

RESEARCH ARTICLE

Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups

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Abstract

1. The stability of a plant community is defined as its ability to resist and be resilient to changes. Plant community stability can be driven by a range of external perturbations as well as by plant community traits. Plant litter traits (species or mass) are widely recognized drivers for plant community composition and diversity changes in grasslands. Yet, the effects of litter traits on the temporal stability of plant communities in natural grasslands are largely unknown.
2. In this study, a field experiment was conducted at an alpine meadow on the Qinghai Tibetan Plateau to quantify the effects of litter from *Elymus nutans*, *Kobresia setchwanensis* and *Ligularia virgaurea* on the temporal stability of plant community biomass at five different mass levels (0, 100, 200, 400 and 600 g/m²). The experiment was conducted over the period from the pre-growth to peak-growth stage between 2017 and 2019, during which temporal stability of plant community biomass was assessed in relation to plant community characteristics.
3. The effects of litter on temporal stability of plant community biomass were mainly driven by the litter mass rather than the litter species. A hump-shaped relationship between litter mass and temporal stability of plant community biomass was found, with the highest stability under intermediate litter mass treatment (200 g/m²). A structural equation model identified that this response was driven by the indirect effects of litter mass on the temporal stability of the biomass of the dominant (forbs) and subdominant (grasses) functional groups in the community and the asynchrony of plant functional groups.
4. The results of this study demonstrate that plant litter traits are important drivers for maintaining plant community stability in natural grasslands, highlighting the importance of grassland management decisions (e.g. grazing intensity) relating to the quantity and quality of litter accumulation.

KEYWORDS

alpine meadow, asynchrony, litter manipulation, plant diversity, temporal stability

1 | INTRODUCTION

Understanding the mechanisms driving the temporal stability of plant community biomass is an important scientific issue in ecology (Brown et al., 2016), as the stability of biomass within a plant community is crucial for maintaining multiple ecosystem functions (Pennekamp et al., 2018). Temporal stability is defined as the capacity of an ecosystem to dampen environmental perturbations over time while retaining ecological functions of interest (Ives & Carpenter, 2007; Pimm, 1984), and it can be impacted by various biotic and abiotic factors (Ma et al., 2017; Xu et al., 2015). Across many ecosystems, the relationship between ecosystem stability and biodiversity has received particular attention (Yang et al., 2012). Multiple aspects of biodiversity may impact the temporal stability of ecosystem processes over time (Craven et al., 2018), and the relationships between diversity and ecosystem temporal stability can vary with ecosystem type (Campbell et al., 2011).

The temporal stability of plant community biomass can be influenced by multiple ecological drivers. Gross et al. (2014) found changes in species richness to be the primary driver of the temporal stability in biodiversity–stability relationships that respond to environmental changes. Several other studies have indicated that temporal stability of the dominant species and/or functional groups is important in maintaining the stability of ecosystems (Hallett et al., 2014; Huang et al., 2020), particularly where the dominant species and/or functional groups account for a considerable proportion (approximately 50%–60% of above-ground biomass) of the community (Ma et al., 2017; Xu et al., 2015). The stability of subordinate species and functional groups contributes relatively less to temporal stability of plant community biomass, but still plays an important role (Huang et al., 2020; Yang et al., 2017). Greater diversity in an ecosystem may enhance temporal stability because of the asynchronous responses of different species to environmental fluctuations (Hautier et al., 2014; Sasaki et al., 2019) and the variable strengths of competition (Loreau & de Mazancourt, 2013). Huang et al. (2020) showed that asynchrony of plant species/functional groups mediates community biomass stability.

In vegetation ecosystems, litter accumulation has been identified as a critical factor that affects all the above-mentioned drivers for plant community diversity (Loydi et al., 2013; Phillips et al., 2016). Plant litter is a pivotal link between above-ground and below-ground ecological processes, has a substantial cascading effect on plant–soil biogeochemical cycling and is an important driver for changes in community structure and functions in ecosystems (Xiao et al., 2015). Conversely, litter accumulation may alter the relative dominance of plant functional groups (Hou et al., 2019) and community composition (Letts et al., 2015), impact the interactions among competing species (Holdredge & Bertness, 2011) and potentially therefore has a considerable influence on temporal stability of plant community biomass.

Both litter mass and litter species are important in determining the effects of plant litter on plant community characteristics. The meta-analysis by Xiong and Nilsson (1999) indicated that litter mass

is a good predictor for the effects of litter on most vegetation variables. Moreover, their analysis indicated that the negative effects of plant litter generally outweigh the positive ones over study periods that are mostly less than three to four seasons. Letts et al. (2015), however, reported litter-plant feedbacks can both promote and inhibit shifts in vegetation composition. The differences in physical and chemical properties (Chomel et al., 2016) of different litter species influence seedling and plant establishment in grasslands (Hovstad & Ohlson, 2008; Loydi et al., 2015). The variation in physical properties of litter species can result in different light, temperature and moisture conditions for plants underneath litter layers (Hou et al., 2019). The chemical differences may produce differences in decomposition, nutrient availability, allelopathy and plant community structure (Facelli & Pickett, 1991). Forbs litter may exert a stronger chemical effect on vegetation because more phytotoxins and nutrients may be released in a short period, whereas grasses litter can have a weaker chemical effect because of its slower rate of decomposition (Xiong & Nilsson, 1999).

In the present study, the aim was to demonstrate the potential impacts of litter on temporal stability of plant community biomass in an alpine meadow of the Qinghai Tibet Plateau (QTP). The QTP is the highest elevation ecoregion in the world, with an area of 2.5 million km² and an average elevation of over 4,000 m. Approximately 65% of the QTP is covered by alpine meadows, and livestock grazing is the main land use (Chen et al., 2013). Recently, the alpine meadows of the QTP have experienced varying degrees of degradation as a result of livestock overgrazing. There are concerns that this issue, which manifests as fast-spreading unpalatable forbs such as *Ligularia virgaurea* rather than palatable perennial grasses or sedges, is detrimental for biodiversity and has harmful consequences for the functioning and stability of the ecosystem (Dong et al., 2013). The cessation of grazing is the proposed approach to restoring degraded grasslands, which would likely alter the composition of plant communities and therefore the species composition of plant litter, in turn leading to an increase in litter biomass (Zou et al., 2016). Such changes to the composition and accumulation of litter can result in variation in litter turnover, thereby altering ecosystem processes such as nutrient cycling (Hong et al., 2021) and plant community characteristics (Zou et al., 2016), which could potentially then impact upon temporal stability of plant community biomass (Isbell et al., 2009). However, little is known about the impact of litter on temporal stability of plant community biomass in the alpine meadows of the QTP.

