



Research article

Litter manipulation enhances plant community heterogeneity via distinct mechanisms: The role of distribution patterns of plant functional composition and niche breadth variability

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ABSTRACT

Plant litter can greatly alter community compositional dynamics and variability of intraspecific interactions in grasslands, and thus the overall ecosystem structure and functions. However, whether plant activity can be driven by plant litter to modify plant community heterogeneity remains poorly explored. We investigate the responses of plant community heterogeneity to litter addition as well as their associated mechanisms. Here we conducted a three-year field experiment in a Tibetan alpine meadow to explore the effects of multiple plant litter addition (five mass levels and three species) on plant communities. We found that the effect of litter manipulation on plant community heterogeneity was mainly driven by litter mass rather than litter species. Higher litter mass manipulation significantly enhanced plant community heterogeneity, which was mainly determined by the niche breadth of forbs and the distribution patterns of functional composition rather than plant diversity. Our findings provide significant insights for understanding the effects of plant litter on grassland ecosystem dynamics to maintain the structure and function of ecosystems. Furthermore, this study suggests that reasonable management practices (e.g., moderate grazing in non-growing seasons) may be pivotal in achieving sustainability of grassland systems through plant litter dynamics.

1. Introduction

Spatial heterogeneity in plant community distribution is an intrinsic feature of terrestrial ecosystems, and is especially critical for maintaining community stability and ecosystem services (Turner et al., 2013; Massé Jodoïn and Guichard, 2019). Plant community heterogeneity is regarded as a vital indicator of ecosystem functioning across diverse grassland ecosystems, including productivity, biodiversity and community structure and succession (Loreau et al., 2013; de Souza Júnior et al., 2014; Sun et al., 2017). Exploring the heterogeneity of grassland plant community is of great significance in understanding the formative mechanism of that plant community under substantial environmental changes. The heterogeneity of plant community is the consequence of ecological selective processes via environmental perturbations and biotic interactions (Ma et al., 2017; Wubs and Bezemer, 2018). Plant community heterogeneity may be largely driven by species reordering and shifts in functional groups within the community (Cleland et al.,

2013; Leffler et al., 2016) and is closely associated with biodiversity and species asynchrony (Song et al., 2020). Moreover, abiotic factors (e.g., nutrients, moisture, etc.) of the soil microenvironment also mediate plant community heterogeneity (Baer et al., 2005; Ulrich et al., 2014). Hence, plant litter that alters the community compositional dynamics and/or the variability of population interactions in grassland ecosystems may have the potential to promote plant community heterogeneity.

Plant litter plays a key role in maintaining the stability of grassland ecosystems (Ma et al., 2022). It can regulate plant species composition (Letts et al., 2015) and alleviate stoichiometric limitation of the soil microenvironment (Xiao et al., 2015). In these ways, it can change the structure and function of grassland ecosystems, such as by altering plant diversity, community productivity and plant asynchrony (Shen et al., 2016; Ma et al., 2022). In addition, changes in plant growth and interspecific interactions in response to litter manipulation could ultimately modify plant community compositional dynamics via distinct effects on different functional groups and/or species (Wang et al., 2010). These

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community properties indicate the contribution of plant litter to plant community heterogeneity, although the driving mechanisms still remain unknown.

In general, the performance and competitive interactions of plants within communities change more strongly under environmental perturbations (Ravenek et al., 2016; Partzsch, 2019). These responses may lead to variations in distribution patterns of plant biomass and population variability, which underpin plant spatial structure and are likely to shape plant community heterogeneity. To explore plant community heterogeneity under plant litter disturbance regimes, we therefore need to determine how the population best adapt to physical and biological conditions, which play an important role in community compositional dynamics. Understanding the level of heterogeneity that maximizes maintenance in a grassland ecosystem is vital when adopting a reasonable management strategy to realize optimal ecological and service functions.

The Tibetan Plateau is the most sensitive ecoregion to environmental change in the world (Chen et al., 2013). The alpine meadows of the Tibetan Plateau are currently undergoing dramatic anthropogenic environmental change, especially that causing the reverse succession of the community, involving decreases in sedge-dominated communities and increases in those dominated by undesirable toxic plants (Wang et al., 2022). The shift in community composition is a significant change that can result in ecological consequences to both—the composition and accumulation dynamics of plant litter. Because of the different chemical constituents of species, shifts in plant community composition and structure greatly increase or decrease litter accumulation (Wang et al., 2020b). Previous studies have found that plant seedling establishment (Donath and Eckstein, 2012), community properties and ecosystem functions are not only responsive to the increase of litter mass but also highly dependent on litter types (Mariotte et al., 2016; Ma et al., 2021). We may therefore expect litter manipulation to affect plant community heterogeneity at a large spatial scale in alpine meadows. Understanding the mechanism of this process will help to indicate the properties and functions of the ecosystem that may be attributed to regulation by grassland litter under various management strategies.

To investigate the responses of plant community heterogeneity, variability of population interactions and biodiversity across scales to litter manipulation and their associated mechanisms, we carried out a three-year field experiment in an alpine meadow with five litter addition mass levels (from 0 to 600 g m⁻²) and three litter species (*Elymus nutans*, *Kobresia setchwanensis* and *Ligularia virgaurea*). The three selected litter species belong to three functional groups—grass, sedge and perennial forb—that differ in their reproductive and dispersal properties, as well as their dominant ecological role in the community. We hypothesized that litter manipulation would strongly affect plant community heterogeneity because of multiple litter-induced direct or indirect effects on plant community compositional dynamics and interspecific interactions. Specifically, to test this hypothesis, we addressed two major questions: (a) how does plant community heterogeneity change in response to litter manipulation, and how do changes differ among litter species? and (b) what are the underlying mechanisms governing the effects of litter manipulation on plant community heterogeneity?

