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RESEARCH ARTICLE

Seasonal nitrogen enrichment alters plant community stability–area relationship through decreased biodiversity, species asynchrony, and population stability

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Abstract

1. Atmospheric nitrogen (N) deposition generally reduces the temporal stability of plant communities (community stability). The positive community stability–area relationship (CSAR) has been reported, but the effects of N deposition on CSAR are unexplored, particularly given that plant N absorption rhythm links with seasonal N enrichment.
2. By conducting an experiment with N additions during autumn, winter, or the growing season in a temperate grassland, we employed the first 6 years' nested plant survey over 0.01–16 m^2 to explore the influence on CSAR.
3. We found that community stability still increased with area under N addition. Seasonal N additions reduced community stability at the local scale (i.e. CSAR intercepts), while N addition in winter or the growing season, but not autumn, reduced CSAR slopes. Moreover, N additions altered the slopes of the relationships between species diversity, species asynchrony, and population stability and area, though the effects varied in magnitude among seasonal inputs. Partial regressions revealed that species diversity exerted stronger pure effects (average about four times in R^2) on stability than area. This benefit was attributed to increased species asynchrony and population stability, even with N-enriched conditions.
4. Our research showed distinct degrees of influence of seasonal N addition on community stability across scales, highlighting that coupling seasonality and spatial scales is warranted for preserving biodiversity to maintain natural ecosystems under N deposition scenarios.

KEYWORDS
biodiversity, community stability, compensatory effect, population stability, seasonal nitrogen deposition, spatial scale, species asynchrony, steppe

1 | INTRODUCTION

The increase in biologically available reactive nitrogen (N) from atmospheric N deposition, resulting from the rapid expansion of industry and agriculture, along with the rising energy production and consumption since the industrial revolution, has become a critical component of ongoing global change (Galloway et al., 2021; Yu et al., 2019). Nitrogen enrichment often promotes aboveground productivity of plant communities (Stevens et al., 2015) and increases species dominance (Bai et al., 2010). However, it also reduces biodiversity (Sanczuk et al., 2024; Stevens et al., 2004) and weakens plant community stability in global grasslands (Hautier et al., 2020; Zhang et al., 2016, 2019).

Most field experimental research on how N deposition affects plant communities relies on N additions during the growing season (spring and summer) (Bai et al., 2010; Bobbink et al., 2010), under the assumption that N deposition primarily occurs during this period (Hertel et al., 2006; Zhang et al., 2012; Zhang, Wang, et al., 2018). However, the substantial increase in reactive N emissions during the non-growing season, driven by the decoupling of human activities from seasonal climatic constraints, has gradually diminished the seasonal differences in N deposition (Cao et al., 2023). Recently, it has been reported that atmospheric N deposition was similar between growing and non-growing seasons, as observed in southern China (Ren et al., 2024). Moreover, experimental studies have shown greater leaching and denitrification under autumn N addition (Cookson et al., 2001) and higher ammonia volatilization under the growing season N addition (Cookson et al., 2001; Zhang et al., 2014), whereas lower N transformation and movement were observed under winter N addition (Hong et al., 2019; Joseph & Henry, 2009). Plants exhibit complex strategies for N uptake, utilization, and storage across seasons to maximize survival and growth, thereby providing crucial ecosystem functions (Hong et al., 2019; Joseph & Henry, 2009; Zhuang et al., 2020). In addition, N deposition occurs not only at the local plot scale but also across broader spatial scales, such as field, basin, region, and ecozone. So far, the effects of seasonal N deposition on the ecosystem functioning of terrestrial natural ecosystems have rarely been reported across multi-spatial scales.

Plant community stability, defined as the inverse of the variability in plant community biomass/cover over time, quantifies the community's capacity to buffer against climatic fluctuations (Pimm, 1984; Tilman et al., 2006). It is a key ecosystem function and tends to increase with area (Wang & Loreau, 2014; Zhang, He, et al., 2018), exhibiting a positive community stability–area relationship (CSAR) (Liang et al., 2025; Wang et al., 2017; Zhang, He, et al., 2018). Theoretically, this positive scaling arises because larger areas typically exhibit reduced stochasticity via spatial averaging and increased environmental heterogeneity, which reduce spatial synchrony among local patches (Wang et al., 2017; Wang & Loreau, 2014). Similarly, biodiversity tends to increase with area, as described by the positive species–area relationship (SAR) (Lu et al., 2024). Biodiversity is widely recognized as a critical driver of community stability across spatial scales. This relationship is underpinned by the spatial insurance hypothesis (Loreau et al., 2003), where asynchronous species responses buffer aggregate community properties against environmental fluctuations. Mechanistically, this stabilization is achieved through two main components: population stability and species asynchrony (Thibaut & Connolly, 2013; Wang et al., 2019). Species asynchrony can be further decomposed into the statistical-averaging effect (SAE), representing the stochastic portfolio effect, and the compensatory effect (CPE) arising from interspecific interactions (Zhao et al., 2022). Together, these processes represent the fundamental biological mechanisms through which biodiversity contributes to community stability across spatial scales, and thus are expected to be closely linked to the emergence of CSAR. While recent advances suggest that the positive scaling of community stability with area is largely attributable to its association with biodiversity (Liang et al., 2025), the synergistic changes in biodiversity and stability with area make it difficult to distinguish the relative roles of area per se versus biodiversity (Zhang, He, et al., 2018). Specifically, it remains unclear whether the increase of stability with sampling area is driven simply by the spatial effect (area per se), the biological effect (biodiversity), or both together (Isbell et al., 2017; Keck et al., 2025). Therefore, teasing apart the relative importance of area per se versus biodiversity is essential for understanding stability mechanisms across scales.

However, N enrichment can reduce plant community stability at both local and larger spatial scales (Zhang et al., 2019). At the local scale, it is well established that N enrichment weakens community stability by reducing biodiversity (Hautier et al., 2015), species asynchrony (primarily the CPE) (Song & Yu, 2015; Zhang et al., 2016), population stability (Chen et al., 2016; Zhang et al., 2016), and dominant species stability (Jia et al., 2022; Zhou et al., 2020), while simultaneously increasing community dominance (Jia et al., 2022; Zhou et al., 2020). These can occur independently or synergistically within local communities (Chen et al., 2016; Zhou et al., 2020). While N-induced instability at larger scales was often attributed to these local effects (Hautier et al., 2020; Yang et al., 2022; Zhang et al., 2019), the cross-scale dynamics remain complex. Interestingly, a recent experimental and meta-analysis study reported that N addition did not significantly alter slopes of the species–area relationships (SAR; Lu et al., 2024). Yet, nutrient enrichment has been shown to generally weaken the relationships between diversity and stability at local and regional scales (Hautier et al., 2015, 2020; Zhang, He, et al., 2018; Zhang et al., 2019). This decoupling implies that N enrichment may disrupt the biological mechanisms that typically translate higher diversity (from SAR) into higher stability. Consequently, N enrichment may weaken the extent to which community stability increases with spatial scales (i.e. the CSAR patterns) even in the absence of changes in SAR slopes. Nevertheless, it remains unclear whether and how changing seasonal patterns of N deposition alter CSAR, and specifically, the relative importance of area versus biodiversity in driving these cross-scale dynamics has yet to be explicitly disentangled.