This study reports the results of a 3-year field experiment that was carried out to investigate the influence of litter species and litter mass on temporal stability of plant community biomass in an alpine meadow on the QTP. Three different litter types from three dominant species that represent different functional groups (*Elymus nutans*—grass, *Kobresia setchwanensis*—sedge and *Ligularia virgaurea*—noxious forb) with five levels of litter mass were employed. *Elymus nutans* and *Kobresia setchwanensis* were the most dominant palatable grass and sedge at the experimental site, respectively, whereas *Ligularia virgaurea* was the fastest-spreading noxious forb at our experimental site, as well as in alpine meadows

in the QTP in general. Previous studies have shown that impacts of litter mass and species can decrease the species dominance (Zou et al., 2016), species richness (Zhang et al., 2019) and asynchrony of plant functional groups (Huang et al., 2020) and increase the variability of the community biomass (Xiong & Nilsson, 1999). These factors are important determinants of temporal stability of plant community biomass (Wu et al., 2020; Zhou et al., 2019). Therefore, we hypothesized in this study that litter species, litter mass and their interaction would significantly impact temporal stability of plant functional groups and community biomass through cascading effects on plant community characteristics such as dominance of plant functional groups, species richness, variability of community biomass and asynchrony of plant functional groups. Based on the observations of previous studies that examined litter impacts on plant community characteristics, we predicted the net effect of litter addition would result a reduction of temporal stability of plant community biomass and that the effect of *Ligularia virgaurea* litter addition would be stronger.

These hypotheses were tested using piecewise structural equation modelling (SEM). The SEM tested whether litter mass, litter species and their interaction altered the temporal stability of plant community biomass via changes in the dominance of plant functional groups, species richness, variability of community biomass, temporal stability of forbs and grasses, and asynchrony of plant functional groups. The specific questions that this paper seeks to answer are as follows: (a) Do the litter species, the litter mass and their interactions have a significant impact upon temporal stability of plant community biomass in the QTP's alpine meadows? (b) Does litter mass or species composition have a greater impact on stability, in which the impact will be more pronounced in litter of *Ligularia virgaurea*? (c) What are the mechanisms driving the impacts of litter on temporal stability of plant community biomass?

2 | MATERIALS AND METHODS

2.1 | Study site

The research was conducted at an alpine meadow site at the north-eastern boundary of the QTP, located in Hongyuan County, China (31°47'N, 102°33'E; 3,485 m a.s.l.). The study site belongs to the continental monsoon climate, in which the annual growth season occurs from the end of April to early October (with the middle of August as the period of peak growth), and the vegetation has an average coverage of more than 80%. The long-term (1961–2013) mean annual temperature is 1.5°C, and the mean annual precipitation is 747 mm—80% of which falls during the growing season, when the average relative humidity is 60%–70%. The soil at the site is classified as Mat Cry-gelic Cambisols (Chinese Soil Taxonomy Research Group, 1995). The vegetation types were *Cyperus*, *Poaceae* and dicotyledon forbs. *Cyperus* species are mainly *Scirpus pumilus*, *Carex thibetica* and *Kobresia Setchwanensis*. *Poaceae* species are mainly *Deschampsia caespitosa* and *Elymus nutans*. Common dicotyledon

forbs include *Saussurea hieracioides*, *Aster tataricus*, *Anemone rivularis*, *Anemone trullifolia*, *Ligularia virgaurea*, *Potentilla fragarioides*. The alpine meadows at the site were subjected to year-round free-grazing by yak.

2.2 | Experimental design

The experimental area at the study site was a moderately degraded grassland. Since 2014, yak have been free grazing the area during the winter. The experimental plots were established in 2017 within a 50 × 50 m area that was fenced to exclude grazing. The plots were arranged in a randomized block design with four replicates for each treatment. Each plot had dimensions of 2 × 2 m and were arranged in blocks. The buffer zone between adjacent plots was at least 1 m. Treatments were randomly assigned to the plots. The treatments included litter from three dominant species at the study site (*E. nutans* [grass], *K. setchwanensis* [sedge] and *L. virgaurea* [noxious forb]) and five litter mass levels for each litter species (0 [control], 100, 200, 400 and 600 g/m²). In late April (before seedlings start to emerge) of each year (2017, 2018 and 2019), all of the above-ground standing litter and fallen material were removed from each plot, and the appropriate litter mass from the litter species was distributed evenly over each plot. Plant litter samples used in the treatments were collected in the preceding year from an adjacent field after plant tissue senescence. The litter samples were air-dried for 1 month and then stored at room temperature for 4 months before being manually cut into lengths of about 1 cm using a hay cutter. Subsamples of the litter from each species were oven-dried at 65°C to a constant mass to calculate the moisture correction factor, and were then accurately weighed to assess the initial litter quantity before being added to the plots.

2.3 | Plant community monitoring

In mid-May of each year, a standard 0.5 × 0.5 m quadrat was permanently established within each plot. In June to August (from the pre-growth to the peak-growth stage) of each year, the plant species within each quadrat were recorded. Species richness in each plot was estimated by the total number of plant species detected in the permanent quadrat. During the same timeframe, 0.5 × 0.5 m quadrats were randomly placed within each plot, and the biomass at ground level within each plot was clipped in the middle of June, July and August. The clipped plants were sorted into forbs, grasses, legumes and sedges, and oven-dried at 65°C to a constant weight to estimate the biomass of community and functional groups. All plant species were classified into the four above-mentioned plant functional groups, in which forbs were classified as the 'dominant functional group' (accounting for 60.1% of the plant community biomass) and grasses were classified as the 'subordinate functional group' (accounting for 23.1% of the plant community biomass). Sedges accounted for 13.6% of the plant community biomass and

legumes—whose responses to litter treatments were negligible—accounted for only 3.2%. Hence, the responses of legumes to litter were not considered for further analysis in this study.

2.4 | Plant community data analysis

The temporal stability of plant community biomass in this study was defined as the ratio of μ/σ , where μ is the temporal average above-ground biomass of a plot over the sampling period, and σ is the temporal standard deviation in the above-ground biomass of a plot over the sampling period (Hautier et al., 2014; Tilman et al., 2006). The same method was used to calculate the temporal stability of the biomass of plant functional groups. The asynchrony of plant functional groups ($1 - \eta$) for each plot was estimated according to Gross et al. (2014):

$$1 - \eta = 1 - (1/n) \sum_i \text{Corr} \left(Y_i, \sum_{j \neq i} Y_j \right),$$

where η is the synchrony of plant functional groups, and Y_i is the above-ground biomass of plant functional group i in a plot of n functional groups over the sampling period. The degree of plant biomass variability was estimated by the response ratio ($100 \times (\text{treatment} - \text{control})/\text{control}$), and Simpson's dominance index was used to estimate plant

functional group biomass (Smith & Wilson, 1996). The data collected over the 3 months of each year from an individual plot were averaged and used for statistical analysis.