2. Materials and methods

2.1. Study site and experimental design

Our research was carried out in an alpine meadow (31°47' N, 102°33' E; 3485 m a.s.l.) at the eastern Tibetan Plateau in Hongyuan county, Sichuan Province, China. The climate is continental cool-temperate monsoon with mean annual precipitation is 747 mm (mainly falling in the growing season from May to September) and the mean annual temperature is 1.5 °C (1961–2013). The soil is classified as Cambisols (Food and Agricultural Organization taxonomy). The dominant and

most common plant species are *Kobresia setchwanensis*, *Elymus nutans*, *Ligularia virgaurea*, *Carex thibetica*, *Scirpus pumilus*, *Saussurea hieracioides*, *Anemone trullifolia*, *Anemone rivularis*, and *Potentilla anserina*.

The litter manipulation experiment was carried out from 2017 to 2019, following a randomized block design. There were five litter addition levels (0 (control), 100, 200, 400, and 600 g m⁻²) and three individual litter species (*E. nutans*, *K. setchwanensis* and *L. virgaurea*) of different functional groups, with four replicates for each treatment. All the treatments were randomized to plots (2 × 2 m each, separated by 1 m buffers) in each block. Plant litter was manipulated annually in late April during 2017–2019. The added litter of each plot was broadcast uniformly by hand. Plant litter samples applied in all experimental plots were collected in the preceding year, air-dried and clipped into roughly 1 cm pieces. To avoid potential environmental effects, all plots were cleared of dead tissues before litter was added. The litter mass application was based on the maximum grassland productivity in the enclosed area (about 400 g m⁻²) of the study site and litter amounting to < 250 g m⁻² showed positive effects on seedling survival (Loydi et al., 2013). The litter treatment levels were adjusted (0, 1/4, 1/2 and 3/2) by the maximum quantity of litter. The detailed experimental design has also been presented in Ma et al. (2021).

2.2. Field sampling and measurements

Above-ground biomass was annually sampled in middle of August of 2017–2019, by clipping all plants tissues at the soil surface in a 0.5 × 0.5 m² strip, which was randomly placed in each plot. The collected plant was sorted into species, oven-dried (65 °C for 48 h), and then weighed. Plants were classified into five functional groups: three forbs—annual, perennial (non-nitrogen fixing) and legumes (nitrogen fixing), and two graminoids—grasses and sedges based on their life and functional forms.

2.3. Data analyses

Plant community heterogeneity (PH) was measured as the mean dissimilarity in functional composition among samples at a site (Collins, 1992), defined as: PH = 1 – plant community similarity (PS), PS = 1 –

$0.5 \sum_{i=1}^S |p_a - p_b|$, where p_a and p_b are the proportional biomass of the

functional group p in a pair of sampling quadrats, and S is the total number of groups. We used biomass-based metrics to calculate plant diversity across scales. Plant functional group diversity index (FDI = $-\sum_i^k p_i \ln p_i$) as the metrics of alpha diversity at local community scale,

where P_i is the proportional biomass of functional group i , summed for all the functional groups measured. The beta diversity was defined as:

$\beta_{simp} = \gamma_{simp} / \alpha_{simp}$, where $\alpha_{simp} = 1 / \sum_{i=1}^4 (k_i \sum_i p_{il}^2)$, $\gamma_{simp} = 1 / \sum_i (\sum_{l=1}^4 k_l p_{il})^2$,

where k_l is the ratio of total biomass of the local community l to that of the aggregate community (i.e., aggregation of the four quadrats) at the larger scale, P_{il} is the proportional biomass of species i in the local community l (Wang and Loreau, 2016; Liang et al., 2021). We used the response ratio of plant biomass to assess the resistance of plant communities to litter treatment. The higher the absolute value of response ratio, the lower the resistance of plants to litter manipulation. The degree of resistance was defined as the formula: resistance = $\ln (B_i/B_0)$, where B_i , B_0 is the biomass of treatment i and control, respectively. The

niche breadth (B_i) of functional group was assessed as: $B_i = 1 / (\sum_{i=1}^r p_{ij}^2)$,

where P_{ij} is the proportional biomass of functional group i in treatment j (Levins, 1968). To test how litter manipulation affects plant community composition, the plant community structure was visualized by nonmetric multidimensional scaling (NMDS) ordinations that were

based on the Bray–Curtis dissimilarity matrices using the vegan package in R (Oksanen et al., 2013), a two-dimensional space to illustrate the differences in plant species composition among litter manipulation treatments. To examine the relationship and interactions between interspecific plant species, co-occurrence network analyses based on spearman's rank was performed using biomass data of species level of plant communities (Wu et al., 2021).

Linear mixed-effects model was performed to determine the effects of year, litter mass, litter species and their interaction on plant community heterogeneity, functional group diversity, biomass ratio and resistance, in which litter species, litter mass and year as fixed factors and plot nested within blocks as random effects. The effects of litter mass, litter species and their interaction on *beta* diversity and niche breadth were also assessed by linear mixed-effects model, in which litter species and litter mass as fixed factors and year as random effects. All statistical analyses were performed using the “predictmeans” and “lme4” packages in R 4.1.0 (R Core Team, 2021). Differences were considered to be statistically significant at $P < 0.05$, and further differences among treatments were investigated by using the Tukey HSD test. In addition, we used piecewise structural equation modelling (SEM) to explore the mechanistic pathways via which litter manipulation influenced plant community heterogeneity (Shipley, 2013) by R version 4.1.0 using the “piecewiseSEM” package (Lefcheck, 2016).

3. Results

3.1. Plant community heterogeneity response to litter manipulation

Plant community heterogeneity was significantly higher under 600 g m⁻² litter mass addition compared with 100 and 200 g m⁻² litter mass addition ($P < 0.001$), while the litter species had no effect ($P > 0.05$) (Table S1; Fig. 1a). In addition, plant community structure significantly differed among the litter mass addition levels and litter species (Fig. 2). The plant communities in the plots that were subjected to high levels of litter manipulation (400 and 600 g m⁻²) were different from the communities with low levels (Fig. 2b).