To investigate how N inputs in different seasons influence CSAR and to disentangle the relative contributions of biodiversity and area to community stability, we have applied N in autumn, winter and the subsequent growing season since 2014 in a Eurasian steppe in Inner Mongolia, China. Here, we employed nested sampling data on plant species cover from 0.01 to 16 m^2 collected over the first 6 years (2015–2020) and hypothesized that (1) N additions would diminish community stability with area, with stronger impacts from autumn and the growing season N addition; (2) seasonal N addition would not alter the relative contributions of plant diversity to community stability as area increases, with biodiversity providing compensatory dynamics (Bai et al., 2004; Liang et al., 2025). We expect this to be robust because the fundamental diversity–stability relationship is anticipated to persist despite N-induced biodiversity loss, thereby maintaining biodiversity as the primary driver of stability relative to spatial effects (Liang et al., 2025).

2 | MATERIALS AND METHODS

2.1 | Study site

The field experiment was conducted in a temperate grassland adjacent to the Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences (116°42' E, 43°38' N), located in the Inner Mongolia Autonomous Region, China. The field was flat and geologically uniform. The long-term (1984–2020) mean annual temperature was 1.1°C and mean annual precipitation was 335.6 mm. The mean monthly temperature ranged from −21.2°C (January) to 19.7°C (July) and mean monthly precipitation from 4.5 mm (January) to 89.1 mm (July). Following the customary seasonal classification guideline for our study grasslands (Bai et al., 2004), there are three seasons in a year, that is, the growing season (May to August), autumn (September to October), and winter (November to next April). Following the Food and Agriculture Organization soil system, soils are Haplic Calcisols. 52 plant species were recorded in this study. Dominant species, defined as those with an average relative above-ground net primary productivity (ANPP) greater than 10% in the control plots, included four perennial grasses—*Leymus chinensis*, *Stipa grandis*, *Achnatherum sibiricum*, and *Agropyron cristatum*—accounting for over 87% of the total community ANPP (Zhang et al., 2023). Annual atmospheric N deposition was far below 1.0 $g\,N\,m^{-2}$ for the past 40 years (Zhu et al., 2025). No fertilizers were applied in the study area before this experiment.

2.2 | Experimental design

The seasonal N addition field experiment was established in July 2014 following a completely random block design (Zhang et al., 2021, 2023). To directly compare the seasonal effects of N deposition, four treatments: the control, N added in late October (autumn N addition), in mid-January without moving snow (winter N addition), and in late May (the growing season N addition) were conducted. Each N treatment was applied as solid ammonium nitrate at 10 $g\,N\,m^{-2}\,year^{-1}$, which is a popular level across global grasslands (Borer et al., 2014). With eight replicates per treatment, the experiment comprised a total of 32 plots. These plots measured $4 \times 4\,m^2$, with 1 m-wide walkways separating the plots and blocks.

2.3 | Field sampling

The plant number and cover in each experimental plot were investigated in every mid-August (during the peak community above-ground biomass period) from 2015 to 2020. Each plot was divided into 16 $1 \times 1\,m^2$ quadrats. A $1 \times 1\,m^2$ frame was used to measure plant cover, which contained 100 evenly spaced 10 cm grids. The cover of each species was visually estimated and then summed across all species to get community-level cover, which may over 100% due to overlapping canopies of various species. For the centre quadrat ($1 \times 1\,m^2$) within each plot, we further investigated it following a fixed nested design (Figure S1). In summary, we obtained nested sampling data of $0.1 \times 0.1\,m^2$, $0.25 \times 0.25\,m^2$, $0.5 \times 0.5\,m^2$, $0.5 \times 1\,m^2$, $1 \times 1\,m^2$, $1 \times 2\,m^2$, $2 \times 2\,m^2$, $4 \times 4\,m^2$ in each plot (Figure S1; Lu et al., 2024).

2.4 | Calculations of biodiversity and ecological stability

The effective number of species, which accounts for both richness and evenness (Hill, 1973; Jost, 2006), was employed as the representation of species diversity, and was calculated as $1 / \sum p_i^2$ (Simpson, 1949), where p_i represents the relative cover of species *i* in a community. We selected this metric to minimize the influence of rare species (Chase & Knight, 2013) and capture dominance effects crucial for stability prediction (Wang & Loreau, 2016). Annual values (2015–2020) were averaged to derive the multi-year mean for analysis.

Community stability (S_{com}) in each scale within the plot was quantified as the ratio of the temporal mean of community cover (μ_{tot}) to its standard deviation (σ_{tot}) across 2015–2020 (Tilman et al., 2006), $S_{com} = \mu_{tot} / \sigma_{tot}$. Following Thibaut and Connolly (2013), population stability (S_{pop}) was quantified as the reciprocal of weighted-average population variability, $\sum_i \frac{\mu_i}{\mu_{tot}} CV_i = \sum_i \frac{\mu_i}{\mu_{tot}} \frac{\sigma_i}{\mu_i} = \sum_i \frac{\sigma_i}{\mu_{tot}}$, i.e., $S_{pop} = \mu_{tot} / \sum_i \sigma_i$, where μ_i and σ_i represented the temporal mean and standard deviation, respectively, of the cover of species *i* in a community within a spatial scale. As the highly correlation between weighted and unweighted population stability (Figure S2; $p < 0.001$), weighted one was used in further analysis. Meanwhile, species asynchrony was calculated as community stability divided by population stability: $\sum_i \sigma_i / \sigma_{tot}$ (Thibaut & Connolly, 2013). It correlated perfectly with the other species asynchrony index (Loreau & de Mazancourt, 2008; calculated as 1−synchrony, ranging from 0 to 1) (Figure S3; $p < 0.001$). Moreover, species asynchrony was decomposed into two separate components: $\mathrm{CPE} = \sqrt{\sum_i \sigma_i^2} / \sigma_{tot}$, and $\mathrm{SAE} = \sum_i \sigma_i / \sqrt{\sum_i \sigma_i^2}$ (Zhao et al., 2022). To meet the normality, above-mentioned variables were log10-transformed.