2.5 | Structural equation modelling

Piecewise SEM was used to explore how litter treatments affected temporal stability of plant community biomass through its impact on plant community characteristics. First, an a priori conceptual model with hypothetical relationships was constructed that contained all possible cascading pathways (Figure 1), assuming that litter mass, litter species and their interaction alter the temporal stability of plant community biomass via changes in the dominance of plant functional groups, species richness, variability of community biomass, temporal stability of forbs and grasses, and asynchrony of plant functional groups. The data were standardized by z-transformation and the plot was used as the random effect. The model was repeatedly simplified by sequentially eliminating non-significant pathways until ultimately a final optimized model was obtained. Only those variables with a variance inflation factor of <5 were included in the same model. We used directed separation tests, Fisher's C statistic and AIC (Akaike information criteria), to assess the goodness-of-model fit (Shipley, 2013). The SEM analyses were performed using the `PIECEWISESEM` package (Lefcheck, 2016) in R version 4.1.0 (R Core Team, 2021).

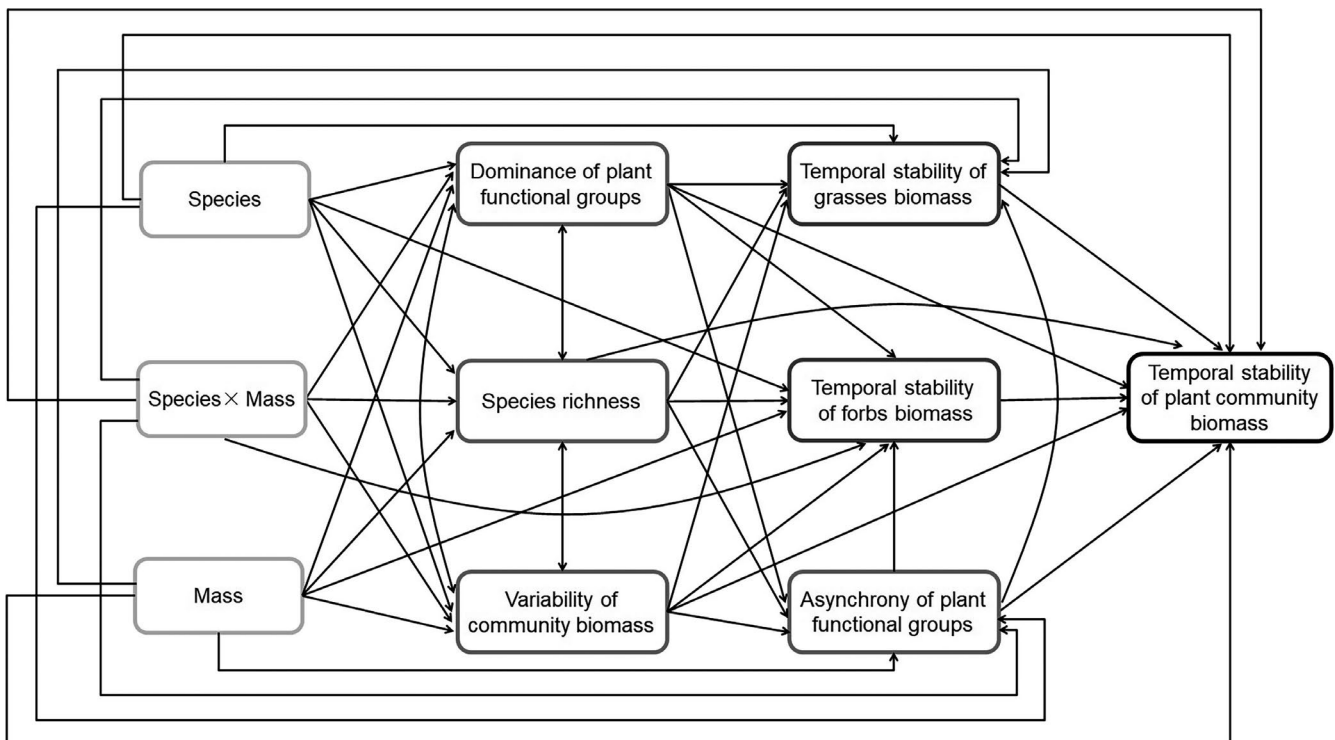


FIGURE 1 Hypothetical causal model for structural equation modelling (SEM) exploring the effects of litter mass, litter species, the interaction of litter mass and litter species, dominance of plant functional groups, species richness, variability of community biomass, asynchrony of plant functional groups and temporal stability of forbs and grasses on community temporal stability in the litter manipulation experiment. Black arrows are hypothesized paths

2.6 | Statistical analysis

A linear mixed-effects model (REML procedure) was used to test the effects of litter species, litter mass, year and their interactions on species richness, dominance of plant functional groups, and plant biomass variability of the community and functional groups. The effects of litter species, litter mass and their interactions on temporal stability of plant community biomass were also assessed by linear mixed-effects model (REML procedure). Litter species, litter mass and year were used as fixed effects, and 'plot' as the random effect. Differences were considered to be statistically significant at $p < 0.05$. All statistical analyses were carried out in R version 4.1.0 (R Core Team, 2021) using the 'lme' function in the lme4 library package.

3 | RESULTS

3.1 | Effects of litter manipulation on temporal stability of plant community biomass

In contrast to our hypothesis (Figure 1), the final SEM predicted that only the litter mass has a significant impact on temporal stability of plant community biomass. The litter species and 'mass \times species' interaction pathways on temporal stability of plant community biomass were not significant to include in the final model (Figure 2). The SEM explained 77% of the variance of temporal stability of plant community biomass with direct effects from the temporal stability of forbs biomass (path coefficient = 0.79; $p < 0.001$), temporal stability of grasses biomass (path coefficient = 0.50; $p < 0.001$) and asynchrony of plant functional groups (path coefficient = 0.27; $p < 0.001$). According to the SEM, the best predictor of temporal stability of plant community biomass is the temporal stability of forbs biomass, which is itself indirectly impacted by litter mass through species richness, dominance of plant functional groups, variability of community biomass and asynchrony of plant functional groups. The temporal stability of grasses biomass is also indirectly impacted by litter mass through the dominance of plant functional groups. The asynchrony of plant functional groups is indirectly impacted by litter mass through the variability of community biomass.

Statistical analysis by the linear mixed-effects model analysis (Figure 3A) confirmed a significant ($p < 0.01$) effect of litter mass on temporal stability of plant community biomass. The effects of litter species and their interaction with litter mass on temporal stability of plant community biomass were not significant. The response of temporal stability of plant community biomass to litter mass was hump-shaped; it increased with increasing litter mass up to 200 g/m² and decreased with further increases in litter mass. The lowest temporal stability of plant community biomass was observed at the highest litter mass treatment of 600 g/m². The effects of litter on the temporal stability of forbs and sedges biomass were non-significant (Figure 3B,D), whereas a significant effect of litter mass on the temporal stability of grasses biomass was observed ($p < 0.01$). The

temporal stability of grasses biomass was significantly lower in the 600 g/m² treatment compared to the control (Figure 3C).