3.2. Beta diversity and functional group diversity response to litter manipulation

Beta diversity was significantly lower in plots treated with *L. virgaurea* treated plots than in those with *K. setchwanensis* ($P < 0.05$; Fig. 1b), while the litter mass addition levels had no effect ($P > 0.05$). The functional group diversity index was significantly increased in the 400 g m⁻² litter treatment compared with the 200 g m⁻² litter treatment ($P < 0.05$), and the effect was greater with *K. setchwanensis* ($P < 0.001$)

(Table S1; Fig. S1). Beta diversity and functional group diversity were largely dependent on litter mass and litter species (all $P < 0.01$; Fig. 1b and S1).

3.3. Biomass distribution patterns, resistance and niche breadth response to litter manipulation

As expected, our results showed that the ratio of below-ground/above-ground biomass ($P < 0.05$) and graminoids/forbs biomass ($P < 0.001$) increased with increasing litter mass addition levels (Table S1; Fig. 3). The effect of litter species on the graminoids/forbs biomass ratio was significantly lower in plots treated with *L. virgaurea* than in those treated with *E. nutans* and *K. setchwanensis* ($P < 0.01$; Fig. 3b), although below-ground/above-ground biomass ratio had no effect ($P > 0.05$; Fig. 3a).

The resistance of both the plant community and annual forbs decreased with increasing litter mass addition levels (all $P < 0.001$; Figs. S2a and b). The resistance of plant community was significantly lower in litter species treated with *L. virgaurea* ($P < 0.001$; Fig. S2a), while the resistance of annual forbs was significantly higher in litter species treated with *K. setchwanensis* ($P < 0.05$; Fig. S2b). The effect of litter mass on the resistance of perennial forbs and sedges varied with litter species (all $P < 0.05$; Figs. S2c and f). Litter manipulation did not affect the resistance of grasses and legumes ($P > 0.05$; Figs. S2d and e).

Litter mass manipulation weakened the niche breadth of annual forbs ($P < 0.05$; Fig. 4a), but did not change the niche breadth of grasses, legumes and sedges ($P > 0.05$; Fig. S3). The effect of litter mass on the niche breadth of perennial forbs varied with litter species ($P < 0.05$; Fig. 4b).

3.4. Interactions among plant species in response to litter manipulation

The ecological networks of the litter treatments were analyzed to evaluate the interaction of plant communities (Fig. S4). The networks of control, treatments of *E. nutans* (600 g m⁻²), *K. setchwanensis* (200, 400 g m⁻²) and *L. virgaurea* consisted of 45–48 nodes and 138–165 edges, showing a high level of inter-community correlation. Other treatment networks showed a similar structure of plant community (consisting of 43–51 nodes and 104–129 edges).

Keystone species in plant networks were altered by litter manipulation (Fig. S4). In the control/*K. setchwanensis* (100 g m⁻²) networks, a higher number of connections between the dominant sedge species *C. thibetica* and *S. pumilus* and other species indicated that *C. thibetica* and *S. pumilus* played a vital role in the plant network (Figs. S4a and f). However, in other treatments, different forb species—mainly *S. hieracioides*, *P. anserina* and *A. rivularis* played a crucial role in the

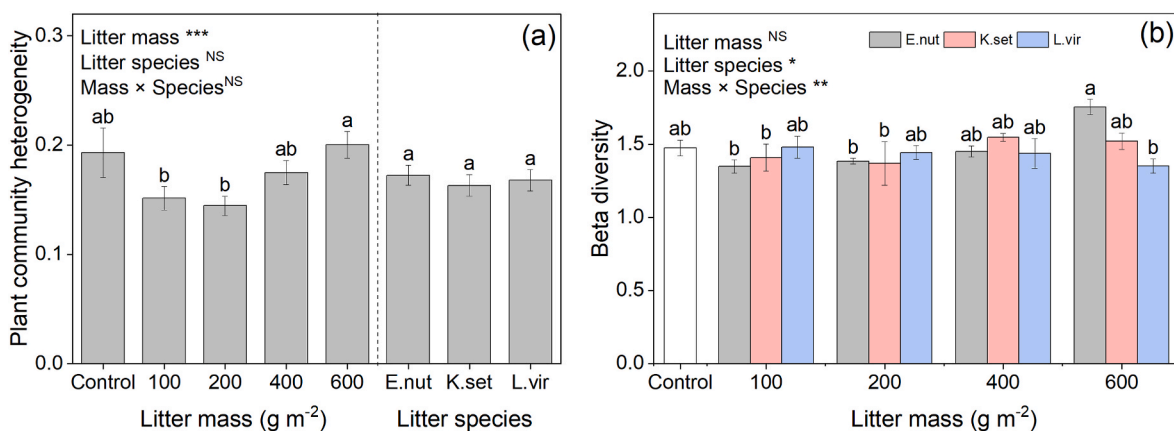


Fig. 1. The effects of litter manipulation on plant community heterogeneity (a) and beta diversity (b). Values are means ± SE. Different letters indicate significant differences at $P < 0.05$ (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. NS, not significant). *E. nutans*—E. nut, *K. setchwanensis*—K. set and *L. virgaurea*—L. vir.