FIGURE 1 Effects of seasonal N additions and area on community stability, species diversity, species asynchrony, and population stability. Relationships between area and (a), community stability, (d), species diversity, (g), species asynchrony, and (j), population stability under seasonal N inputs, and the slopes of their linear relationships (b, e, h, and k, respectively). Lines were fitted across sampling areas using all replicate plots ($n = 8$) per treatment. Effects of seasonal N inputs on (c), community stability, (f), species diversity, (i), species asynchrony, and (l), population stability based on two-way ANOVA, with treatment effects shown regardless of sampling area. Different letters in panels b, c, e, f, h, i, k, and l denote statistically significant treatment differences ($p < 0.05$). Note that the area indicated by the arrow in panel (a) is the unit area, that is, $\log_{10}$ (Area) = 0 (Area = 1 m^2).

2.5 | Replication Statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	Plot (seasonal N additions)	8, 8, 8, 8
Community	Plot (areas: $0.1 \times 0.1\,m^2$, $0.25 \times 0.25\,m^2$, $0.5 \times 0.5\,m^2$, $0.5 \times 1\,m^2$, $1 \times 1\,m^2$, $1 \times 2\,m^2$, $2 \times 2\,m^2$, $4 \times 4\,m^2$)	32, 32, 32, 32, 32, 32, 32, 32

Note: This design includes 8 nested sampling areas per plot × 8 plots per treatment × 4 seasonal N treatments = 256 total sampling units per year.

2.6 | Statistical analyses

First, linear mixed-effects models were applied to test the impacts of sampling area, seasonal N input, and their interactions on community stability, species diversity, population stability, and species asynchrony, using the 'nlme' package. Block was set as a random factor in models. A posteriori comparisons were conducted at $\alpha = 0.05$. Simple linear regressions were conducted to examine the relationships between area and all response variables, as well as pairwise relationships among species diversity, population stability, species asynchrony, CPE, and SAE, and community stability.

Second, partial regressions were applied to compare the magnitude of the relationships of area, species diversity, species asynchrony, and population stability with community stability while statistically controlling for other variables. Residuals of community stability were derived from regressions against the control variables and represent variation independent of those effects. Hierarchical partitioning was further used to identify key predictors driving community stability ('rdacca.hp' package; Lai et al., 2022).

Finally, structural equation modelling (SEM) was applied to identify the pathways linking area to ultimate community stability under all treatments, utilizing the "piecewiseSEM" package (Lefcheck, 2016) and incorporating block as a random factor via 'nlme' package. An initial conceptual model was developed based on theory and previous empirical studies (Figure S4; Thibaut & Connolly, 2013; Zhang et al., 2016). Model fit was evaluated using Shipley's test of *d*-separation, Fisher's *C* statistic, and the Akaike information criterion, retaining only pathways supported by non-significant Fisher's *C* ($p > 0.05$). In the final SEM, following Thibaut and Connolly (2013), community stability must be entirely explained ($R^2 = 100\%$) by species asynchrony and population stability (also see Liang et al., 2025). Standardized net effects were calculated as the sum of direct and indirect effects (derived by multiplying path coefficients along causal pathways). Additionally, the relative strengths of species asynchrony and population stability were statistically compared using an *F*-test for equality of variances on the log10-transformed components.

All analyses and figures were conducted with R version 4.2.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Effects of seasonal N input on community stability–area relationship (CSAR)

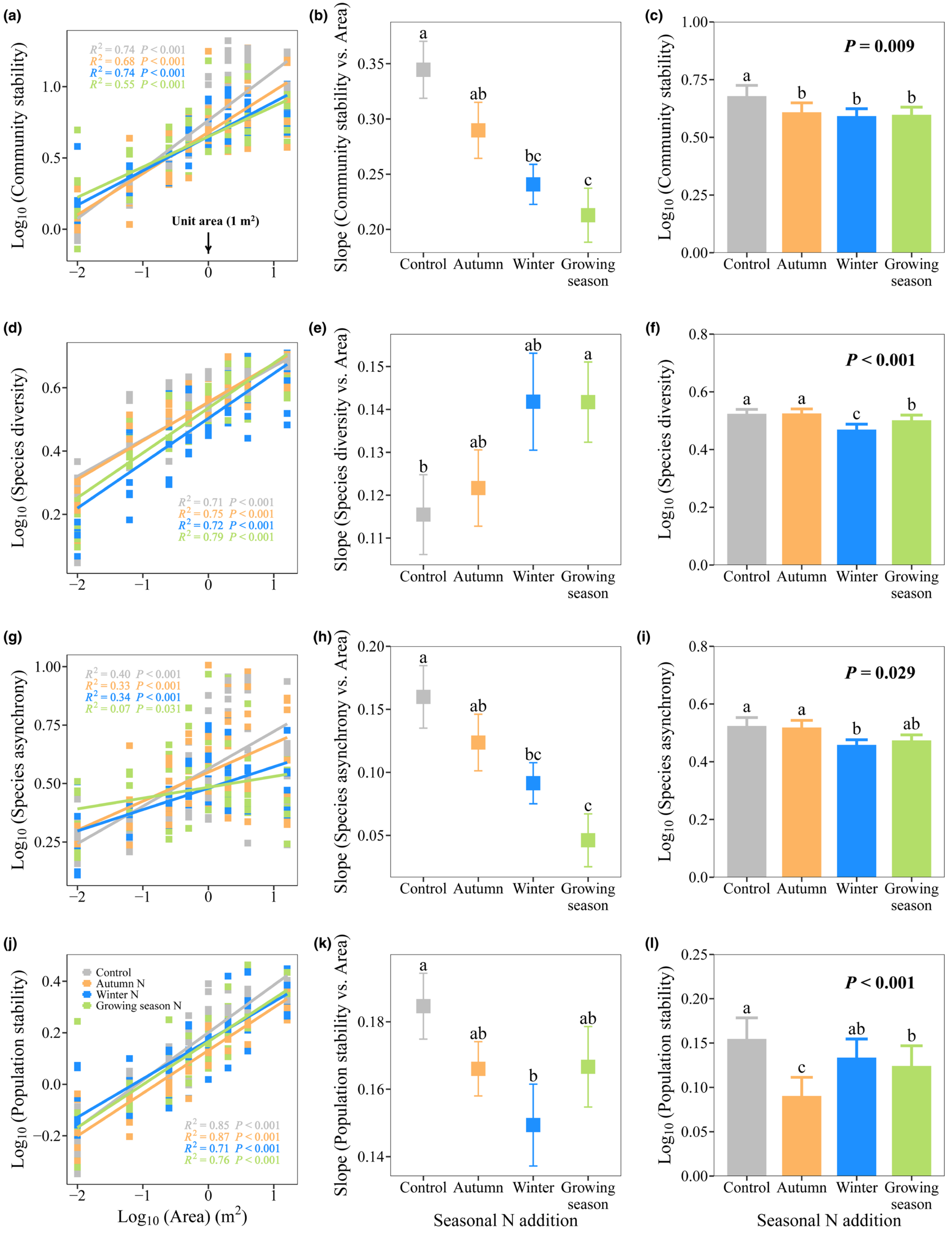
Community stability (Figure 1a; Table S1; Figure S5; $F_{7,217} = 103.4$, $p < 0.001$), species diversity (Figure 1d; Table S1; $F_{7,217} = 103.4$, $p < 0.001$), species asynchrony (Figure 1g; Table S1; $F_{7,217} = 23.4$, $p < 0.001$), and population stability (Figure 1j; Table S1; $F_{7,217} = 167.9$, $p < 0.001$) increased with area irrespective of N input.