3.2 | Plant community response to litter manipulation

Over the 3-year experimental period, litter treatments had significant effects on plant community characteristics (Figure 4; Table S1). There was a significant effect of litter mass and litter species ($p < 0.001$ for both) on species richness (Figure 4A). The species richness decreased with increasing litter mass, and the 400 and 600 g/m² treatments showed significantly lower ($p < 0.05$) species richness compared to the control. The plant species richness was significantly lower ($p < 0.05$) in plots treated with *L. virgaurea* litter compared to those treated with *E. nutans* or *K. setchwanensis* litter (Figure 4A). The effect of litter mass on the dominance of plant functional groups varied with litter species (P -value for mass \times species interaction < 0.05) (Figure 4B). The asynchrony of plant functional groups was significantly ($p < 0.05$) impacted by litter species, and there was a significant difference between that in the plots treated with *E. nutans* litter compared to those with *K. setchwanensis* litter (Figure 4C). Plant community biomass showed a significant ($p < 0.001$) negative response to litter species and litter mass (Figure 4D), and the response was greater in the 400 and 600 g/m², and *L. virgaurea* litter treatments.

4 | DISCUSSION

Natural grasslands host a diverse range of plant species with a variety of life strategies that respond to multiple perturbations over time to maintain ecosystem stability. The present study demonstrates that plant litter—an important plant community trait—can impact the temporal stability of plant community biomass in grasslands. This response is mainly driven by the indirect effects of litter mass on the temporal stability of the biomass of forbs and grasses (the dominant and subdominant functional group in the community), and the asynchrony of plant functional groups (Figure 2). Results also showed that manipulating the litter mass can potentially help to maintain a greater temporal stability of plant community biomass. Specifically, a hump-shaped relationship was found between litter mass and temporal stability of plant community biomass (Figure 3A), with the highest temporal stability of plant community biomass observed in the intermediate litter treatment of 200 g/m². This finding is consistent with Xiong and Nilsson (1999), who concluded that positive effects of litter on vegetation occur where the litter quantity is below 200 g/m².

Although previous studies have demonstrated the importance of plant diversity and the heterogeneity of plant functional groups on ecological stability (Huang et al., 2020; Zhou et al., 2019), the present study makes some notable further advances. First, to the best of our knowledge, this study is the first in which the impacts of multi-level

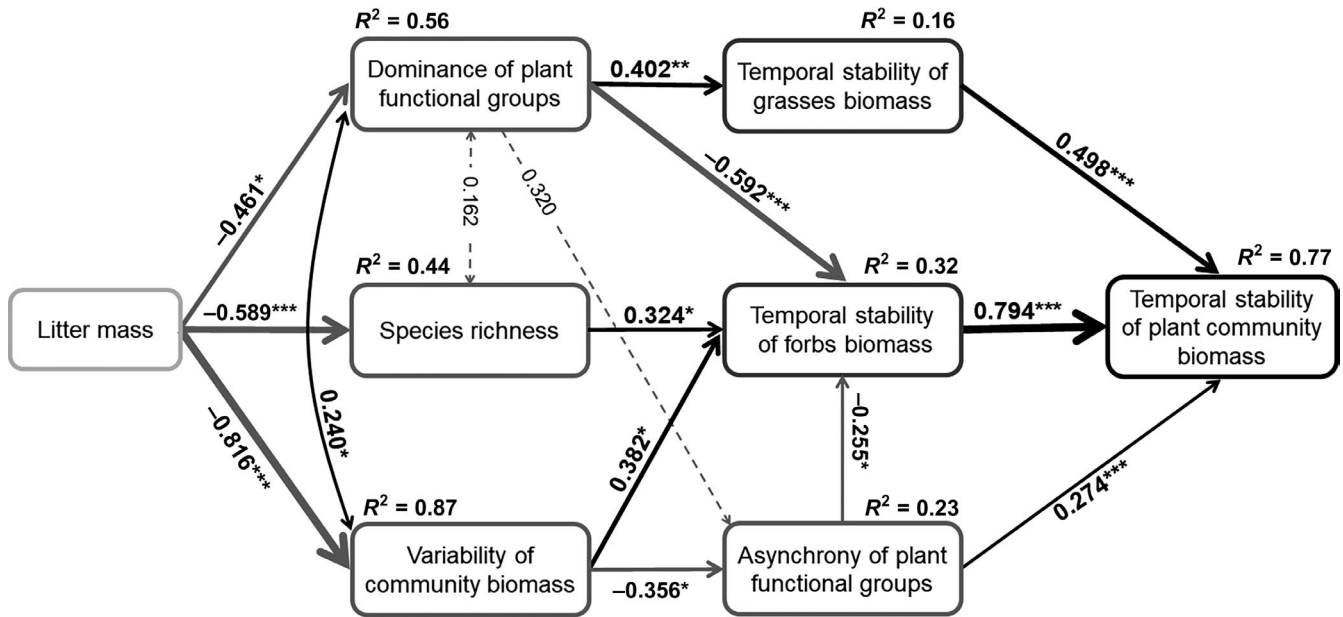
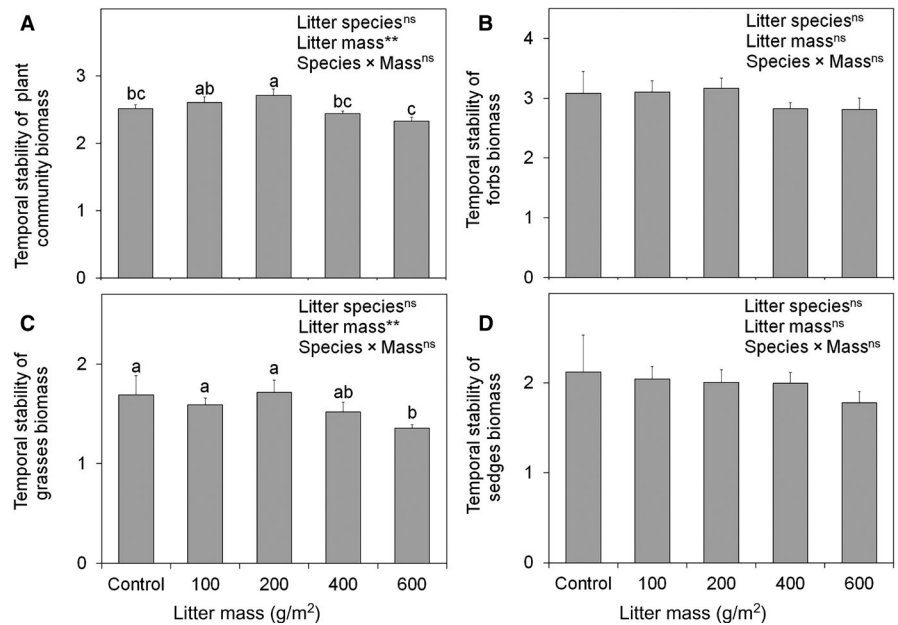