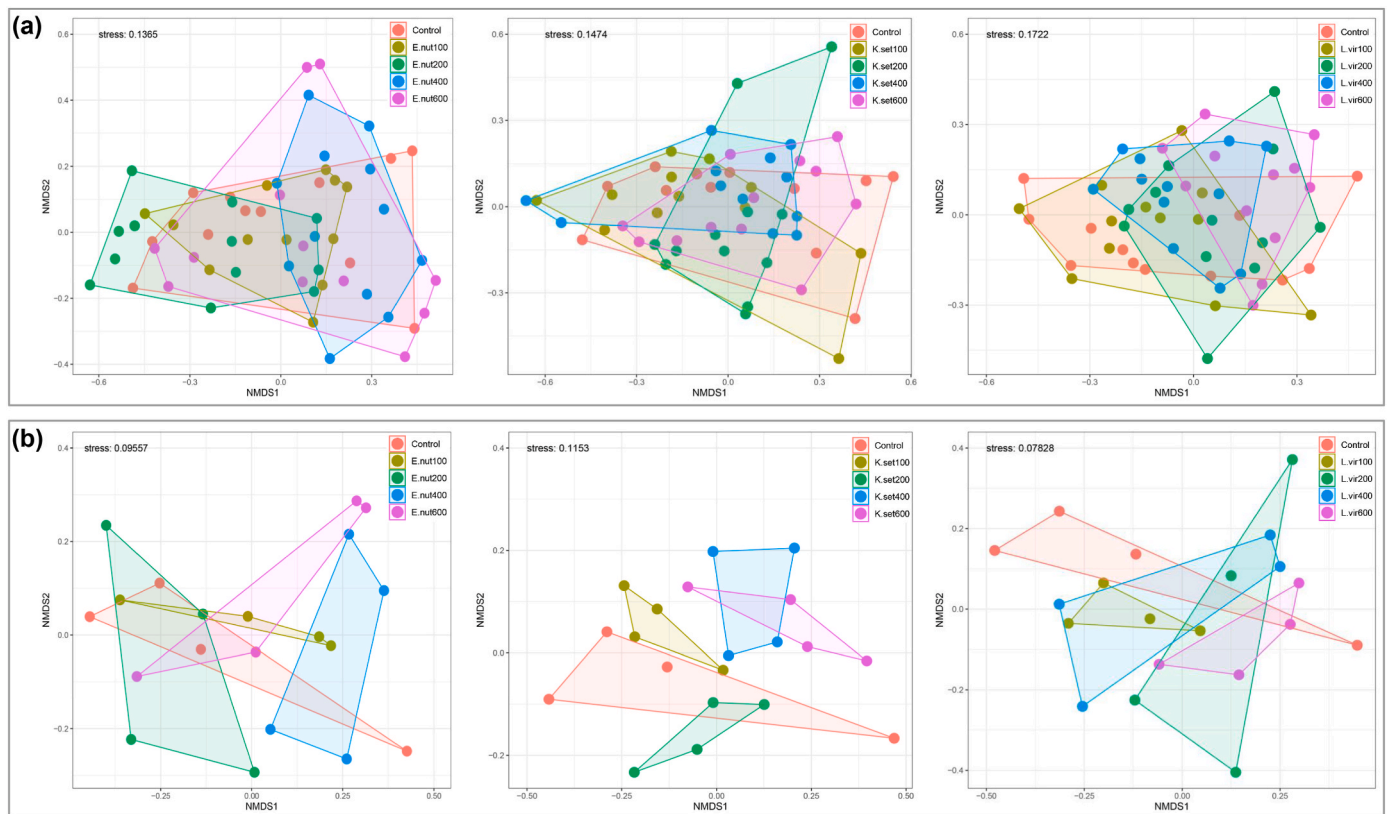


Fig. 2. Non-metric multidimensional scaling (NMDS) ordination plots of plant community structure among treatments in two-dimensional space, across all years (a) and the last year 2019 (b) based on Bray-Curtis distance.

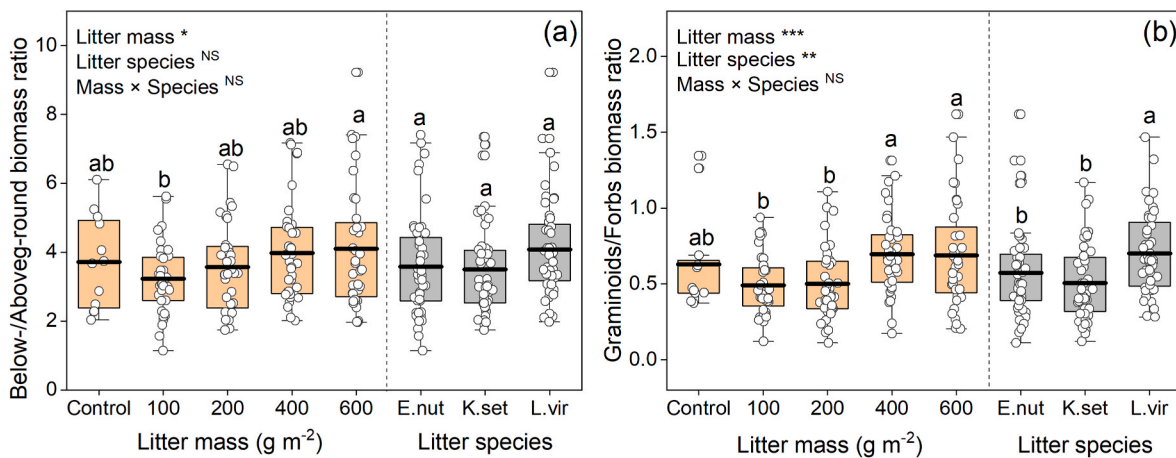


Fig. 3. The effects of litter manipulation on ratio of below-ground/above-ground biomass (a), graminoids/forbs above-ground biomass (b). Box plots show mean; box edges, first quartile and third quartile; and whiskers, minimum and maximum. Different letters indicate significant differences at $P < 0.05$ (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). NS, not significant). *E. nutans*–*E. nut*, *K. setchwanensis*–*K. set* and *L. virgaurea*–*L. vir*.

community (Fig. S4b–e, g–m).

3.5. Main drivers of plant community heterogeneity

The SEM analysis (Fig. 5) suggested that litter mass manipulation mediates plant community heterogeneity mainly through changes in graminoids/forbs biomass ratio and niche breadth of annual forbs, which were respectively positively (path coefficient = 0.33) and negatively (path coefficient = -0.22) correlated with plant community heterogeneity. In addition, plant community heterogeneity was also negatively (path coefficient = -0.59) associated with niche breadth of

perennial forbs.