All N input decreased CSAR intercepts (Figure S6), with reductions from 10.94% to 14.91% compared with the control. CSAR slopes were also significantly reduced under winter and growing season N additions (Figure 1b). In contrast, the growing season N addition significantly increased the SAR slope (Figure 1e). Seasonal N input reduced plant community stability across areas (Figure 1c; Table S1; $F_{3,217} = 3.9$, $p = 0.009$), while both winter and the growing season N additions significantly reduced species diversity (Figure 1f). There was no interaction between sampling area and seasonal N additions on community stability (Table S1; $F_{21,217} = 1.6$, $p = 0.058$) and species diversity (Table S1; $F_{21,217} = 0.8$, $p = 0.060$).

Only the growing season N input significantly reduced the slope of the species asynchrony–area relationship (Figure 1h; Figure S7), while winter N input significantly reduced the slope of the population stability–area relationship (Figure 1k). Winter N input significantly reduced species asynchrony (Figure 1i; Table S1; $F_{3,217} = 3.1$, $p = 0.029$), while both autumn and the growing season N inputs decreased population stability (Figure 1l; Table S1; $F_{3,217} = 8.2$, $p < 0.001$).

3.2 | The roles of biodiversity and sampling area in influencing community stability

Species diversity, population stability, and species asynchrony were all positively correlated with community stability across


(a)
Log10 (Community stability)
$R^2 = 0.74$ $P < 0.001$
$R^2 = 0.68$ $P < 0.001$
$R^2 = 0.74$ $P < 0.001$
$R^2 = 0.55$ $P < 0.001$
Unit area (1 m²)
(b)
Slope (Community stability vs. Area)
a
ab
bc
c
Control
Autumn
Winter
Growing season
(c)
Log10 (Community stability)
$P = 0.009$
a
b
b
b
(d)
Log10 (Species diversity)
$R^2 = 0.71$ $P < 0.001$
$R^2 = 0.75$ $P < 0.001$
$R^2 = 0.72$ $P < 0.001$
$R^2 = 0.79$ $P < 0.001$
(e)
Slope (Species diversity vs. Area)
b
ab
ab
a
(f)
Log10 (Species diversity)
$P < 0.001$
a
a
c
b
(g)
Log10 (Species asynchrony)
$R^2 = 0.40$ $P < 0.001$
$R^2 = 0.33$ $P < 0.001$
$R^2 = 0.34$ $P < 0.001$
$R^2 = 0.07$ $P = 0.031$
(h)
Slope (Species asynchrony vs. Area)
a
ab
bc
c
(i)
Log10 (Species asynchrony)
$P = 0.029$
a
a
b
ab
(j)
Log10 (Population stability)
Control
Autumn N
Winter N
Growing season N
$R^2 = 0.85$ $P < 0.001$
$R^2 = 0.87$ $P < 0.001$
$R^2 = 0.71$ $P < 0.001$
$R^2 = 0.76$ $P < 0.001$
Log10 (Area) (m²)
(k)
Slope (Population stability vs. Area)
a
ab
b
ab
Seasonal N addition
(l)
Log10 (Population stability)
$P < 0.001$
a
c
ab
b
Seasonal N addition

areas (Figure S8; all $p < 0.001$). Partial regressions indicated that the pure spatial effect of area (Figure 2a; controlling for diversity, $R^2 = 0.02–0.15$) explained less variance in community stability than the pure biological effect of species diversity (Figure 2b; controlling for area, $R^2 = 0.26–0.38$). In contrast, species asynchrony (Figure 2c) and population stability (Figure 2d) remained positively correlated with community stability even after controlling for all other mentioned variables and explained more variance than area (Figure 2a) or species diversity (Figure 2b) when controlling only for each other. In addition, the relative importance of these variables in predicting community stability was similar among experimental treatments (Table 1), with species diversity being about two to four times more important than area (Table 1).

In addition, irrespective of seasonal N input, the SEMs showed that biodiversity mediated the indirect effects of area on community stability, which was directly promoted by species asynchrony and population stability (Figure 3). Species diversity exerted a strong standardized total effect (0.70–0.77) on community stability (Figure 3; Figure S9), highlighting that diversity acts as the primary mediator through which area (total effect = 0.38–0.55) influences stability, conforming to the findings (Figure 2a,b; Table 1) in the previous paragraph. The positive correlation between species asynchrony and population stability disappeared under winter N input (Figure 3c), while area negatively affected species asynchrony under the growing season N input (Figure 3d). The standardized effect of area on community stability via population stability consistently exceeded that via species asynchrony (Figure S10). Although hierarchical partitioning and SEM yielded slightly different rankings of predictor importance, an *F*-test for equality of variances confirmed that the contributions of species asynchrony and population stability were not statistically different ($F = 1.18$, $p > 0.05$).