FIGURE 2 A piecewise structural equation model to illustrate the pathways of litter mass effect on temporal stability of community biomass. Numbers next to arrows indicate the standard path coefficient of each pathway. Arrow width is proportional to the strength of the relationship. Black and grey solid arrows represent significant positive and negative pathways, respectively. Grey dashed arrows indicate non-significant pathways but critical to final model fit. R^2 indicates the proportion of variance explained for each dependent variable in the model. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Fisher's $C = 21.199$, $p = 0.732$ and $AIC = 103.199$

FIGURE 3 Effects of litter mass on temporal stability of biomass of plant community (A), forbs (B), grasses (C) and sedges (D). Letters indicate significant differences at $p < 0.05$ (** $p < 0.01$. ns, not significant). Values are mean \pm SE



litter manipulation (litter species, litter mass and their interaction) on temporal stability of plant community biomass have been assessed. Previous studies have examined the responses of temporal stability of plant community biomass to external perturbations such as climate warming (Ma et al., 2017), grazing (Li et al., 2020) and nitrogen deposition (Zhou et al., 2020). Second, while most previous studies on the temporal stability of plant community biomass of grasslands were examined only during the peak plant growth stage, our study covered the full plant growth period from the pre-growth to peak-growth stage, which can better reveal the stability of grassland

community dynamics. Third, it has been demonstrated here that, under litter manipulation, the responses of the temporal stability of dominant and subdominant functional group biomass are more important for the temporal stability of plant community biomass than the asynchrony of plant functional groups, which is in contrast to the observations reported by Zhou et al. (2019).

The temporal stability of forbs biomass was found in this study to be the main contributor to the variation in temporal stability of plant community biomass (Figure 2), and this can be attributed to the substantial plant community biomass (60.1%) and species richness

(70.5%) accounted for by forbs in the experimental community. Many forb species are relatively sensitive to perturbations owing to their weak ability to acquire resources under litter manipulation (Wang et al., 2010). At our experimental site, the forbs functional group included a morphologically and phylogenetically diverse group of species containing Asteraceae, Ranunculaceae and 12 other different families, which may have differential susceptibility to perturbations under litter treatments, thereby impacting the temporal stability of plant community biomass. In contrast, Zhou et al. (2019) reported that temporal stability of plant community biomass was not significantly correlated with the temporal stability of forbs biomass, despite forbs being the dominant functional group in the community, in a climate change simulation experiment conducted at an alpine meadow site on the QTP.

In our experiment, the addition of litter reduced the biomass production of forbs (Figure S1a) without altering its temporal stability (Figure 3B), which suggests that the litter treatments decreased its temporal variation. The treatments with larger additions of litter mass (400 and 600 g/m²) resulted in higher variability in community biomass (Figure 4D) and reduced dominance of plant functional groups (Figure 4B), thus impacting the stability of forbs biomass and thereby the temporal stability of plant community biomass. This was evident from the results of the SEM, in which litter mass showed a direct negative impact on species richness, the variability of community biomass and the dominance of plant functional groups, and an indirect negative impact on the asynchrony of plant functional

groups, which then significantly influenced the stability of forbs (Figure 2).

Grasses, which constituted the subdominant functional group in our experimental site, accounted for 23.1% of the total plant community biomass and there was a significant impact on temporal stability of plant community biomass (Figure 2). Other previous studies have also observed that the temporal stability of subordinate species influences the temporal stability of plant community biomass (Ma et al., 2020; Yang et al., 2017). At high levels of litter mass addition (600 g/m²), the temporal stability of grasses biomass was significantly lower than in the control (Figure 3C), and the SEM identified that this effect was driven indirectly via litter mass impacting the dominance of plant functional groups (Figure 2).

The SEM also identified the asynchrony of plant functional groups as another key driver of temporal stability of plant community biomass (Figure 2). Specifically, litter mass was found to affect the asynchrony of plant functional groups by altering the variability of community biomass (Figure 2), with the larger litter mass treatments increasing the biomass variability of forbs and sedges to a greater extent (Figure S1a,c) but stabilizing that of grasses (Figure S1b). This may have resulted in a greater variability of community biomass (Figure 4D) and probably caused a high degree of asynchrony in plant functional groups (Figure 2). Different plant species possess different functional traits, and their responses to litter disturbances can also be different (Loreau & De Mazancourt, 2008), leading to asynchronous responses to litter. Zhou et al. (2019) and Huang et al. (2020) reported that the

