



## Compensatory effect dominates the stabilizing effects of species asynchrony in semiarid grassland after N and P addition

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### ABSTRACT

Semiarid grassland ecosystems on the Loess Plateau in China are constrained by persistent nitrogen (N) and phosphorus (P) limitations owing to historical soil erosion. N and P fertilization have a significant influence on grassland productivity and stability. However, the underlying mechanisms across different grassland community types remains poorly understood. A six-year split-plot field experiment was conducted to explore how N and P additions influence stability in short grass (SG) and tall forb (TF) communities, and to elucidate the roles of population stability (dominant or non-dominant species) and species asynchrony, specifically compensatory (CPE) and statistical-averaging (SAE) effects, in stabilizing the community. In SG community, the stability was jointly driven by species asynchrony (64.65 %) and population stability (35.35 %), with CPE accounting for 77.94 % of species asynchrony and dominant species stability contributing 91.84 % to population stability. The stability of the TF community was primarily driven by species asynchrony (84.40 %), with a major contribution from CPE (86.99 %). Overall, species asynchrony, particularly CPE, played a key role in stabilizing grasslands under N and P additions. However, SG and TF communities exhibiting divergent pathways. N and P additions destabilized CPE by shifting the dominant species composition in SG community and causing species richness decline in TF community. Fertilization strategies should prioritize moderate levels of N for the SG and low levels for the TF community to prevent biodiversity loss and promote long-term stability. Different community types were strongly influenced by the levels of N inputs, highlighting the need to integrate regional N deposition dynamics into fertilization strategies to achieve sustainable grassland restoration on the Loess Plateau.

### 1. Introduction

The Loess Plateau is considered one of the most ecologically fragile regions in China, having experienced severe soil erosion and degradation from centuries of intensive land use (Gong et al., 2023). Since the implementation of the Grain-for-Green Program, restoration efforts have significantly improved vegetation cover and soil conservation (Gong et al., 2023; Li et al., 2019). However, historical soil erosion, compounded by substantial losses in soil fertility, has led to critically low levels of soil available nitrogen (N) and phosphorus (P) (Wen and Zhen, 2020). Grasslands in this region face persistent challenges, including

slow ecological succession, simplified community structures, and diminished ecosystem services (Feng et al., 2020; Song et al., 2025). Therefore, identifying effective nutrient management strategies is crucial to optimize the ecological and economic potential of these grasslands. However, the continuous increase in N deposition in recent decades has caused a pronounced imbalance in N and P inputs across semiarid grassland ecosystems in China (Liu et al., 2011; Zhu et al., 2016). The entire Loess Plateau region has experienced N deposition rates of 13–20 kg N ha<sup>-1</sup> a<sup>-1</sup>, whereas the P deposition rates have remained exceptionally low (less than 0.17 kg P ha<sup>-1</sup> a<sup>-1</sup>), resulting in a high N:P deposition ratio of 94–150 (Zhu et al., 2016). This imbalance

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has shifted nutrient limitation from traditional N limitation to co-limitation by both N and P. These changes have introduced considerable uncertainty in developing effective fertilization strategies for grassland restoration across this region (Li et al., 2016; Liu et al., 2011; Peng et al., 2019).

Semiarid grassland ecosystems on the Loess Plateau are highly vulnerable and exhibit low stability owing to variable precipitation and frequent droughts (Luo et al., 2024; Wang et al., 2022). Consequently, achieving long-term ecosystem stability has become the primary goal of restoration efforts of semiarid grasslands (Bai et al., 2022; Xu et al., 2021). The Loess Plateau encompasses a diverse array of grassland types, shaped by complex interactions between successional stages and topographical variations. These distinct grasslands are dominated by different functional groups, thereby posing substantial challenges for implementing standardized fertilization strategies (Sun et al., 2017; Yu et al., 2020). Our previous study revealed that N and P addition exerted significantly different effects on diversity, community composition, and population stability across various grassland types (Chen et al., 2020, 2021). Meanwhile, various studies have demonstrated that nutrient enrichment exhibited varying effects on grassland stability through multiple ecological mechanisms, such as species asynchrony, population stability, and biodiversity, across different grassland ecosystems (Hautier et al., 2014; Zhang and Wang, 2023; Zhang et al., 2016; Zhao et al., 2022). These findings underscore the need to explore the mechanisms underlying the variation in stability among grassland types during fertilization-based restoration processes on the Loess Plateau.