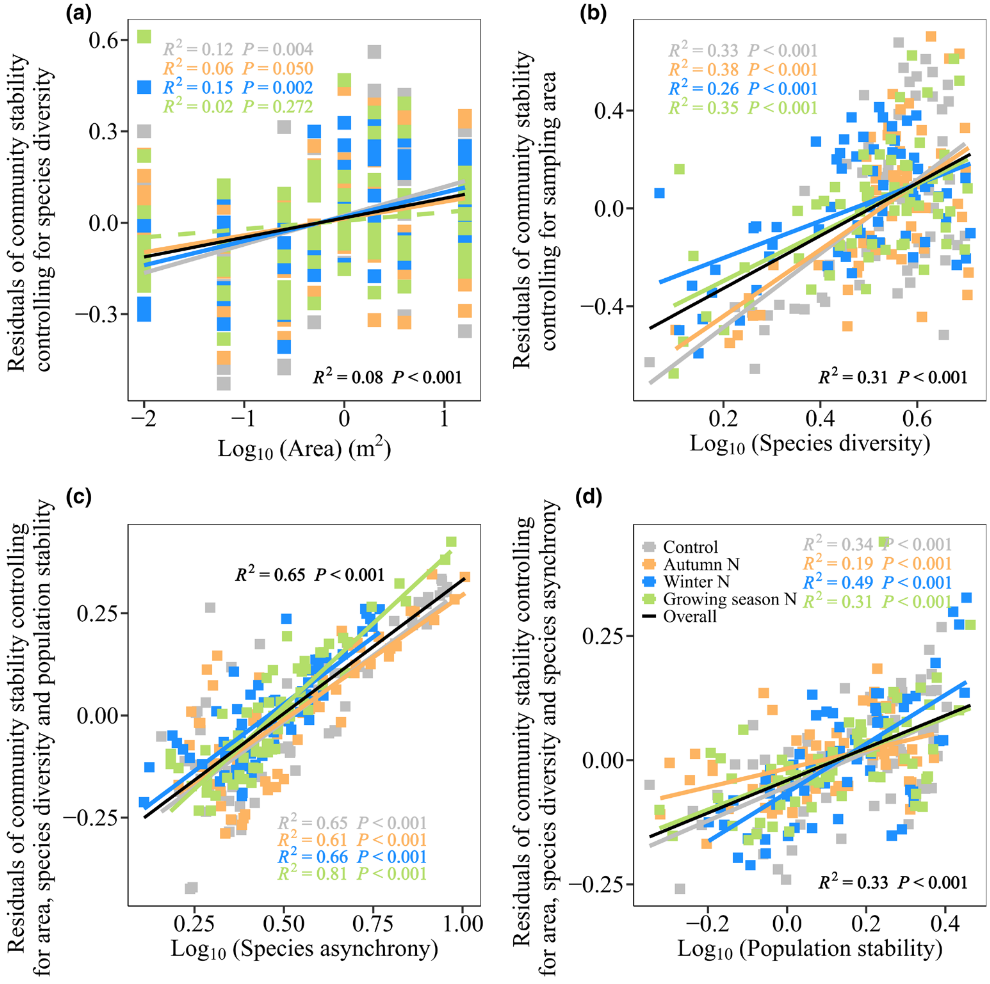


FIGURE 2 Relationships between area, species diversity, species asynchrony, and population stability and residuals of community stability. Residuals of community stability were extracted from linear regressions of community stability against the indicated controlling variables (i.e. the variation independent of the control variables). The panels display the relationships between: (a) area and residuals of community stability (controlling for species diversity); (b) species diversity and residuals of community stability (controlling for area); (c) species asynchrony and residuals of community stability (controlling for area, species diversity, and population stability); and (d) population stability and residuals of community stability (controlling for area, species diversity, and species asynchrony). Colours represent experimental treatments and the black line represents overall results.

TABLE 1 The relative importance in predicting community stability under seasonal nitrogen (N) additions based on hierarchical partitioning.

	Control		Autumn N addition		Winter N addition		Growing season N addition	
	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)
Area	0.05*	5.25	0.06*	6.23	0.07*	6.87	0.05*	5.29
Species diversity	0.18***	17.71	0.19***	18.99	0.15**	15.07	0.19***	19.45
Population stability	0.31***	31.18	0.30***	30.27	0.40***	39.99	0.35***	34.53
Species asynchrony	0.46***	45.86	0.45***	44.51	0.38***	38.08	0.41***	40.73
Total	1	100	1	100	1	100	1	100

Note: "Species diversity" is the value of effective number of species. Asterisks indicate significant correlations (*$p<0.05$; **$p<0.01$; ***$p<0.001$), based on permutation tests with 999 randomizations.

For species asynchrony, its two components, that is, CPE and SAE, were positively correlated with species asynchrony (Figure 4a,b; all $p<0.001$) and community stability (Figure 4c,d; all $p<0.001$). These positive correlations remained robust after statistically controlling for the effects of area (Figure S11). Nitrogen input in winter or the growing season significantly reduced CPE, while winter N input significantly decreased SAE across areas (Figure S12). Community stability was mostly positively correlated with CPE, but not with SAE at each specific area (Figure S13). For population stability, it was attributable to dominant species stability, increasing with more dominant species considered (Figure S14).

4 | DISCUSSION

We assessed the impact of seasonal N inputs on the community stability–area relationship (CSAR) and the underlying process using nested plant cover data over the first six consecutive years in a field grassland experiment. Extending the theoretical framework of Liang et al. (2025), this represents the first field study to detect the effect of N enrichment on CSAR. Partially contrasting with our first hypothesis, only winter and the growing season N enrichment significantly decreased CSAR slopes, while all treatments reduced intercepts. Supporting our second hypothesis, we found that biodiversity acted as the primary mediator of the area effect regardless of N inputs. Furthermore, community stability was proximately driven by species asynchrony (regulated by CPE) and population stability (regulated by dominant species). These direct mechanisms exerted stronger effects than distal drivers (area or species diversity). The hierarchy remains robust under seasonal N additions.

4.1 | Effects of seasonal N input on community stability with area

Community stability increased with area under ambient and seasonal N-enriched conditions. This positive CSAR in the unfertilized grassland was consistent with results from theoretical models (Liang et al., 2025; Wang et al., 2017; Wang & Loreau, 2014) and field surveys (Liang et al., 2025; Zhang, He, et al., 2018). Recent experimental studies have shown that community stability at the regional scale is generally higher than that at the local scale (Hautier et al., 2020; Li et al., 2023; Zhang et al., 2019; Zhu et al., 2024), though these studies were limited to two spatial scales with different regional areas, such as 1.25 m^2 (Li et al., 2023), 3 m^2 (Hautier et al., 2020), 5 m^2 (Zhu et al., 2024), and 10 m^2 (Zhang et al., 2019). Our study extended these findings by using nested sampling over eight continuous spatial scales (up to 16 m^2). Theoretically, originated from the dynamics of local communities, the spatial insurance effect is expected to improve community stability at larger scales (Loreau et al., 2003; Wang & Loreau, 2014, 2016). In our study, species diversity, species asynchrony, and population stability increase as the area increases, which enhances community stability and maintains the positive CSAR.

