

RESEARCH ARTICLE

Decoupled responses of above- and below-ground stability of productivity to nitrogen addition at the local and larger spatial scale

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Abstract

Temporal stability of net primary productivity (NPP) is important for predicting the reliable provisioning of ecosystem services under global changes. Although nitrogen (N) addition is known to affect the temporal stability of aboveground net primary productivity (ANPP), it is unclear how it impacts that of belowground net primary productivity (BNPP) and NPP, and whether such effects are scale dependent. Here, using experimental N addition in a grassland, we found different responses of ANPP and BNPP stability to N addition at the local scale and that these responses propagated to the larger spatial scale. That is, N addition significantly decreased the stability of ANPP but did not affect the stability of BNPP and NPP at the two scales investigated. Additionally, spatial asynchrony of both ANPP and BNPP among communities provided greater stability at the larger scale and was not affected by N addition. Our findings challenge the traditional view that N addition would reduce ecosystem stability based on results from aboveground dynamics, thus highlighting the importance of viewing ecosystem stability from a whole system perspective.

KEYWORDS

metacommunity, multiple spatial scales, nitrogen deposition, semi-arid grassland, spatial asynchrony, temporal stability

1 | INTRODUCTION

Global nitrogen (N) availability is rapidly increasing due to the accelerating industrialization and N fertilizer utilization (Galloway et al., 2008), with consequences for ecosystem functioning, including productivity and its stability (Cardinale et al., 2012). Here, stability is defined as the invariability of net primary productivity (NPP) over time and measured as the ratio of the temporal mean of NPP to its standard deviation (Donohue et al., 2016; Tilman, 1999). NPP can be measured at different hierarchical levels: populations of different species, local communities, and metacommunities (Wilcox et al., 2017a); and can be partitioned into aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP). Although

N addition usually increases ANPP (Bai et al., 2010; Isbell et al., 2013; Tilman, 1987), the magnitude of increase in temporal variability may be greater and thereby reduce temporal stability (Rosenzweig, 1971; Tilman, 1996; but see Grman et al., 2010; Yang et al., 2011). However, most studies to date focused primarily on the temporal stability of ANPP at relatively small spatial scales (i.e., within single local communities) (Hector et al., 2010; Tilman, 1996). These studies found that N addition usually reduces the local stability of ANPP (Hautier et al., 2014; Xu et al., 2015; Zhang et al., 2016). Whether N addition affects the stability of BNPP and NPP and whether these effects propagate to larger spatial scales remain unknown.

A recent hierarchical framework makes it possible to quantify the processes driving ecosystem stability at multiple spatial scales

(Wang et al., 2019b; Wang & Loreau, 2014, 2016). According to this framework, higher temporal stability at the local scale (alpha stability) may result from two processes: higher temporal stability of all species (species stability) (Zhang et al., 2016) and higher asynchronous dynamics among species (species asynchrony) (Loreau et al., 2003). Higher temporal stability at the larger spatial scale (gamma stability) may result from higher alpha stability and higher asynchronous dynamics among local communities (spatial asynchrony) (Liang et al., 2021; Wang & Loreau, 2014, 2016; Wilcox et al., 2017a).

Using this framework, recent studies found that the negative impact of N addition on alpha stability of ANPP may propagate to larger spatial scales (Hautier et al., 2020; Zhang et al., 2019). These studies show that fertilization reduces alpha stability of ANPP by decreasing species asynchrony (Hautier et al., 2020; Valencia et al., 2020; Xu et al., 2015; Zhang et al., 2019). The reduction of alpha stability of ANPP directly propagates to decrease gamma stability of ANPP (Hautier et al., 2020; Zhang et al., 2019). Additionally, N addition may reduce gamma stability of ANPP by reducing spatial asynchrony (Hautier et al., 2020; but see Zhang et al., 2019). Furthermore, these studies have shown that the impact of N addition on stability at multiple spatial scale may depend on biodiversity. That is, the reduction of local plant diversity (alpha diversity) or the reduction of variation in species composition among communities (beta diversity) in response to N addition lead to a reduction in species asynchrony or spatial asynchrony and to a decline of ANPP stability at the local and larger spatial scales (Hautier et al., 2014, 2020).

Although this framework considers dynamics of ANPP, processes should apply similarly to BNPP. However, limitations of sampling species-level BNPP are constraining the applicability of such framework at the local scale (i.e., species stability and species asynchrony require species-level productivity data), but not at the larger spatial scale at which community-level BNPP data can be collected. This allows to assess the contribution of alpha stability and spatial asynchrony of both ANPP and BNPP to stabilize productivity at the larger spatial scale.