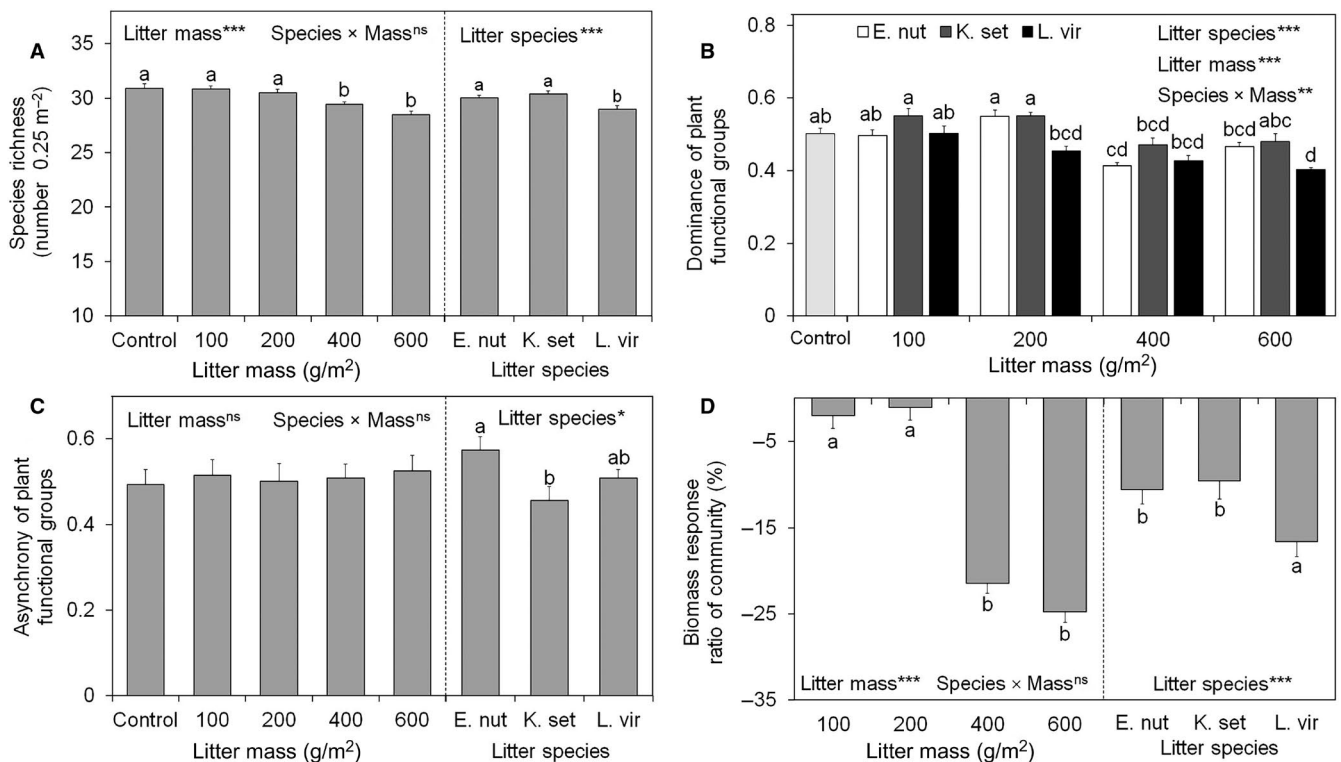


FIGURE 4 Effects of litter species and mass on species richness (A), dominance of plant functional groups (B), asynchrony of plant functional groups (C) and biomass response ratio of community (D). The letters indicate significant differences at $p < 0.05$ (* $p < 0.05$, *** $p < 0.001$, ns, not significant). Values are mean \pm SE. E. nut–*E. nutans*, K. set–*K. setchwanensis* and L. vir–*L. virgaurea*

asynchrony of plant functional groups was the key determinant for temporal stability of plant community biomass in their study site, rather than climate change or nitrogen addition. A positive relationship between temporal stability of plant community biomass and species asynchrony has also been reported previously by Wu et al. (2020), while Yang et al. (2017) reported a negative effect of daytime warming on temporal stability of plant community biomass in a semi-arid temperate steppe, partly due to its positive effect on species asynchrony. Other studies have reported no effect (Sasaki et al., 2019) or a negative effect (Chi et al., 2019) of species asynchrony on temporal stability of plant community biomass.

The present study revealed that the litter mass treatments in our experimental plots significantly impacted the species richness (Figure 4A), thereby impacting the temporal stability of plant community biomass (Figure 2)—a finding that has also been observed in several previous studies (Huang et al., 2020; Kohli et al., 2019). However, in our study, the effect of species richness on temporal stability of plant community biomass was indirect, by changing the temporal stability of forbs biomass (Figure 2). This is perhaps attributable to the very little variation in species richness that occurred (disappearance of only one or two rare species out of a total 30 species per 0.25 m²) under the higher litter mass addition treatments (Figure 4A). The high diversity in our experimental plots may have resulted in a poor relationship between temporal stability of plant community biomass and species richness, as studies on biodiversity and the functioning of ecosystems typically show the strongest relationships at lower levels of species richness (Venail et al., 2015). Several previous studies have also shown plant diversity to not be the main factor maintaining temporal stability of plant community biomass in natural grasslands (Ma et al., 2020; Sasaki & Lauenroth, 2011). In contrast, Zhou et al. (2020) showed that high species richness contributed to a higher temporal stability of plant community biomass. In the present study, it was found that greater litter mass addition reduced the species richness (Figure 4A), probably due to the suppression of seedling establishment by reduced species recruitment (Mariotte et al., 2016; Zhang et al., 2019) and limited light availability affecting species recruitment (Liu et al., 2018).

The SEM did not identify litter species as having a significant impact on plant community characteristics or temporal stability of plant community biomass. However, the linear mixed-effect model analysis of direct effects indicated litter responses to plant community characteristics were stronger under *L. virgaurea* than *E. nutans* or *K. setchwanensis* litter addition (Figures 3 and 4; Figure S1). This observation is consistent with our hypothetical prediction and possibly related to the different decomposition rates of the three litter species. It was estimated from a separate litter bag experiment (data not presented) that the mass losses of *L. virgaurea*, *E. nutans* and *K. setchwanensis* were 49.6%, 23.3% and 36.1%, respectively, during late April to mid-August. The faster decomposition rates associated with *L. virgaurea* litter may have facilitated higher light availability for seedlings and released more secondary compounds or toxins to the soil (Saito et al., 2015), which potentially affected the composition of the plant communities (Shi et al., 2018).

The present results have great significance for maintaining community stability in alpine meadows located on the QTP, which are becoming increasingly vulnerable to degradation via external perturbations. Grazing exclusion is the recommended practice for restoring degraded grasslands, but a limitation of this approach would be substantial litter mass accumulation, which has been shown to instigate negative impacts on grassland community characteristics (Zou et al., 2016). The result of the present study—that greater litter mass negatively impacted temporal stability of plant community biomass—reinforces this finding. However, it was also found that a litter mass accumulation up to 200 g/m² would be beneficial in terms of enhancing temporal stability of plant community biomass. Therefore, one could argue that rational grazing to facilitate beneficial levels of litter accumulation would enhance plant community stability. In support of this argument, Loydi et al. (2013) also reported positive effects of low and medium litter accumulation (<500 g/m²) on seedling emergence and enhanced seedling survival at low litter accumulation (<250 g/m²) in grassland ecosystems.

The encroachment of unpalatable and poisonous plant species in alpine meadows on the QTP is considered to be a serious threat in terms of grassland degradation (Xie et al., 2014). A high proportion of poisonous plants in grassland plant communities will result in greater litter mass accumulation as animals avoid ingestion of these plants. In the present study, it was found that higher litter mass and litter from *L. virgaurea*—a dominant poisonous plant found on the QTP—had a strong impact on plant community characteristics. Therefore, we can speculate that one possible mechanism by which the rapid spread of poisonous plants in alpine meadows facilitates grassland degradation is the negative feedback of their litter to the plant community stability. These findings highlight the importance of considering litter feedback effects on grassland community stability in grazing management decisions.

5 | CONCLUSIONS

This study demonstrated that plant litter is an important but previously unrecognized mechanism regulating the temporal stability of plant community biomass of alpine meadows on the QTP. The functional group stability of forbs and grasses and the asynchrony of plant functional groups were found to be the key drivers regulating temporal stability of plant community biomass, as compared to plant diversity and variability of community biomass. Our study provides important empirical evidence for the potential role of litter effects in the temporal stability of dominant/subdominant plant functional groups, and thus suggests a positive litter dynamics feedback cycle that serves as valuable information when developing sustainable grassland management strategies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

F.H. conceived the ideas and designed the methodology; Z.M., Y.Z. and J.W. conducted the field experiment and collected the data; F.H. and Z.M. performed the statistical analyses and modelling, and prepared the manuscript. All authors revised the manuscript and contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.ksn02v752> (Ma et al., 2021).