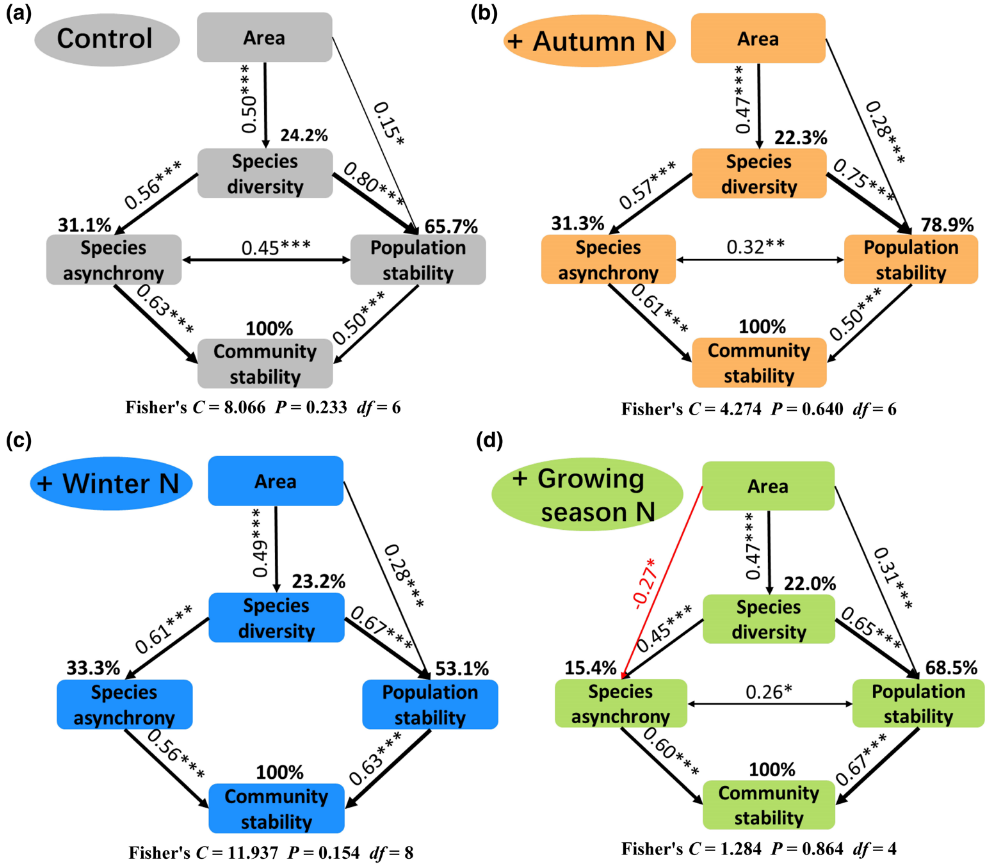


FIGURE 3 Structural equation modelling illustrating the pathways of area affecting community stability under seasonal N additions. (a), Control, and adding N during (b), autumn, (c) winter, and (d) the subsequent growing season. Positive and negative effects are shown with black and red arrows, respectively. Solid and dashed lines represent significant (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) and non-significant ($p > 0.05$) coefficients. The standardized coefficients are shown near the lines. R^2 values, reflecting the proportion of variance explained, are presented above the variables. All variables were log10-transformed. Sample size: $n = 8$ plots per treatment.

For CSAR, its slope reflects the rate at which community stability increases as area expands (Wang et al., 2017), while its intercept represents the community stability at the unit area (i.e. 1 m^2 in this study). We found that N input in any seasons could significantly decrease CSAR intercepts, while N input during winter or the growing season, not autumn lowered CSAR slopes. The decline in intercepts suggests that N enrichment reduced local-scale community stability, possibly due to destabilized dominant species in our natural grassland. It also suggests reduced population stability and weakened compensatory dynamics within small scales. The observed distinction between the effects of seasonal N additions likely arises from seasonal differences in soil biogeochemical processes and freeze–thaw dynamics. In autumn, relatively warm soil temperatures maintain microbial activity. Given that non-growing season N is primarily retained by soil biota (Ma et al., 2020), N added in autumn is likely subject to substantial microbial immobilization. Furthermore, driven by rain and snowmelt, this N tends to leach into deeper soil layers. Crucially, it undergoes two distinct periods of freeze–thaw cycles (early winter freezing and spring thawing). This prolonged exposure to environmental fluctuations might increase N losses via leaching and denitrification (Cookson et al., 2001), thereby buffering the immediate N availability in spring and resulting in weaker negative effects on community stability across spatial scales (unchanged slope). In contrast, low winter temperatures suppress microbial activity. Winter added N is largely retained in the snowpack and concentrates in the surface soil upon melting (Li et al., 2020). Crucially, the release of this accumulated N coincides with the single period of spring freeze–thaw cycles. During this period, freeze–thaw events promote the rapid release of inorganic N, creating a substantial early-season N pulse in the topsoil (Joseph & Henry, 2009). This single-pulse mechanism synchronizes nutrient supply with the onset of the growing season, significantly reducing local stability and decreasing the CSAR slope. Moreover, N input in the growing season is immediately available, promoting the dominance of fast-growing nitrophilous species and intensifying competitive exclusion, which decrease compensatory dynamics among species (Bai et al., 2010), causing the reduction in both local stability (lower intercept) and spatial scaling of stability (flatter slope). Our finding provides new insight into the scale-dependent impact of N input on community stability across larger spatiotemporal scales: N input during winter or the growing season may have stronger destabilizing effects on plant community at broader spatial scales, similar to the overall N effects when