BNPP usually contributes more to NPP than ANPP in grasslands (Gao et al., 2008; Gherardia & Sala, 2020; Peek, 2007). Hence, it is important to understand the temporal stability BNPP and how it contributes to the stability of NPP. Plants may allocate relatively more biomass aboveground with increasing N availability (Gao et al., 2011; Peng et al., 2017; Wang et al., 2019a), resulting in larger responses in above- than belowground. Empirical evidence that BNPP is less sensitive than ANPP to increased precipitation (Wilcox et al., 2017b), suggests that BNPP may be more conservative than ANPP in its responses to environment fluctuations. Moreover, Wang et al. (2019a) reported that the response pattern of NPP to N addition corresponded more closely to ANPP than to BNPP in a temperate steppe. Whether the temporal stability of ANPP, BNPP, and NPP at multiple spatial scales show similar responses to N addition remains unclear.

To investigate the responses of temporal stability of ANPP, BNPP, and NPP to N addition and their associated mechanisms at multiple spatial scales, we carried out a field experiment with six N

addition rates (from 0 to 50 g N m⁻² yr⁻¹) in a temperate steppe. We hypothesized that (1) N addition would reduce the temporal stability of ANPP but not BNPP at both local and larger spatial scales, and (2) asynchronous dynamics among species and among communities at local and larger spatial scales would regulate stability. In summary, we aimed to examine the difference of ANPP, BNPP, and NPP stability in their responses to N addition and to understand the factors driving the temporal stability of productivity at multiple spatial scales.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was carried out in a temperate meadow steppe (50°10'46.1"N, 119°22'56.4"E) near the Erguna Forest-Steppe Ecotone Research Station, Inner Mongolia, China. The grassland had been used for forage harvest before 2013. The long-term mean annual precipitation of the site is 363 mm, and the mean annual temperature is -2.45°C, ranging from -28.0°C in January to 19.1°C in July (1957–2016). The soil is classified as chernozem according to the Food and Agricultural Organization of the United Nations classification. Six C₃ perennial species dominated the community, *Leymus chinensis*, *Stipa baicalensis*, *Artemisia frigida*, *Thermopsis lanceolata*, *Cymbaria dahurica*, and *Carex duriuscula*, which together make up >90% of the total aboveground biomass.

2.2 | Experimental design

The N addition experiment was carried out from 2014 to 2020, following a randomized block design (Yang et al., 2019). There were six rates of N addition (i.e., 0, 2, 5, 10, 20, and 50 g N m⁻² yr⁻¹) crossed with two types of N compounds (NH₄NO₃ and CO(NH₂)₂), with eight replicates for each treatment. We selected those two types of N compounds to compare the different effects of inorganic and organic N types. The annual ambient atmosphere N deposition was <2 g N m⁻² yr⁻¹ in this region (Yu et al., 2019). No fertilizer was received prior to this experiment. Thus, the lowest addition level (2 g N m⁻² yr⁻¹) in this study was close to the ambient N deposition. The use of higher N addition rates served as a proxy for N fertilization activities and/or long-term extreme N addition in temperate grasslands (Zhang et al., 2017). The area of each plot was 10 m × 10 m. Within each block, all the treatments were randomized to plots, which were separated by 1 m walkways.

Nitrogen fertilizers were added annually since 2014, in late May. Fertilizers were mixed with sand (because of the low amount of added fertilizer at low addition rates) and broadcast uniformly by hand. Sand was sieved through less than 2 mm in size, washed in water, and then dried at 250°C for 1 h. To avoid potentially confounding effects, all plots received the same amount of sand (0.5 kg per plot).

2.3 | Field sampling and measurement

ANPP was estimated from the peak aboveground biomass at mid-August (Bai et al., 2004). Aboveground biomass was annually sampled from 2014 to 2020, by clipping all vascular plants at the soil surface in a 1 m × 1 m quadrat, which was randomly placed in each plot without spatial overlap of quadrats among years and at least 0.5 m inside the border of each plot to avoid edge effects. This was used to represent the community at local spatial scale. All plants were sorted to species, oven-dried at 65°C for 48h, and then weighed.

BNPP was estimated using the ingrowth core method (Steingrobe et al., 2001). At the beginning of the growing season in each year, three holes of 7 cm diameter and 50 cm depth were drilled into the soil vertically in each plot, with a distance of at least 1 m between each hole. The collected soil was sieved (mesh size 2 mm) to sort out rocks, organic debris and other non-root material from roots. After that, polyester mesh bags (mesh size 1 mm) were inserted into the holes with a PVC tube with diameter of 7 cm and length of 70 cm. The PVC tube was pulled out a few centimeters and root-free sieved soil was filled in and compressed to a density comparable with the bulk soil. This procedure was repeated until the mesh bag was completely filled. The BNPP sampling started from the third year of N addition. In mid-September of each year from 2016 to 2020, the polyester mesh bags were carefully pulled out of the holes and the soil was sieved as described above to sort out roots from non-root material and minimize sampling uncertainty. All root samples were washed before being oven-dried at 75°C for 48 h. BNPP was estimated based on the average of root biomass of three ingrowth cores from each plot. NPP for each plot was calculated as the sum of ANPP and BNPP.

