (2016). Mosaic‐pattern vegetation formation and dynamics driven by the water‐wind crisscross erosion. Journal of Hydrology, 538, 355–362. https://doi.org/10.1016/j.jhydrol.2016.04.030
Xia, J., & Wan, S. (2013). Independent effects of warming and nitrogen addition on plant phenology in the Inner Mongolian steppe. Annals of Botany, 111, 1207–1217. https://doi.org/10.1093/aob/mct079
Xiong, S., & Nilsson, C. (1999). The effects of plant litter on vegetation: A meta ‐ analysis. Journal of Ecology, 87, 984–994. https://doi.org/10.1046/j.1365‐2745.1999.00414.x
Zhang, A., Zhang A, Wang D, Wan S. Litter addition increases plant diversity by suppressing seeding in a semiard grassland. Northern China. Ecol Evol. 2019;9:9907–9915. https://doi.org/10.1002/ece3.5532