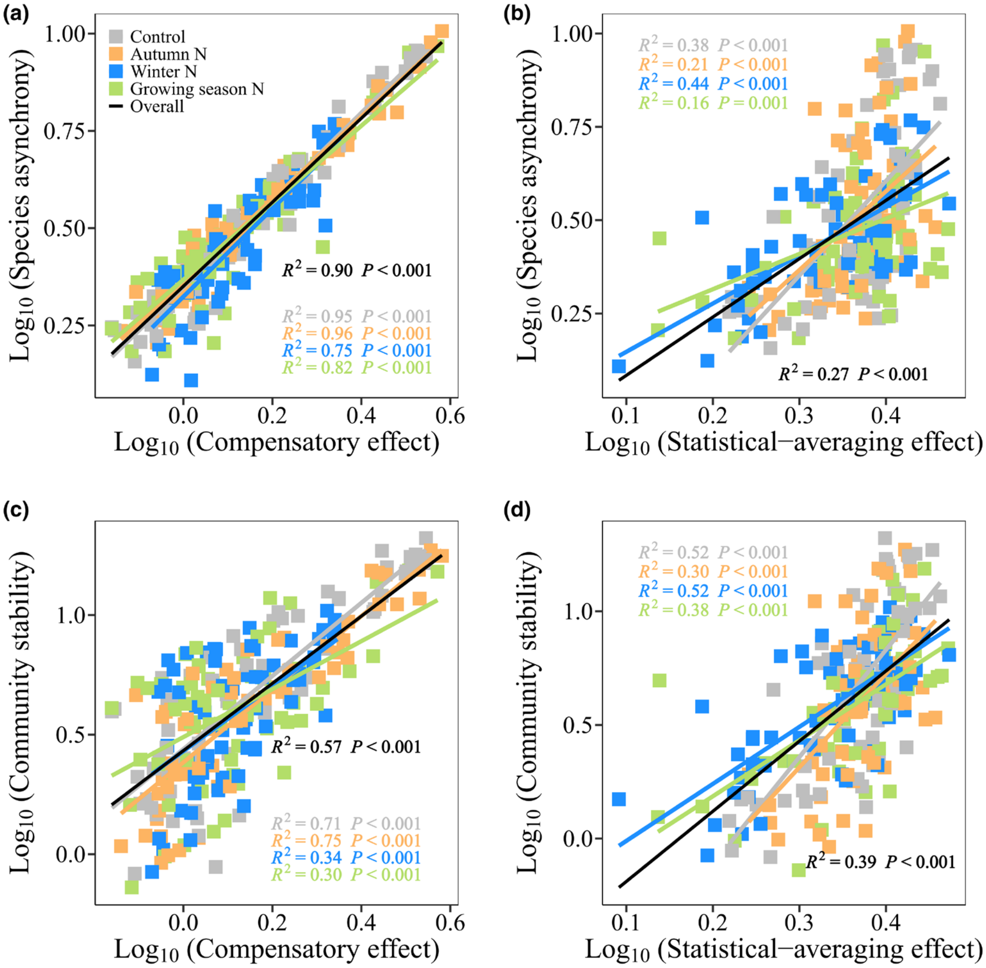


FIGURE 4 Relationships between two components, that is, compensatory effect (CPE) and statistical-averaging effect (SAE), of species asynchrony and community stability. Relationships between (a), CPE and (b), SAE and species asynchrony. Relationships between (c), CPE and (d), SAE and community stability. Colours represent experimental treatments and the black line represents overall results.

all seasonal treatments are considered (Figure 5). This may result from greater biotic homogenization across space and reduced spatial asynchrony under these treatments, which limit stability accumulation with area. This pattern highlights the loss of spatial insurance within the grassland ecosystem. However, consistent with the CSAR framework proposed by Wang et al. (2017), we recognize that this amplification trend may vary when scaling across ecosystem boundaries. Future research is therefore needed to investigate these dynamics across different ecosystems and ecotones, where landscape heterogeneity might alter the scaling of stability.

Despite moderate statistical interactions (Table S1), N addition induced a divergent scaling pattern: steepening the SAR slope while dampening the CSAR slope. The increase in the SAR slope induced by the growing season N input aligns with scale-dependent responses of biodiversity to N enrichment (Chalcraft et al., 2008; Lan et al., 2015), as N enrichment likely promoted the dominance of nitrophilous species (Bai et al., 2010). Although acting as a strong filter that reduced local diversity more than regional diversity, this dominance did not imply spatial homogenization. Rather, priority effects likely allowed different dominant species to persist across patches, maintaining compositional dissimilarity (Chalcraft et al., 2008) and steepening the species accumulation curve. Crucially, however, such structural heterogeneity failed to translate into stability gains. N-induced functional homogenization likely synchronized population fluctuations (Zhang et al., 2019), weakening spatial insurance effects, and decoupling diversity patterns from stability scaling. Therefore, relying solely on SAR patterns or local-scale assessments (e.g. plot scale) risks underestimating ecological vulnerability and N-induced destabilization (Figure 5). Moreover, growing season N addition may even overestimate stability loss at larger scales due to reductions in both the CSAR slope and intercept. Overall, future field studies in other natural ecosystems might consider both the seasonality and spatial scales of atmospheric N deposition.

4.2 | The importance of biodiversity on community stability with area

We found that plant community stability increased with species diversity, species asynchrony, and population stability across spatial

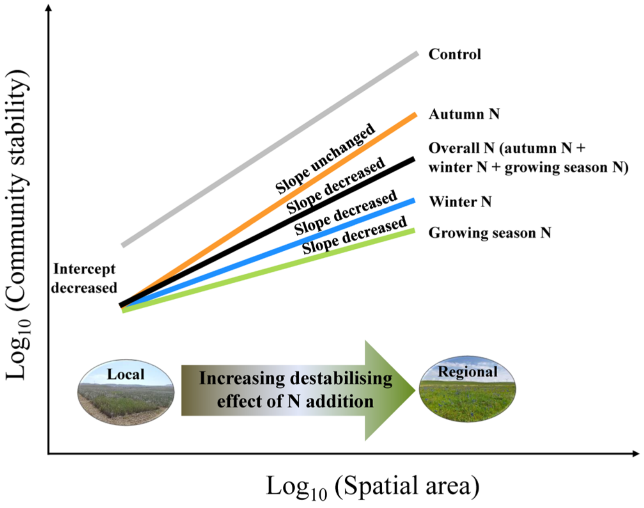


FIGURE 5 Scenario of seasonal nitrogen (N) inputs on community stability–area relationship (CSAR) within an ecosystem. Colours correspond to seasonal N enrichment scenarios. It suggests that previous N enrichment in the growing season or winter may overestimate the negative effect of annual N deposition on community stability at the larger spatial scales as the unchanged CSAR slope under autumn N event.

scales under seasonal N enrichment, confirming that these biotic factors (Chen et al., 2016; Tilman et al., 2006; Zhang et al., 2016) remain important stabilizing mechanisms. Nevertheless, their synergistic responses to area make it difficult to tease apart the individual effects of these biotic factors and area on community stability (Loreau, 1998; Zhang et al., 2016). Direct comparisons revealed that species diversity exhibited significantly steeper regulatory slopes than area despite comparable explanatory power (Figure S15). Furthermore, we found that the explanatory power of area on stability effectively dropped (R^2 from 0.72–0.79 to 0.02–0.15) when controlling for species diversity, whereas the diversity effect remained relatively robust (R^2 from 0.46–0.59 to 0.26–0.38). Together with the SEM, these results indicate a hierarchy in which area provides the spatial foundation, while biodiversity is the primary pathway through which spatial extent is translated into community stability. This supports and extends the theoretical framework proposed by Liang et al. (2025). We acknowledge this dominance of biotic mechanisms likely reflects the limited environmental heterogeneity within our local spatial extent (0.01–16 m^2), whereas abiotic heterogeneity is expected to play a more independent role in generating spatial asynchrony at larger scales (Wang et al., 2017).

Consistent with previous theoretical work (Liang et al., 2025; Thibaut & Connolly, 2013), species asynchrony and population stability jointly drove community stability with comparable effects. Meanwhile, species asynchrony and population stability remained robustly positively correlated with residuals of community stability after controlling for the other variables under N-enriched conditions, extending the theoretical argument by Liang et al. (2025) again. Consistent with Meng et al. (2024), area directly affected population stability, as larger areas support larger populations that better buffer environmental fluctuations and random events. We also observed a positive relationship between species diversity and population stability (Figure S8). This discrepancy may reflect system-specific mechanisms, such as reduced species dominance and enhanced niche complementarity in our temperate grassland, promoting a greater population-level temporal stability. The statistical strength (R^2) of the relationship between dominant species stability and population stability was strengthened with the number of dominant species considered, reaching 74%. This supports the mass ratio hypothesis (Grime, 1998), indicating that as the cumulative biomass of dominant species increases, they increasingly dictate the aggregate stability of the community. This suggests that dominant species played a major role in enhancing population stability, as previous work has been reported (Grman et al., 2010; Sasaki & Lauenroth, 2011).