2.4 | Diversity, stability and asynchrony

For consistency, diversity, stability, and asynchrony were calculated with the data over the five years of the experiment (2016–2020). Alpha diversity indices (species richness and Simpson) were measured for each community. Species richness is the number of plant species recorded in each plot. Simpson is the inverse of the weighted average of Simpson index:

$$\alpha_{\text{simp}} = 1/\sum_{l=1}^8 \omega_l \phi_l \quad (1)$$

where $\phi_l = \sum_i^S p_{il}^2$, p_{il} represents the relative biomass of species i in the local community l and S is the number of species in the local community l , ω_l is the ratio of total biomass of the local community l to that of the aggregate community (i.e., aggregation of the eight quadrats) at the large scale (Wang & Loreau, 2016). Because Simpson index and species richness exhibited similar trends along the N addition gradient (Figure S1), and the strong correlation between them ($r = .91$ [95%] confidence intervals [CIs] = 0.69–0.98), we used Simpson index as alpha diversity

in our models. Following theoretical models (Wang & Loreau, 2014, 2016), the gamma diversity was defined as:

$$\gamma_{\text{simp}} = 1/\sum_i p_i^2 \quad (2)$$

where $p_i = \sum_{l=1}^8 \omega_l p_{il}$ denotes the relative biomass of species i in the aggregate community at the large scale. Beta diversity was defined as the multiplicative partitioning of abundance-based gamma diversity:

$$\beta_{\text{simp}} = \gamma_{\text{simp}}/\alpha_{\text{simp}} \quad (3)$$

We used the R functions “specnumber” and “diversity” from the vegan package to calculate species richness and Simpson indices, respectively.

The temporal stability of productivity (ANPP, BNPP, or NPP) was calculated as the ratio of temporal mean to standard deviation over 5 years of the experiment (2016–2020) (Wang & Loreau, 2014; Zhang et al., 2019). Species stability was calculated as the weighted average of local species stability across all species and the eight plots per treatment. Alpha stability was calculated as the weighted average of community stability across eight plots per treatment, and Gamma stability was calculated as the temporal stability of the total biomass of eight plots under the same treatment. They were calculated as:

$$\text{Species stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_{i,k} \sqrt{\nu_{ii,kk}}} \quad (4)$$

$$\text{Alpha stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_k \sqrt{\sum_{i,j} \nu_{ij,kk}}} \quad (5)$$

$$\text{Gamma stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sqrt{\sum_{i,j,k,l} \nu_{ij,kl}}} \quad (6)$$

We defined species asynchrony as the variance-weighted correlation across species, and spatial synchrony as the variance-weighted correlation across communities:

$$\text{Species asynchrony} = \frac{\sum_{i,k} \sqrt{\nu_{ii,kk}}}{\sum_k \sqrt{\sum_{i,j} \nu_{ij,kk}}} \quad (7)$$

$$\text{Spatial asynchrony} = \frac{\sum_k \sqrt{\sum_{i,j} \nu_{ij,kk}}}{\sqrt{\sum_{i,j,k,l} \nu_{ij,kl}}} \quad (8)$$

where $\mu_{i,k}$ denotes the mean of species i in local community k , and $\nu_{ij,kl}$ denotes the covariance between species i in local community k and species j in local community l .

For ANPP, we calculated the temporal variability and synchrony as defined by Equations (4)–(8). We used the R function “var.partition,” which was developed by Wang et al. (2019b) to calculate asynchrony and stability across spatial scales for ANPP. The R function