Previous studies have provided valuable insights into the critical roles of diversity, population dynamics, and interspecies interactions in shaping grassland stability (Xu et al., 2022; Zhang et al., 2019a; Zhou et al., 2019). According to a widely accepted framework, community stability consists of two fundamental components: population stability and species asynchrony (Wagg et al., 2022; Zhang et al., 2016; Zhao et al., 2022). Population stability plays a critical role in buffering community productivity against fluctuations, especially when dominant species demonstrate strong stability (Hou et al., 2023; Liu et al., 2019; Zhang and Wang, 2023). Nutrient addition can substantially alter population stability through species turnover and composition shifts (Zhang et al., 2016; Zhou et al., 2019). Nutrient addition typically favors fast-growing, nutrient-responsive species characterized by lower stability, while suppressing slower-growing species that generally possess greater stability, ultimately leading to a reduction in population stability (Avolio et al., 2014; Bai et al., 2010).

Species asynchrony is a key driver of community stability that reflects the extent to which species exhibit offset fluctuations in their abundances (Valencia et al., 2020; Xu et al., 2015). Empirical studies have demonstrated that higher species asynchrony enhances community stability through two main mechanisms: compensation (CPE) and statistical averaging effect (SAE) (Zhang et al., 2016; Zhao et al., 2022). Nutrient addition-induced changes in species diversity modulate the stabilizing role of species asynchrony by influencing CPE and SAE (Lisner et al., 2024; Zhang et al., 2025; Zhao et al., 2022). CPE occurs when the population declines of some species are offset by increases in others (Bai et al., 2004; Gan et al., 2025). Under natural conditions, CPE is often promoted by the coexistence of species with heterogeneous resource-use strategies that respond differently to environmental change (Bai et al., 2004). Meanwhile, SAE posits that communities with higher species richness are statistically more stable because independent fluctuations among species tend to offset one another (Kalyuzhny et al., 2014; Song and Yu, 2015). However, excessive nutrient addition often weaken CPE by favoring a subset of fast-growing, nutrient-responsive species with homogeneous resource-use strategies and undermine SAE by reducing biodiversity through mechanisms such as light competition and soil acidification (DeMalach et al., 2017; Gan et al., 2025; Hautier et al., 2014; Song and Yu, 2015). These destabilizing consequences highlight the importance of evaluating how changes in species turnover and richness influence CPE and SAE under nutrient addition across

diverse grassland types on the Loess Plateau.

Numerous studies have investigated the effects of diversity, species asynchrony, and population stability on community stability under nutrient addition (Gan et al., 2025; Liu et al., 2019; Song and Yu, 2015). However, the mediating roles of population stability (dominant or non-dominant species), CPE, and SAE in stabilizing the community, particularly the influence of N and P addition on these processes across different grassland types, remain unclear. For instance, the following aspects remain unclear: how species turnover affects the influence of population stability on community stability, whether nutrient addition primarily weakens SAE through species loss, and whether nutrient addition alters species compensation dynamics to override the SAE. Addressing these critical knowledge gaps is necessary to develop targeted fertilization strategies that enhance productivity and preserve the stability of various types of grasslands on the Loess Plateau. Accordingly, we conducted a six-year experiment involving the addition of N and P in two contrasting grassland types—short grass (SG) and tall forb (TF) communities—on the Loess Plateau. Specifically, our study aimed to: (1) examine the differential species turnover patterns between the two communities under various addition levels of N and P, and their influence on population stability and CPE; (2) evaluate the relative contributions of dominant and non-dominant species stability to overall population stability under N and P addition; and (3) elucidate the contrasting effects of nutrient-induced diversity loss on community stability across different grassland types, with particular emphasis on the roles of CPE and SAE.