In addition, species asynchrony, arising from both CPE and SAE, could promote community stability in local communities (Zhao et al., 2022). Both winter and growing season N addition significantly reduced CPE, driven by the increased dominance of synchronous species that dampened compensatory dynamics. Conversely, winter N also reduced SAE, primarily attributed to severe species loss that undermined the statistical portfolio effect. Nevertheless, the largely consistent relationships between CPE/SAE and stability across N treatments in our study suggest that these effects, as emergent properties of species-rich communities, represent general stabilizing mechanisms robust to N enrichment. It has been reported that SAE played a dominant role in stabilizing plant community across North American grasslands (Zhao et al., 2022), whereas CPE mediated plant community stability in Chinese northern temperate grasslands, that is, our field grassland (Bai et al., 2004). The seasonal N inputs did not alter the strong contribution of CPE to both species asynchrony and community stability over areas in the Chinese northern temperate grasslands. Taken together, it emphasizes the critical importance of species diversity, which was positively associated with both population stability and species asynchrony, in promoting community stability across spatial scales, in both ambient (Liang et al., 2025) and N-enriched grasslands. While our 6-year experiment captures the initial dynamics of seasonal N enrichment, long-term studies suggest that sustained N inputs drive non-random species turnover, favouring N-tolerant, fast-growing species while excluding N-sensitive species, leading to community-level acclimation over decadal timescales. Consequently, we expect the CSAR slope to stabilize at a chronically lower baseline rather than continue to decline indefinitely. To verify these broad spatiotemporal projections, future research combining long-term and multi-site networks will be essential.

5 | CONCLUSION

This study quantitatively explored multi-spatial scale community stability with seasonal N addition in a northern temperate grassland. We found the magnitude (slope) of the positive community stability–area relationship was reduced under the growing season or winter N addition. Biodiversity, which was positively associated with species asynchrony (primarily driven by compensatory dynamics) and population stability (primarily driven by dominant species stability), acted as the proximate driver mediating the stability–area relationship, maintaining its central role in promoting stability under both ambient and seasonal N-enriched conditions. These findings timely extend the most recent theoretical framework (Liang et al., 2025) to N enrichment scenarios. Practically, conserving biodiversity to maintain community stability requires integrating spatial and temporal dimensions into management: prioritizing large, contiguous habitats to maximize spatial buffering while advocating for temporally targeted emission reductions during sensitive dormant periods.

AUTHOR CONTRIBUTIONS

Yunhai Zhang designed the study and performed the research, Yuqiu Zhang, Xu Chen, and Zhengru Ren collected data, Yuqiu Zhang, Carly J. Stevens, Weiyu Lu, and Yunhai Zhang performed the analyses, Yuqiu Zhang wrote the first draft of the manuscript, Carly J. Stevens and Yunhai Zhang supervised, reviewed, and edited the writing, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest in this work.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at Science Data Bank: https://doi.org/10.57760/sciencedb.16115 (Zhang et al., 2026).

STATEMENT ON INCLUSION

Our study involved collaboration between researchers based in the country where the study was conducted and an international partner from the UK. All authors were actively involved from the early stages of study design, data collection, and interpretation to ensure that local ecological knowledge and context were incorporated throughout the research process. Findings have been shared with local collaborators, and relevant literature from regional scientists has been cited where appropriate.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Results of analysis of linear mixed-effects models for the effects of seasonal N additions (N), Sampling area (A), and their interaction on community temporal stability, species diversity, species asynchrony, and population stability during the experiment period (2015–2020). Block was used as a random factor. Degrees of freedom (*df*), *F*-test values, and *p*-values are given.

Figure S1. The design of multi-scale sampling.

Figure S2. Relationships between weighted and unweighted population stability. Solid lines represent the significant regressions ($p < 0.05$). Colours represent the experimental treatments and the black line represents the overall results.

Figure S3. Relationships between two measures of species asynchrony. Solid lines represent the significant regressions ($p < 0.05$). Colours represent the experimental treatments and the black line represents the overall results.

Figure S4. The initial structural equation model for sampling area on community stability. All plausible pathways were considered, on the basis of theoretical and empirical studies.

Figure S5. Effects of seasonal N additions on community stability in different sampling areas. Different letters among the columns indicate differences among the treatments ($p < 0.05$). Error bars indicate 1 SE.

Figure S6. Changes in the intercept of community stability–sampling area linear relationships under seasonal N additions.

Figure S7. Effects of seasonal N additions on the relationships between sampling area and species asynchrony. The relationships are fitted using (a), quadratic functions, (b), piecewise linear regressions, for species asynchrony and the sampling area.

Figure S8. Correlations between community stability, species diversity, species asynchrony, and population stability. Asterisks indicate significant correlations at $p < 0.05$ (*), $p < 0.01$ (**) or $p < 0.001$ (***).

Figure S9. Standardized total effects of sampling area and species diversity on community stability under seasonal N additions. The standardized total effects values were derived from the structural equation models (SEMs) of Figure 3.

Figure S10. Standardized effects of sampling area on community stability through population stability and species asynchrony under seasonal N additions. The standardized effects values were derived from the structural equation models (SEMs) of Figure 3.

Figure S11. Partial correlations between the two components of species asynchrony, that is, compensatory effect (CPE) and statistical-averaging effect (SAE), and overall species asynchrony and community stability independent of sampling area effects. All plotted variables represent residuals extracted from linear regressions against sampling area. The panels display the relationships between: (a) residuals of CPE and residuals of species asynchrony; (b) residuals of SAE and residuals of species asynchrony; (c) residuals of CPE and residuals of community stability; and (d) residuals of SAE and residuals of community stability. Colours represent the experimental treatments and the black line represents the overall results.

Figure S12. Effects of seasonal N additions on the compensatory effect and statistical-averaging effect in different sampling areas. Inset plots show the mean compensatory effect and statistical-averaging effect under seasonal N additions. Different letters among the columns indicate differences among the treatments ($p < 0.05$). Error bars indicate 1 SE.

Figure S13. Effects of seasonal N additions on the relationships between community stability and the compensatory effect or statistical-averaging effect across sampling areas. Relationships between community stability and (a), the compensatory effect, and (b), statistical-averaging effect across sampling areas (0.01–16 m^2).

Figure S14. Relationships between population stability and stability of dominant species (*Stipa grandis*, *Leymus chinensis*, *Achnatherum sibiricum*, and *Agropyron cristatum*). Solid lines represent the significant regressions ($p < 0.05$).

Figure S15. Comparison of the regulatory strength (slope), explanatory power (R^2), and statistical significance (*p*-values) of area versus species diversity in explaining community stability across 32 experimental plots. Panels (a) and (b) show relationships between community stability and species diversity and area, respectively. Panels (c, d and e) summarize slopes, R^2 values, and *p*-values for individual regressions. Colours represent the experimental treatments.

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