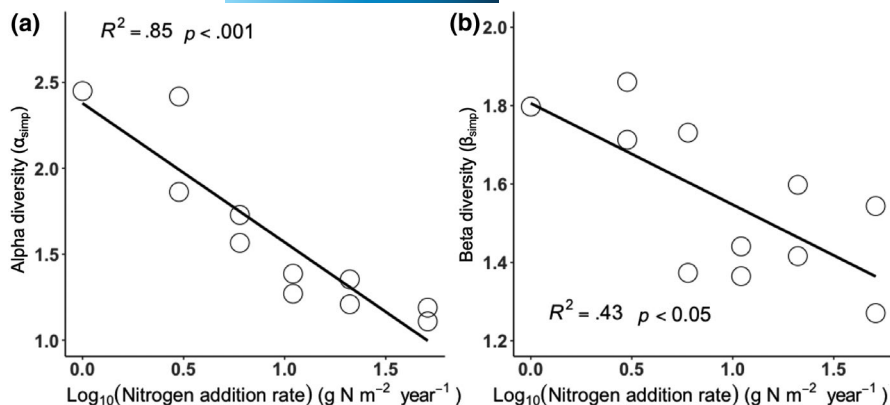


FIGURE 1 Changes of alpha diversity and beta diversity with increasing N addition rates. (a) alpha diversity (α_{simp} , the average Simpson index of a 1-m² plot in the same treatment across 2016–2020) (b) beta diversity ($\beta_{\text{simp}} = \gamma_{\text{simp}} / \alpha_{\text{simp}}$). The two points at each N addition rate is the value of each N compound addition. Solid lines are corresponding regression lines

“var.partition” takes the raw data of time series of species biomass at each plot as input and returns variability and synchrony metrics at different hierarchical levels. Because we had no species-level BNPP, the calculation of stability of both BNPP and NPP were limited to Equations (4) and (7). We developed the new R function “var.partition.new” based on R function “var.partition” (Appendix S1) to calculate asynchrony and stability across spatial scales for BNPP and NPP, respectively, which takes the raw data of time series of community data at each plot as input and returns variability and synchrony metrics.

2.5 | Statistical analysis

Stability and asynchrony values were logarithm transformed to meet the normality requirement for data analyses. To assess the effects of N addition rate and N addition type on plant diversity (alpha and beta diversity) and the stability (alpha and gamma stability) of ANPP, BNPP, and NPP, we used analysis of variance with N addition rate as the continuous variable, and N type as the categorical variable (Table S1). As there was no interaction between N addition rate and type in affecting diversity and stability (all $p > .05$; Table S1), data of the two N compound types were combined for further analyses. To examine how diversity and stability variables were related with N addition rate, a linear regression model was performed. We used Duncan’s test to compare the slope of productivity with precipitation among the six N rates.

To identify the significant pathways through which N addition influenced the hierarchical ANPP, BNPP, and NPP stability, we used structural equation modeling (SEM) using the R package “piecewiseSEM” (Lefcheck, 2016), mixed-effect models was used in SEM with function lme () in nlme package. We conducted hypothetical causal models including all possible pathways (Figure S2). Prior to the analysis, variance inflation factors were calculated to assess the multi-collinearity of predictor variables. Then, we simplified the initial model by eliminating nonsignificant pathways and state variables based on regression weight estimates. Overall fitness of the piecewise SEM was evaluated using Shipley’s test of d-separation, Fisher’s C statistic and AIC to ensure that no potential pathways between variables (log-transformed) were lost. We considered the collection

of hypothesized relationships being consistent with the data when P for the Fisher’s C test was greater than the threshold of significance (i.e., $p > .05$). All analyses were conducted using R version 4.0.2 (R Development Core Team, 2020).

3 | RESULTS

Alpha diversity ($p < .001$; slope = -0.21 ± 0.03 ; Figure 1a), beta diversity ($p = .017$; slope = -0.26 ± 0.09 ; Figure 1b), and alpha ($p = .009$; slope = -0.53 ± 0.15 ; Figure 2a) and gamma stability of ANPP ($p = .017$; slope = -0.61 ± 0.19 ; Figure 2a) significantly decreased with increasing N addition rates. In contrast, increasing N addition rates had no detectable impact on either alpha or gamma stability of BNPP (both $p > .05$; Figure 2b) and NPP (both $p > .05$; Figure 2c), as well as spatial asynchrony of ANPP, BNPP, and NPP (all $p > .05$; Figure 3).

The SEM results showed that the negative impact of N addition on alpha and gamma stability was partly mediated through the decline in local species diversity. The decline in alpha diversity simultaneously reduced species asynchrony and increased species stability of ANPP. Because the negative impact through species asynchrony was stronger than the positive impact on species stability, this resulted in an overall negative effect of N addition on alpha and gamma stability (Figure 4). Nitrogen addition also reduced beta diversity, but this did not affect spatial asynchrony of ANPP. Combining all these pathways, N addition increased species stability of ANPP (total effect size (TES) = 0.605), but decreased alpha (TES = -0.608) and gamma (TES = -0.547) stability of ANPP. In contrast, N addition had no impact on spatial asynchrony, and alpha and gamma stability of either BNPP or NPP (Figure 4). The response pattern of NPP stability corresponded more closely to BNPP stability ($p = 0.067$; Figure 4) than to ANPP stability.