4. Discussion

Plant community compositional dynamics and population variability have great potential to reveal the underlying mechanisms of plant community heterogeneity in response to environmental change (Collins et al., 2017). In our study, plant community heterogeneity was lower when conditioned by low-levels of plant litter manipulation. Our results further showed that the distribution patterns of functional composition and niche breadth rather than plant diversity promoted

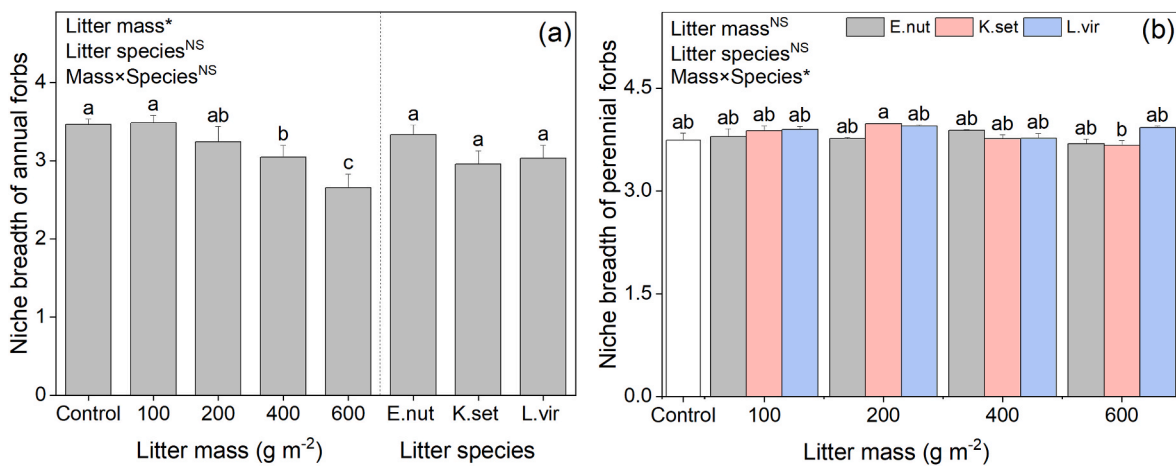


Fig. 4. The effects of litter manipulation on niche breadth of annual forbs (a) and perennial forbs (b). Values are means ± SE. Different letters indicate significant differences at $P < 0.05$ (* $P < 0.05$; NS, not significant). *E. nutans*–*E. nut*, *K. setchwanensis*–*K. set* and *L. virgaurea*–*L. vir*.

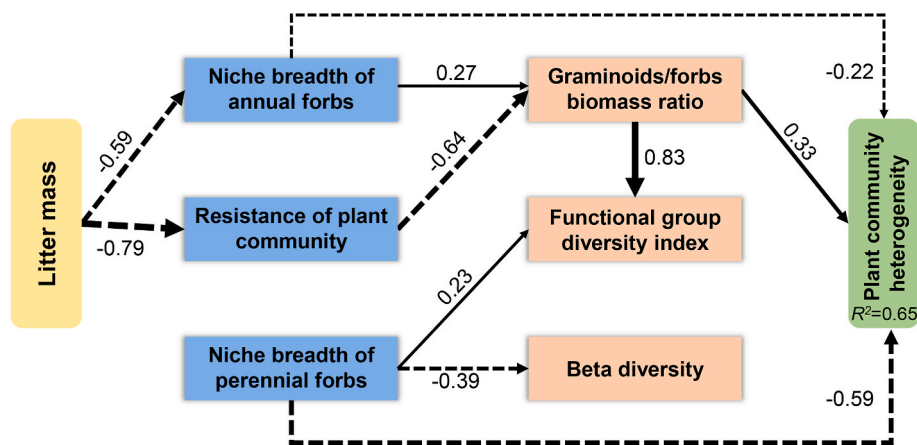


Fig. 5. Structural equation models of the direct and indirect effects of litter mass manipulation on plant community heterogeneity. Solid and dashed black arrows represent positive and negative paths ($P < 0.05$). The width of the arrow indicates the strength of the relationship. Values associated with the arrows represent standardized path coefficients. R^2 indicate the variance explained by the model. The final model fitted the data well: Fisher’s C = 40.33, $P = 0.21$ and AIC = 96.33.

plant community heterogeneity under plant litter manipulation. Collectively, the study indicated that the alpine meadow was regulated by plant litter mass accumulation and population-specific properties, which implied that this ecologically important system may be vulnerable to plant litter dynamics under diversified grassland management strategies.

Our study demonstrated that plant litter manipulation could change distribution patterns of functional composition by changing the niche breadth of annual forbs and the resistance of the plant community, thereby altering plant community heterogeneity (Fig. 5). We also found that the niche breadth of annual forbs and perennial forbs strongly and directly affected plant community heterogeneity (Fig. 5). Importantly, plant litter shifts interactions among plant species, which, in turn, affect the community functional patterns that determine plant community heterogeneity. This may be explained by the greater variety of species interactions within the heterogeneous communities (Fig. S4). Moreover, the effect of plant community heterogeneity in our study was more likely due to changes in functional group asynchrony (Ma et al., 2022). These results were thus consistent with previous findings that species spatial distribution patterns (Cleland et al., 2013) and species asynchrony (Song et al., 2020) are largely associated with plant community heterogeneity. Contrary to our expectations, we found that, while plant diversity varied significantly, it did not affect plant community heterogeneity (Figs. 1 and 5 and S1). This was partly due to the fundamentally higher

biodiversity in the study, whereas plant community heterogeneity was more sensitive to low diversity (Liu et al., 2016). In addition, the soil nutrient environment was generally stimulated by the dynamics of plant litter (Sun et al., 2018), which led to the replacement of plant species adapting to these soil changes (van der Putten et al., 2013). This affected the utilization rate of resources by plants, indirectly regulated the spatial distribution pattern of populations and enhanced the heterogeneity of plant communities (Ulrich et al., 2014).