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REFERENCES

- Brown, B. L., Downing, A. L., & Leibold, M. A. (2016). Compensatory dynamics stabilize aggregate community properties in response to multiple types of perturbations. *Ecology*, *97*, 2021–2033. <https://doi.org/10.1890/15-1951.1>
- Campbell, V., Murphy, G., & Romanuk, T. N. (2011). Experimental design and the outcome and interpretation of diversity-stability relations. *Oikos*, *120*, 399–408. <https://doi.org/10.1111/j.1600-0706.2010.18768.x>
- Chen, H., Zhu, Q., Peng, C. H., Wu, N., Wang, Y. F., Fang, X. Q., Gao, Y. H., Zhu, D., Yang, G., Tian, J. Q., Kang, X. M., Piao, S. L., Ouyang, H., Xiang, W. H., Luo, Z. B., Jiang, H., Song, X. Z., Zhang, Y., Yu, G. R., ... Wu, J. H. (2013). The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biology*, *19*, 2940–2955. <https://doi.org/10.1111/gcb.12277>
- Chi, Y. G., Xu, Z. W., Zhou, L., Yang, Q. P., Zheng, S. X., & Li, S. P. (2019). Differential roles of species richness versus species asynchrony in regulating community stability along a precipitation gradient. *Ecology and Evolution*, *9*, 14244–14252. <https://doi.org/10.1002/ece3.5857>
- Chinese Soil Taxonomy Research Group. (1995). *Chinese soil taxonomy* (pp. 58–147). Science.
- Chomel, M., Guittonny-Larchevêque, M., Fernandez, C., Gallet, C., DesRochers, A., Paré, D., Jackson, B. G., & Baldy, V. (2016). Plant secondary metabolites: A key driver of litter decomposition and soil nutrient cycling. *Journal of Ecology*, *104*(6), 1527–1541. <https://doi.org/10.1111/1365-2745.12644>
- Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., ... Manning, P. (2018). Multiple facets of biodiversity drive the diversity-stability relationship. *Nature Ecology & Evolution*, *2*, 1579–1587. <https://doi.org/10.1038/s41559-018-0647-7>
- Dong, Q. M., Zhao, X. Q., Wu, G. L., Shi, J. J., & Ren, G. H. (2013). A review of formation mechanism and restoration measures of 'black-soil-type' degraded grassland in the Qinghai-Tibetan Plateau. *Environmental Earth Sciences*, *70*, 2359–2370. <https://doi.org/10.1007/s12665-013-2338-7>
- Facelli, J. M., & Pickett, S. T. A. (1991). Plant litter: Its dynamics and effects on plant community structure. *Botanical Review*, *57*, 1–32. <https://doi.org/10.1007/bf02858763>
- Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Wayne Polley, H., Reich, P. B., & van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist*, *183*, 1–12. <https://doi.org/10.1086/673915>
- Hallett, L. M., Hsu, J. S., Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gherardi, L. A., Gross, K. L., Hobbs, R. J., Turnbull, L., & Suding, K. N. (2014). Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology*, *95*, 1693–1700. <https://doi.org/10.1890/13-0895.1>
- Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., Lind, E. M., MacDougall, A. S., Stevens, C. J., Bakker, J. D., Buckley, Y. M., Chu, C., Collins, S. L., Daleo, P., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., ... Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, *508*, 521–525. <https://doi.org/10.1038/nature13014>
- Holdredge, C., & Bertness, M. D. (2011). Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions*, *13*, 423–433. <https://doi.org/10.1007/s10530-010-9836-2>
- Hong, J. T., Lu, X. Y., Ma, X. X., & Wang, X. D. (2021). Five-year study on the effects of warming and plant litter quality on litter decomposition rate in a Tibetan alpine grassland. *Science of The Total Environment*, *750*. <https://doi.org/10.1016/j.scitotenv.2020.142306>
- Hou, D. J., He, W. M., Liu, C. C., Qiao, X. G., & Guo, K. (2019). Litter accumulation alters the abiotic environment and drives community successional changes in two fenced grasslands in Inner Mongolia. *Ecology and Evolution*, *9*, 9214–9224. <https://doi.org/10.1002/ece3.5469>
- Hovstad, K. A., & Mikael, O. (2008). Physical and chemical effects of litter on plant establishment in semi-natural grasslands. *Plant Ecology*, *196*, 251–260. <https://doi.org/10.1007/s11258-007-9349-y>
- Huang, M. J., Liu, X., & Zhou, S. R. (2020). Asynchrony among species and functional groups and temporal stability under perturbations: Patterns and consequences. *Journal of Ecology*, *108*, 2038–2046. <https://doi.org/10.1111/1365-2745.13418>
- Isbell, F., Polley, H. W., & Wilsey, B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: Patterns and processes. *Ecology Letters*, *12*, 443–451. <https://doi.org/10.1111/j.1461-0248.2009.01299.x>
- Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, *317*, 58–62. <https://doi.org/10.1126/science.1133258>
- Kohli, M., Borer, E. T., Kinkel, L., & Seabloom, E. W. (2019). Stability of grassland production is robust to changes in the consumer food web. *Ecology Letters*, *202*, 707–716. <https://doi.org/10.1111/ele.13232>
- Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. <https://doi.org/10.1111/2041-210X.12512>
- 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 Ecology*, *2163*, 357–370. <https://doi.org/10.1007/s11258-014-0436-6>