4 | DISCUSSION

By simultaneously examining the responses of temporal stability of ANPP, BNPP, and NPP to N addition, we found that ANPP and BNPP stability responses were decoupled. Nitrogen addition reduced

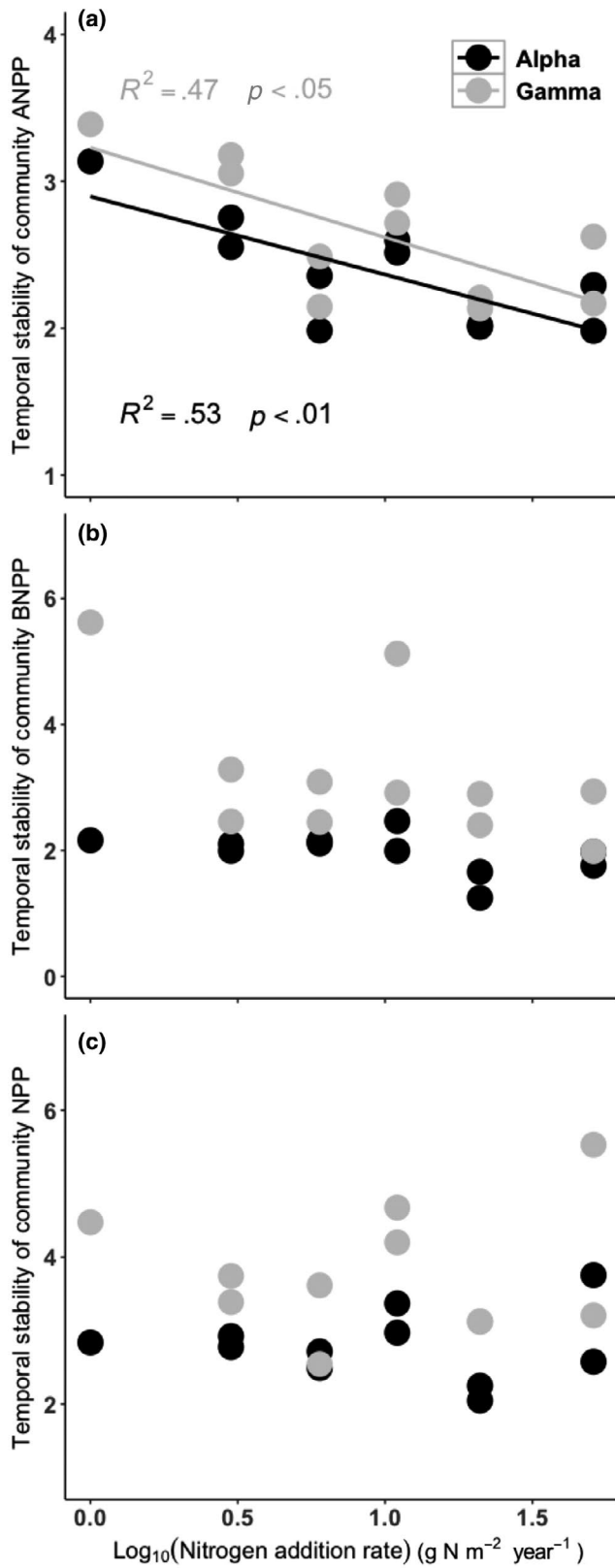


FIGURE 2 Changes of the temporal stability of aboveground net primary productivity (ANPP, a), belowground net primary productivity (BNPP, b), and total net primary productivity (NPP, c) with increasing N addition rates at multiple scales. The two points at each N addition rate is the value of each N compound addition