Much research on plant litter effects on biodiversity has focused on plant alpha diversity, which has produced varied results depending on different grassland types (Letts et al., 2015; Mariotte et al., 2016; Zhang et al., 2019). In particular, our study has reported that litter addition had positive effects on the plant functional group index and that the effects varied with litter species (Fig. S1). This may be attributed to shifts in variability of plant population interactions, which were strongly associated with different plant growth dynamics (inhibited or promoted) of functional types (Fig. 4, S2 and S4). Additionally, the shifts in the graminoids/forbs biomass ratio and niche breadth of perennial forbs were likely to have a greater effect on maintaining plant functional group diversity under litter manipulation (Fig. 5). As predicted, we also observed that plant litter maintained the community beta diversity (Fig. 1b), which may be due to the stronger changes in niche breadth of perennial forbs (Fig. 5). Another possible explanation was that litter manipulation weakened the stature of dominant species/functional

groups and enhanced the stature of rare species/functional groups, increasing the common species in the communities (Figs. 3 and 4 and S4). This may have led to more marked effects on community beta diversity, as indicated in some previous studies of arid and semiarid grasslands (Yang et al., 2014), and semi-natural grasslands (Ohara et al., 2015).

Spatial distribution patterns of functional composition in plant communities were expected to follow as a consequence of the functional composition and species trait variability within communities, such as the changes in allocation of plant population and the differentiation of vegetation ecotypes (Browning et al., 2014; Sun et al., 2017). As expected, manipulating the plant litter greatly shifted the spatial distribution patterns of functional composition (Fig. 3), indicating that litter promoted plant growth divergence. Forbs and graminoids were the two main plant functional groups in our study site, and the increased ratio of graminoids/forbs above-ground biomass in high litter mass treatments could be attributed to the lower resistance of forbs (annual and perennial), the higher resistance of sedges and stable resistance of grasses (Figs. S2 and 5). Another possibility was that higher niche breadth of forbs (annual and perennial) and stable niche breadth of graminoids (grasses and sedges) may be more advantageous for the graminoids/forbs above-ground biomass ratio (Figs. 4 and 5 and S3). Likewise, the below-ground/above-ground biomass ratio was highest in the maximum litter mass treatment in our study, presumably because of greater changes in the physical environment above-ground associated with less biomass, which did not affect below-ground biomass (Marotte et al., 2016; Ma et al., 2021). Remarkably, the changed resistance and niche breadth of plant functional groups, which were likely due to the changed competition hierarchy of the competing species within the communities were greatly disturbed by plant litter (Fig. S4). Plant litter had particularly strong impacts on community environmental resources, allowing plants with competitive advantages for optimal acquisition of space resources to become keystone species (Ravenek et al., 2016; Partzsch, 2019), thereby changing interspecific competition and coexistence (Fig. S4) and facilitating resistance and niche breadth shifts in plant functional groups.

In our study, ecological functioning and species interaction responses to litter manipulation were characterized by litter species effecting diverse changes in plant communities, however, these effects were stronger under the poisonous perennial forb–*L. virgaurea* treatment. Generally, forbs are relatively easier to be decomposed by microbes compared with grasses (Liu et al., 2018), in a process which can release more allelochemicals into the soil (Saito et al., 2015) and increases competition for above-ground resources (e.g., light and radiation) (Zhang et al., 2019), which further contributes to coexistence and competitive interactions of plants at the population level.

Notably, researches have increasingly recognized the importance of exploring optimum management strategies to maintain the stability of grassland ecological functions. Grassland degradation is understood to allow the spread of unpalatable plants (Li et al., 2014), and enclosure is widely recognized as an effective practice both to curb grassland degradation and quickly restore degraded grassland (Wang et al., 2020a). In turn, higher above-ground biomass produced in these grassland systems could result in a thicker litter layer, which will greatly impact plants performance and competitive interactions and regulate community ecological functioning, thereby regulating plant community heterogeneity. We therefore propose that controlling litter accumulation through the management practice of moderate grazing in non-growing periods is important to weaken the negative effects of litter and achieve sustainability of grassland systems.

5. Conclusions

In conclusion, our study showed that plant litter manipulation promoted plant community heterogeneity in the alpine meadow, and the effect was enhanced with increasing litter mass addition levels rather

than by litter species. The distribution patterns of functional composition and niche breadth variability of annual/perennial forbs were strongly linked to plant community heterogeneity. Our experiment highlights the importance of understanding variations in plant community properties and ecological functioning when evaluating litter effects on plant community heterogeneity, which since these factors have vital implications for maintaining the structure and function of grassland ecosystems. These findings indicate that grassland ecosystems can be characterized by plant litter dynamics, and that reasonable management practices may be particularly pivotal in achieving sustainability of grassland systems.

Credit author statement

Fujiang Hou conceived the ideas and designed methodology. Zhouwen Ma conducted the field experiment and collected the data. Fujiang Hou, Zhouwen Ma and Lan Li performed the statistical analyses and modelling. Fujiang Hou and Zhouwen Ma prepared the manuscript. All authors revised the manuscript and contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

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

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115877>.

References

- Baer, S.G., Collins, S.L., Blair, J.M., Knapp, A.K., Fiedler, A.K., 2005. Soil heterogeneity effects on tallgrass prairie community heterogeneity: an application of ecological theory to restoration ecology. *Restor. Ecol.* 13, 413–424. <https://doi.org/10.1111/j.1526-100x.2005.00051.x>.
- Browning, D.M., Franklin, J., Archer, S.R., Gillan, J.K., Guertin, D.P., 2014. Spatial patterns of grassland–shrubland state transitions: a 74-year record on grazed and protected areas. *Ecol. Appl.* 24, 1421–1433. <https://doi.org/10.1890/13-2033.1>.
- Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., et al., 2013. The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biol.* 19, 2940–2955. <https://doi.org/10.1111/gcb.12277>.
- Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gross, K.L., Gherardi, L.A., Hallett, L.M., Hobbs, R.J., Hsu, J.S., Turnbull, L., Suding, K.N., 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* 94, 1687–1696. <https://doi.org/10.1890/12-1006.1>.
- Collins, S.L., 2006. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* 73, 2001. <https://doi.org/10.2307/1941450>, 1992.
- Collins, C.D., Banks-Leite, C., Brudvig, L.A., Foster, B.L., Cook, W.M., Damschen, E.I., et al., 2017. Fragmentation affects plant community composition over time. *Ecography* 40, 119–130. <https://doi.org/10.1111/ecog.02607>.