- Li, Y., Dong, S. K., Gao, Q. Z., Zhang, Y., Liu, S. L., Ganjurjav, H., Hu, G. Z., Wang, X. X., Yan, Y. L., Wu, H. B., Gao, X. X., Li, S., & Zhang, J. (2020). Rotational grazing promotes grassland aboveground plant biomass and its temporal stability under changing weather conditions on the Qinghai-Tibetan Plateau. *Land Degradation and Development*, 31, 2662–2671. <https://doi.org/10.1002/ldr.3596>
- Liu, J. S., Cui, Y., Li, X. F., Wilsey, B. J., Isbell, F., Wan, S. Q., Wang, L., & Wang, D. L. (2018). Reversal of nitrogen-induced species diversity declines mediated by change in dominant grass and litter. *Oecologia*, 188, 921–929. <https://doi.org/10.1007/s00442-018-4252-x>
- Loreau, M., & de Mazancourt, C. (2008). Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172, 48–66. <https://doi.org/10.1086/589746>
- Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115. <https://doi.org/10.1111/ele.12073>
- Loydi, A., Donath, T. W., Eckstein, R. L., & Otte, A. (2015). Non-native species litter reduces germination and growth of resident forbs and grasses: Allelopathic, osmotic or mechanical effects? *Biological Invasions*, 17, 581–595. <https://doi.org/10.1007/s10530-014-0750-x>
- 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. *Journal of Ecology*, 101, 454–464. <https://doi.org/10.1111/1365-2745.12033>
- Ma, F. F., Zhang, F. Y., Quan, Q., Song, B., Wang, J. S., Zhou, Q. P., & Niu, S. L. (2020). Common species stability and species asynchrony rather than richness determine ecosystem stability under nitrogen enrichment. *Ecosystems*, 24(3), 686–698. <https://doi.org/10.1007/s10021-020-00543-2>
- Ma, Z. Y., Liu, H. Y., Mi, Z. R., Zhang, Z. H., Wang, Y. H., Xu, W., Jiang, L., & He, J. S. (2017). Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications*, 8, 15378. <https://doi.org/10.1038/ncomms15378>
- Ma, Z., Zeng, Y., Wu, J., Zhou, Q., & Hou, F. (2021). Data from: Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.ksn02v752>
- 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. *Applied Vegetation Science*, 20, 28–39. <https://doi.org/10.1111/avsc.12291>
- Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E. A., Ganesanandamoorthy, P., Garnier, A., Griffiths, J. I., Greene, S., Horgan, K., Massie, T. M., Mächler, E., Palamara, G. M., Seymour, M., & Petchey, O. L. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112. <https://doi.org/10.1038/s41586-018-0627-8>
- Phillips, C. L., Murphey, V., Lajtha, K., & Gregg, J. W. (2016). Asymmetric and symmetric warming increases turnover of litter and unprotected soil C in grassland mesocosms. *Biogeochemistry*, 128, 217–231. <https://doi.org/10.1007/s10533-016-0204-x>
- Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326. <https://doi.org/10.1038/307321a0>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- 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>
- Sasaki, T., & Lauenroth, W. K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166, 761–768. <https://doi.org/10.1007/s00442-011-1916-1>
- Sasaki, T., Lu, X. M., Hirota, M., & Bai, Y. F. (2019). Species asynchrony and response diversity determine multifunctional stability of natural grasslands. *Journal of Ecology*, 107, 1862–1875. <https://doi.org/10.1111/1365-2745.13151>
- Shi, G. X., Wang, W. Y., Jiang, S. J., Cheng, G., Yao, B. Q., Feng, H. Y., & Zhou, H. K. (2018). Effects of the spreading of *Ligularia virgaurea* on soil physicochemical property and microbial functional diversity. *Chinese Journal of Plant Ecology*, 42, 126–132. <https://doi.org/10.17521/cjpe.2017.0111>
- 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>
- Smith, B., & Wilson, J. B. (1996). A consumer's guide to evenness indices. *Oikos*, 76, 70–82. <https://doi.org/10.2307/3545749>
- Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632. <https://doi.org/10.1038/nature04742>
- Venail, P., Gross, K., Oakley, T. H., Narwani, A., Allan, E., Flombaum, P., Isbell, F., Joshi, J., Reich, P. B., Tilman, D., van Ruijven, J., Cardinale, B. J., & Fox, C. (2015). Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Functional Ecology*, 29, 615–626. <https://doi.org/10.1111/1365-2435.12432>
- 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 and Soil*, 331, 377–389. <https://doi.org/10.1007/s11104-009-0259-8>
- Wu, Q., Ren, H. Y., Wang, Z. W., Li, Z. G., Liu, Y. H., Wang, Z., Li, Y. H., Zhang, R. Y., Zhao, M. L., Chang, S. X., & Han, G. D. (2020). Additive negative effects of decadal warming and nitrogen addition on grassland community stability. *Journal of Ecology*, 108, 1442–1452. <https://doi.org/10.1111/1365-2745.13363>
- 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>
- Xie, T. P., Zhang, G. F., Zhao, Z. G., Du, G. Z., & He, G. Y. (2014). Intraspecific competition and light effect on reproduction of *Ligularia virgaurea*, an invasive native alpine grassland clonal herb. *Ecology and Evolution*, 4, 827–835. <https://doi.org/10.1002/ece3.975>
- Xiong, S. J., & Nilsson, C. (1999). The effects of plant litter on vegetation: A meta-analysis. *Journal of Plant Ecology*, 87, 984–994. <https://doi.org/10.1046/j.1365-2745.1999.00414.x>
- Xu, Z. W., Ren, H. Y., Li, M. H., Van Ruijven, J., Han, X. G., Wan, S. Q., Li, H., Yu, Q. I., Jiang, Y., & Jiang, L. (2015). Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *Journal of Ecology*, 103, 1308–1316. <https://doi.org/10.1111/1365-2745.12441>
- Yang, H. J., Jiang, L., Li, L. H., Li, A., Wu, M. Y., & Wan, S. Q. (2012). Diversity-dependent stability under mowing and nutrient addition: Evidence from a 7-year grassland experiment. *Ecology Letters*, 15, 619–626. <https://doi.org/10.1111/j.1461-0248.2012.01778.x>
- Yang, Z. L., Zhang, Q., Su, F. L., Zhang, C. H., Pu, Z. C., Xia, J. Y., Wan, S. Q., & Jiang, L. (2017). Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology*, 23, 154–163. <https://doi.org/10.1111/gcb.13391>
- Zhang, A., Wang, D., & Wan, S. Q. (2019). Litter addition decreases plant diversity by suppressing seeding in a semiarid grassland, Northern China. *Ecology and Evolution*, 9, 9907–9915. <https://doi.org/10.1002/ece3.5532>

- Zhou, B. R., Li, S., Li, F., Dong, S. K., Ma, F. L., Zhu, S. C., Zhou, H. K., & Stufkens, P. (2019). Plant functional groups asynchrony keep the community biomass stability along with the climate change—a 20-year experimental observation of alpine meadow in eastern Qinghai-Tibet Plateau. *Agriculture, Ecosystems & Environment*, 282, 49–57. <https://doi.org/10.1016/j.agee.2019.06.002>
- Zhou, M., Yang, Q., Zhang, H. J., Yao, X. D., Zeng, W. J., & Wang, W. (2020). Plant community temporal stability in response to nitrogen addition among different degraded grasslands. *Science of The Total Environment*, 729, <https://doi.org/10.1016/j.scitotenv.2020.138886>
- Zou, J. R., Luo, C. Y., Xu, X. L., Zhao, N., Zhao, L., & Zhao, X. Q. (2016). Relationship of plant diversity with litter and soil available nitrogen in an alpine meadow under a 9-year grazing exclusion. *Ecological Research*, 31, 841–851. <https://doi.org/10.1007/s11284-016-1394-3>

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