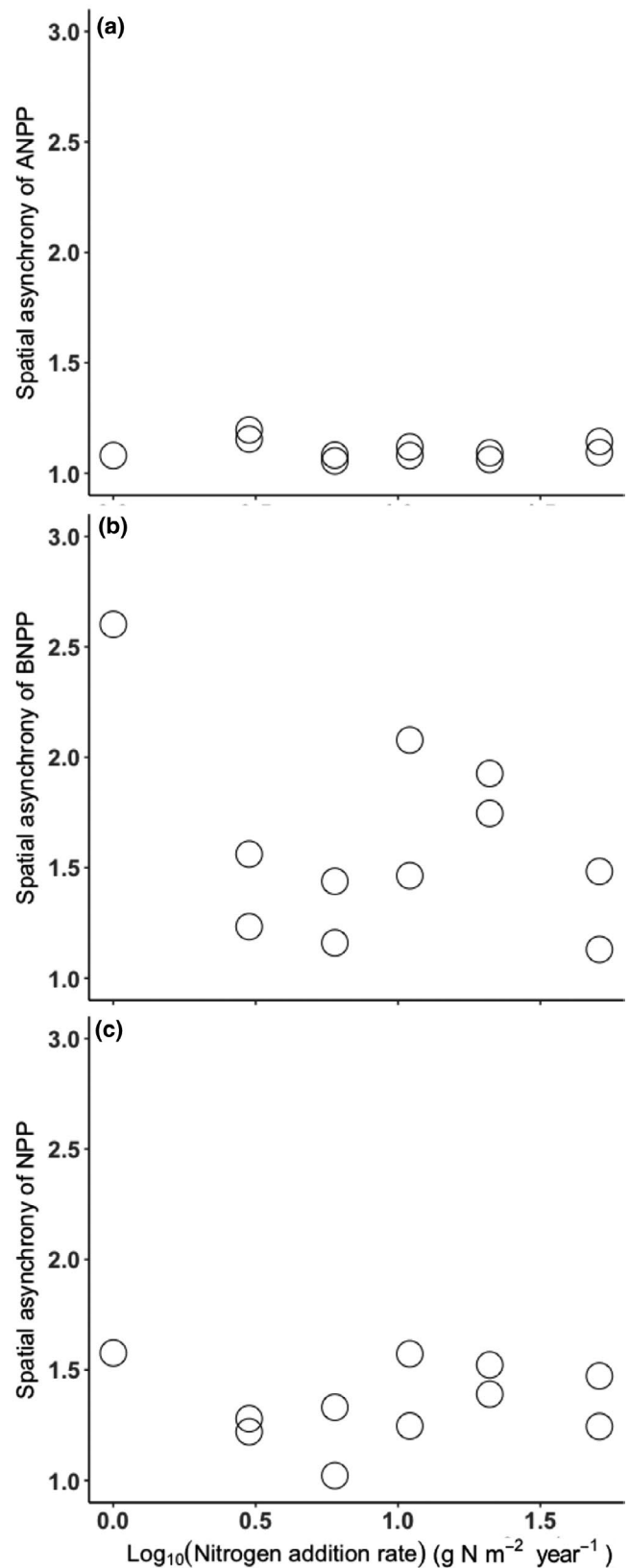


FIGURE 3 Changes of spatial asynchrony of aboveground net primary productivity (ANPP, a), belowground net primary productivity (BNPP, b), and total net primary productivity (NPP, c) with increasing N addition rates. The two points at each N addition rate is the value of each N compound addition

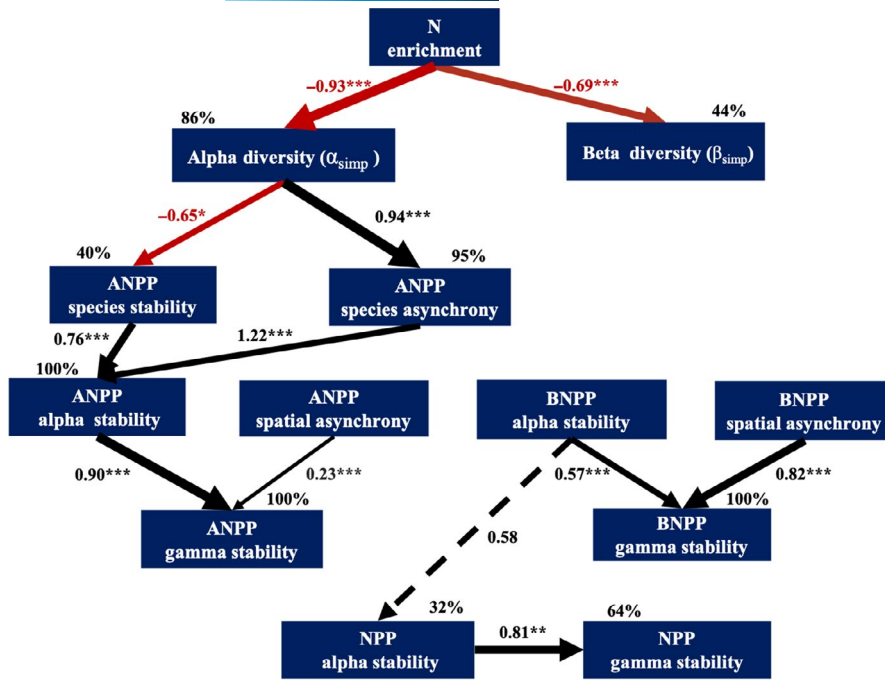


FIGURE 4 Structural equation modelling (SEM) showing the direct and indirect effects of N enrichment on grassland biodiversity and ecosystem stability at multiple scales (AIC = 208.712, Fisher's C = 130.712, p -value = .237). Solid black and red arrows represent significant positive and negative coefficient, respectively (asterisks denote significant levels: *, $p \leq 0.05$; **, $p \leq 0.01$; and ***, $p \leq 0.001$, respectively), and dashed black arrow represents marginal significant coefficient ($0.05 < p < 0.1$). Percentages next to endogenous variables indicate the variance explained by the model (R^2) [Colour figure can be viewed at wileyonlinelibrary.com]