- Core Team, R., 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- de Souza Júnior, M.B., Ferreira, F.F., de Oliveira, V.M., 2014. Effects of the spatial heterogeneity on the diversity of ecosystems with resource competition. *Physica A* 393, 312–319. <https://doi.org/10.1016/j.physa.2013.08.045>.
- Donath, T.W., Eckstein, R.L., 2012. Litter effects on seedling establishment interact with seed position and earthworm activity. *Plant Biol.* 14, 163–170. <https://doi.org/10.1111/j.1438-8677.2011.00490.x>.
- Lefcheck, J.S., 2016. PIECEWISESEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573579 <https://doi.org/10.1111/2041-210X.12512>.
- Leffler, A.J., Klein, E.S., Oberbauer, S.F., Welker, J.M., 2016. Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia* 1811, 287–297. <https://doi.org/10.1007/s00442-015-3543-8>.
- Letts, B., Lamb, E.G., Mischkolz, J.M., Romo, J.T., 2015. Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. *Plant Ecol.* 216, 357–370. <https://doi.org/10.1007/s11258-014-0436-6>.
- Levins, R., 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press.
- Li, Y.Y., Dong, S.K., Liu, S.L., Wang, X.X., Wen, L., Wu, Y., 2014. The interaction between poisonous plants and soil quality in response to grassland degradation in the alpine region of the Qinghai-Tibetan Plateau. *Plant Ecol.* 215, 809–819. <https://doi.org/10.1007/s11258-014-0333-z>.
- Liang, M., Liang, C., Hautier, Y., Wilcox, K.R., Wang, S., 2021. Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales. *Ecol. Lett.* 24, 2054–2064. <https://doi.org/10.1111/ele.13826>.
- Liu, C., Song, X.X., Wang, L., Wang, D.L., Zhou, X.M., Liu, J., Zhao, X., Li, J., Lin, H.J., Wan, S.Q., 2016. Effects of grazing on soil nitrogen spatial heterogeneity depend on herbivore assemblage and pre-grazing plant diversity. *J. Appl. Ecol.* 53, 242–250. <https://doi.org/10.1111/1365-2664.12537>.
- Liu, W.X., Allison, S.D., Li, P., Wang, J., Chen, D.M., Wang, Z.H., Yang, S., Diao, L.W., Wang, B., Liu, L.L., 2018. The effects of increased snow depth on plant and microbial biomass and community composition along a precipitation gradient in temperate steppes. *Soil Biol. Biochem.* 124, 134–141. <https://doi.org/10.1016/j.soilbio.2018.06.004>.
- Loreau, M., de Mazancourt, C., Duffy, E., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115. <https://doi.org/10.1111/ele.12073>.
- Loydi, A., Eckstein, R.L., Otte, A., Donath, T.W., Gómez-Aparicio, L., 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. *J. Ecol.* 101, 454–464. <https://doi.org/10.1111/1365-2745.12033>.
- Ma, Z.W., Wang, Y.X., Wang, H.A.B.M., Zhang, Z.M., Hou, F.J., 2017. Litter and its functions in grazing ecosystems. *Acta praeaculturae sinica* 26, 201–212. <https://doi.org/10.11686/cyxb2016342>.
- Ma, Z.W., Wu, J., Li, L., Zhou, Q.P., Hou, F.J., 2021. Litter-induced reduction in ecosystem multifunctionality is mediated by plant diversity and cover in an alpine meadow. *Front. Plant Sci.* 12, 773804 <https://doi.org/10.3389/fpls.2021.773804>.
- Ma, Z.W., Zeng, Y.F., Wu, J., Zhou, Q.P., Hou, F.J., 2022. Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Funct. Ecol.* 36, 148–158. <https://doi.org/10.1111/1365-2435.13935>.
- Mariotte, P., Spotswood, E.N., Farrer, E.C., Suding, K.N., Fraser, L., 2016. Positive litter feedbacks of an introduced species reduce native diversity and promote invasion in Californian grasslands. *Appl. Veg. Sci.* 20, 28–39. <https://doi.org/10.1111/avsc.12291>.
- Massé Jodoin, J., Guichard, F., 2019. Non-resource effects of foundation species on meta-ecosystem stability and function. *Oikos* 128, 1613–1632. <https://doi.org/10.1111/oik.06506>.
- Ohara, R.G., Ushimaru, A., Verheyen, K., 2015. Plant beta-diversity is enhanced around grassland-forest edges within a traditional agricultural landscape. *Appl. Veg. Sci.* 18, 493–502. <https://doi.org/10.1111/avsc.12166>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.B., Simpson, G., Solymos, P., Stevenes, M.H.H., Wagner, H., 2013. *Vegan: community ecology package*. FR package version 2.0–10. <http://CRAN.Rproject.org/package=vegan>.
- Partzsch, M., 2019. Warming differently affects the inter- and intraspecific interactions among semi-dry grassland species. *Perspect. Plant Ecol.* 40, 12548 <https://doi.org/10.1016/j.ppees.2019.125481>.
- Ravenek, J.M., Mommer, L., Visser, E.J.W., van Ruijven, J., van der Paaau, J.W., Smit-Tiekstra, A., de Caluwe, H., de Kroon, H., 2016. Linking root traits and competitive success in grassland species. *Plant Soil* 407, 39–53. <https://doi.org/10.1007/s11104-016-2843-z>.