stability of ANPP at the local and larger spatial scale but did not affect stability of either BNPP or NPP at the two scales investigated. These results imply that belowground stability response cannot be predicted based on ANPP responses and that NPP responses depend more on BNPP than ANPP responses to N enrichment. Our findings challenge the perspective that N addition would destabilize primary productivity based on results from aboveground (Hautier et al., 2014; Zhang et al., 2016) and thus highlight the importance of a whole ecosystem perspective (Hui & Jackson, 2006).

The negative effects of N addition on stability of ANPP propagated from local to larger spatial scales, as alpha stability was the major driver of gamma stability (Figure 4). The N-induced reduction in alpha stability is consistent with results from other studies (Hautier et al., 2014; Zhang et al., 2016). Our SEM results further showed that the losses of alpha diversity following N addition reduced local scale stability of ANPP by reducing asynchronous dynamics among species and increasing species stability of ANPP, but the role of species asynchrony was stronger than that of species stability, resulting in an overall negative impact of N addition on local stability (Figure 4). These results highlight the importance of plant diversity and asynchronous dynamics among species in driving functional stability (Wang et al., 2021; Xu et al., 2015, 2021), which may help to stabilize ecosystem functioning at larger spatial scales under N addition (Zhang et al., 2019). Although beta diversity decreased with N addition but did not contribute to gamma stability in our ecosystem. Similarly, plant beta diversity decreased linearly with N addition in a temperate steppe due to increased directional environmental filtering (Liu et al., 2021). The lack of contribution of beta diversity to spatial asynchrony contrasts with theoretical and experimental evidence (Liang et al., 2021; Wang & Loreau, 2014, 2016; Wang et al., 2021). For example, Wang et al. (2021) reported the general positive contribution of beta diversity to gamma stability using

a meta-analysis of 39 grassland biodiversity experiments. However, this result is in line with observational and experimental studies showing that beta diversity did not contribute to gamma stability (Wilcox et al., 2017a; Zhang et al., 2019).

Contrary to the theoretical prediction that spatial asynchrony would be positively correlated with beta diversity (Wang & Loreau, 2016), we found that beta diversity was a poor predictor for spatial asynchrony (Figure 4). Likewise, Wilcox et al. (2017a) found no association between beta diversity and spatial asynchrony in a global-scale analysis with 62 herbaceous communities, highlighting the complexity of the relationship between beta diversity and spatial asynchrony in natural ecosystems. Hautier et al. (2020) found that fertilization reduced the strength of the relationship between beta diversity and spatial asynchrony. Both the lack of the response of spatial asynchrony to N amendment and its weak relationship with beta diversity may be driven by strong community-level responses to temporal variation in precipitation and species-level demographic stochasticity (Zhang et al., 2019). In our study, both ANPP and its responses to N addition were highly sensitive to the interannual variation of precipitation (Figure S3). These results suggest that the spatial insurance effect played an important role in driving ANPP stability at the larger spatial scale and that such effect would not be related with beta diversity.

Consistent with theoretical predictions (Wang & Loreau, 2014, 2016) and empirical evidence (Wang et al., 2021; Wilcox et al., 2017a; Zhang et al., 2019), we found that asynchronous dynamics among local communities contribute to stabilize primary productivity at the larger spatial scale, leading to higher gamma stability compared with alpha stability (Figures 2a and 4). Small-scale spatial heterogeneity of both soil properties and plant communities widely exist in grasslands (Hodapp et al., 2018; Zhou et al., 2008). The spatial heterogeneity of soil plays an active role in maintaining

plant species richness in a semiarid grassland (Zhou et al., 2008). Furthermore, grasslands with more spatially heterogeneous composition have significantly higher rates of annual turnover (Hodapp et al., 2018), which would contribute to the observed spatial asynchrony.

In contrast to the negative impact of N addition on stability of ANPP, we did not find evidence that N addition affected the stability of either BNPP or NPP. This result challenges prediction of N addition impacts on the stability of primary production, based solely on evidence from aboveground productivity (Hautier et al., 2020; Zhang et al., 2019). Several reasons might explain the lower sensitivity of BNPP stability than ANPP stability to N enrichment and thus the decoupling in their responses. First, biomass allocation is plastic (Hui & Jackson, 2006; Poorter et al., 2012). For instance, more biomass would be allocated to aboveground in the wet years due to the alleviation of water limitation in this semiarid grassland (Wang et al., 2019a). In our study, the ANPP:BNPP ratio changed from 1.1 to 2.1 with increasing N addition rates (Figure S4a). Plants would allocate proportionally more biomass to aboveground for light competition in response to N addition (Gao et al., 2011; Peng et al., 2017; Wang et al., 2019a), which would contribute to the higher sensitivity to interannual variation of precipitation under N addition. Second, soil is a good buffer to protect the belowground system from climatic variations. Results from a global data set showed that BNPP is less affected by climate than ANPP across global grasslands (Sun et al., 2020), which is also supported by our results of the relationship between precipitation and ANPP or BNPP (Figure S3). In our study, the slopes of precipitation–ANPP relationship increased significantly with N addition rates, with larger values than those of precipitation–BNPP relationship, indicating that ANPP was more sensitive to the interannual variations of natural precipitation (Figure S3). The stability of BNPP observed in our study was in line with the results of a transect study along a precipitation gradient across short-grass steppe, mixed-grass prairie, and tallgrass prairie (Luo et al., 2017), which reported that the increases of precipitation had limited effect on BNPP. Third, roots are extremely plastic in architecture, morphology, and the search for nutrient patches (Cahill & McNickle, 2011; Padilla et al., 2013). The dominate species in our ecosystem (*L. chinensis*, *C. duriuscula*, and *A. frigida*) vary greatly in root traits, including root diameter, root branching intensity, first-order root length, and mycorrhizal colonization (Li et al., 2017). The complementarity and trade-offs in resource foraging may facilitate higher stability of BNPP (Kraft et al., 2015; Zemunik et al., 2016). Although f_{BNPP} , the fraction of BNPP to NPP, decreased from 50% to 38% with increasing N rates (Figure S4b), BNPP still plays an important role in stabilizing stability of NPP at higher N addition rates. Together, our results highlight the importance of including the stability of BNPP for understanding the impacts of eutrophication on the stability of primary productivity.

Nitrogen addition decreased stability of ANPP at local and larger spatial scales, but such pattern did not propagate to stability of either BNPP or NPP. We found strong contribution of both alpha stability and spatial asynchrony of BNPP to gamma stability of BNPP,

as well as strong contribution of alpha stability of NPP to gamma stability of NPP, indicating that N addition did not reduce the contribution of alpha stability and spatial asynchrony of BNPP and NPP on gamma stability of BNPP and NPP. These findings further highlight that different mechanisms underlie the maintenance of stability of above- and belowground parts. To our knowledge, this is the first evidence from belowground perspectives showing the role of spatial asynchrony in driving larger spatial scale stability of primary productivity. More asynchronous dynamics among local communities (spatial asynchrony) can lead to higher stability at the larger spatial scale (gamma stability) (Hautier et al., 2020), which reflects the presence of spatial insurance (Loreau et al., 2003; Wang et al., 2019b). Nitrogen addition would lead to more homogeneous community composition in diverse grasslands due to losses of local species richness and reduced species turnover (Roth et al., 2013). Both species richness and species evenness significantly decreased with increasing N addition rate in this ecosystem (Yang et al., 2019). Our results indicated that primary production as the fundamental ecosystem function is more conservative than community composition with respect to the spatial variation in response to N addition. Such conservative characteristics of the spatial variation of primary production is a strong guarantee for the temporal stability of primary productivity at larger spatial scales under the scenario of N addition.

Our short-term results could reflect transient dynamics in response to N addition. Whether these short-term results could be translated to longer temporal scales needs to be tested. However, previous experiments looking at short- and longer-term dynamics in the same experiment suggest that the impacts of N addition on stability are consistent through time (Hautier et al., 2014, 2020). Compared with that of ANPP, the responses of BNPP to N addition are less understood, which retards our understanding of the patterns and drivers of BNPP stability. More works from different grassland ecosystems focusing the long-term responses of BNPP to N addition are critically needed to test the generality of our results.

5 | CONCLUSIONS

At both local and larger spatial scales, N addition decreased the stability of ANPP, but did not affect the stability of both BNPP and NPP in this temperate steppe. The responses of NPP stability to N addition were more similar with that of BNPP stability than ANPP stability, highlighting the importance of belowground production in driving ecosystem level responses. Although recent studies reported the role of spatial asynchrony of ANPP in stabilizing gamma stability of ANPP (Hautier et al., 2020; Zhang et al., 2019), our results highlight the importance of spatial asynchrony from both the belowground and whole ecosystem perspectives.

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AUTHOR CONTRIBUTIONS

XTL and XGH designed the research. GJY and ZJZ collected the data. GJY, XTL, and YH developed research questions and analyzed the data. GJY wrote the draft with contributions and input from all authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: at <https://doi.org/10.5061/dryad.7sqv9s4tn>

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