- Saito, Y., Iga, S., Nakashima, K., Okamoto, Y., Gong, X., Kuroda, C., Tori, M., 2015. Terpenoids from *Ligularia virgaurea* collected in China: the first example of two bakkane derivatives with an anhydride-type ring C and nineteen new chemical constituents. *Tetrahedron* 71, 8428–8435. <https://doi.org/10.1016/j.tet.2015.09.011>.
- Shen, Y., Chen, W.Q., Yang, G.W., Yang, X., Liu, N., Sun, X., Chen, J.S., Zhang, Y.J., 2016. Can litter addition mediate plant productivity responses to increased precipitation and nitrogen deposition in a typical steppe? *Ecol. Res.* 31, 579–587. <https://doi.org/10.1007/s11284-016-1368-5>.
- Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology* 94, 560–564. <https://doi.org/10.1890/12-0976.1>.
- Song, S.S., Zhu, J.L., Zheng, T.L., Tang, Z.Y., Zhang, F., Ji, C.J., Shen, Z.H., Zhu, J.X., 2020. Long-term grazing exclusion reduces species diversity but increases community heterogeneity in an alpine grassland. *Front. Ecol. Evol.* 8, 66. <https://doi.org/10.3389/fevo.2020.00066>.
- Sun, C.L., Chai, Z.Z., Liu, G.B., Xue, S., 2017. Changes in species diversity patterns and spatial heterogeneity during the secondary succession of grassland vegetation on the Loess Plateau, China. *Front. Plant Sci.* 8, 1465. <https://doi.org/10.3389/fpls.2017.01465>.
- Sun, Y., He, X.Z., Hou, F.J., Wang, Z.F., Chang, S.H., 2018. Grazing increases litter decomposition rate but decreases nitrogen release rate in an alpine meadow. *Biogeosciences* 15, 4233–4243. <https://doi.org/10.5194/bg-15-4233-2018>.
- Turner, M.G., Donato, D.C., Romme, W.H., 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landsc. Ecol.* 28, 1081–1097. <https://doi.org/10.1007/s10980-012-9741-4>.
- Ulrich, W., Piwczynski, M., Zaplata, M.K., Winter, S., Schaaf, W., Fischer, A., 2014. Small-scale spatial variability in phylogenetic community structure during early plant succession depends on soil properties. *Oecologia* 175, 985–995. <https://doi.org/10.1007/s00442-014-2954-2>.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Schweitzer, J.A., Suding, K.N., de Vooorde, T.F.J.V., Wardle, D.A., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276. <https://doi.org/10.1111/1365-2745.12054>.
- Wang, S.P., Loreau, M., 2016. Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* 19, 510–518. <https://doi.org/10.1111/ele.12582>.
- Wang, C.T., Long, R.J., Wang, Q.L., Liu, W., Jing, Z.C., Zhang, L., 2010. Fertilization and litter effects on the functional group biomass, species diversity of plants, microbial biomass, and enzyme activity of two alpine meadow communities. *Plant Soil* 331, 377–389. <https://doi.org/10.1007/s11104-009-0259-8>.
- Wang, Y.X., Sun, Y., Chang, S.H., Wang, Z.F., Fu, H., Zhang, W.G., Hou, F.J., 2020a. Restoration practices affect alpine meadow ecosystem coupling and functions. *Rangel. Ecol. Manag.* 73, 441–451. <https://doi.org/10.1016/j.rama.2020.01.004>.
- Wang, J., Liu, W.X., Li, P., Jia, Z., Deng, M.F., Yang, S., Liu, L.L., 2020b. Long-term deepened snow cover alters litter layer turnover rate in temperate steppes. *Funct. Ecol.* 34, 1113–1122. <https://doi.org/10.1111/1365-2435.13531>.
- Wang, Y.X., Wu, Z., Wang, Z.F., Chang, S.H., Qian, Y.Q., Chu, J.M., Jia, Z.Q., Zhou, Q.P., Hou, F.J., 2022. Ecosystem coupling and ecosystem multifunctionality may evaluate the plant succession induced by grazing in alpine meadow. *Front. Plant Sci.* 13, 839920 <https://doi.org/10.3389/fpls.2022.839920>.
- Wu, X.F., Yang, J.J., Ruan, H., Wang, S.N., Yang, Y.R., Naem, I., Wang, L., Liu, L., Wang, D.L., 2021. The diversity and co-occurrence network of soil bacterial and fungal communities and their implications for a new indicator of grassland degradation. *Ecol. Indic.* 129, 107989 <https://doi.org/10.1016/j.ecolind.2021.107989>.
- Wubs, E.R.J., Bezemer, T.M., 2018. Plant community evenness responds to spatial plant-soil feedback heterogeneity primarily through the diversity of soil conditioning. *Funct. Ecol.* 32, 509–521. <https://doi.org/10.1111/1365-2435.13017>.
- Xiao, C., Janssens, I.A., Zhou, Y., Su, J., Liang, Y., Guenet, B., 2015. Strong stoichiometric resilience after litter manipulation experiments: a case study in a Chinese grassland. *Biogeosciences* 12, 757–767. <https://doi.org/10.5194/bg-12-757-2015>.
- Yang, J., Chu, P.F., Chen, D.M., Wang, M.J., Bai, Y.F., 2014. Mechanisms underlying the impacts of grazing on plant α , β and γ diversity in a typical steppe of the Inner Mongolia grassland. *Chinese Journal of Plant Ecology* 38, 188–200. <https://doi.org/10.3724/SP.J.1258.2014.00017>.
- Zhang, A., Wang, D., Wan, S.Q., 2019. Litter addition decreases plant diversity by suppressing seeding in a semiarid grassland, Northern China. *Ecol. Evol.* 9, 9907–9915. <https://doi.org/10.1002/ece3.553>.