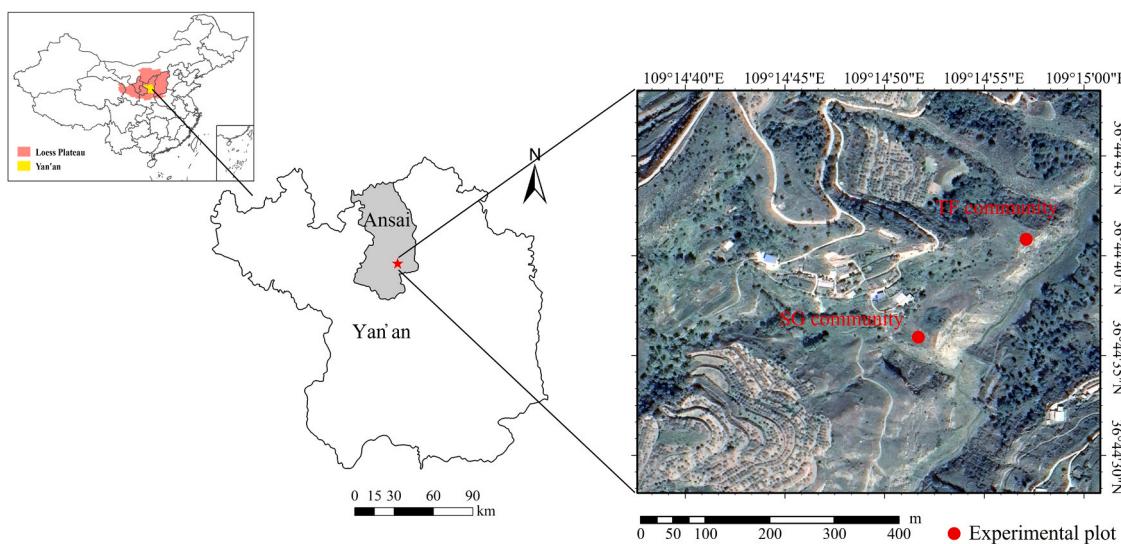
## 2. Materials and methods

### 2.1. Study site

This study was conducted in the Zhifanggou watershed within the Ansai District of Yan'an City, Shaanxi Province, northwest China ( $36^{\circ} 42' 42''$ – $36^{\circ} 46' 28''$  N,  $109^{\circ} 13' 46''$ – $109^{\circ} 16' 03''$  E) (Fig. 1). This region is situated at the forest–grassland ecotone, and experiences a semiarid temperate climate. Temperatures range from a minimum of  $-6.9^{\circ}\text{C}$  in January to a maximum of  $22.6^{\circ}\text{C}$  in July (Xiong et al., 2021). The mean annual precipitation from 1951 to 2016 is 528.8 mm, with approximately 82.2 % occurring during the growing season (May–September) (Figure S2). The typical soil type in this area is Huangmian soil, classified as Calcaric Cambisol according to the FAO FAO and ISRIC, 1988; Zhang et al., 2019b). The landscape is characterized by typical loess hilly-gully terrain. Common vegetation includes xerophytic herbaceous species, such as *Bothriochloa ischaemum*, *Artemisia gmelinii*, *Artemisia giralddii*, *Lespedeza davurica*, and *Stipa bungeana* (Xiong et al., 2021).

### 2.2. Experimental design

In 2017, two distinct representative grasslands [short grass (SG) and tall forb (TF) communities] with similar slopes and orientations were selected (Fig. 1). The SG community was dominated by *S. bungeana*, *B. ischaemum*, and *L. davurica*. The TF community was dominated by *A. gmelinii* and *A. mongolica*. The functional classifications of the major species in the two communities are shown in Table S1. The experiment involving N and P addition was designed in a split-plot layout. Within each block, four main plots ( $4.0\text{ m} \times 4.0\text{ m}$ ) were established, corresponding to four levels of N addition: 0 (N0), 25 (N25), 50 (N50), and  $100\text{ kg N ha}^{-1}\text{ yr}^{-1}$  (N100). Additionally, four subplots ( $2.0\text{ m} \times 2.0\text{ m}$ ) were assigned within each main plot, corresponding to four levels of P addition: 0 (P0), 20 (P20), 40 (P40), and  $80\text{ kg P}_2\text{O}_5\text{ ha}^{-1}\text{ yr}^{-1}$  (P80). The experimental design included 12 main plots and 48 subplots per grassland community (Figure S1). The lowest level of N addition (N25) was applied to match the atmospheric N deposition rate on the Loess Plateau, which is approximately  $21.76\text{ kg N ha}^{-1}\text{ yr}^{-1}$  (Liang et al., 2016). The N50 and N100 treatments represented approximately two- and four-fold higher than atmospheric N deposition to assess the



**Fig. 1.** Geographical location of the short grass (SG) and tall forb (TF) communities on the Loess Plateau in China.

potential consequences of elevated N input. N addition levels were consistent with previous grassland fertilization studies conducted in the Ansai District (Zhang et al., 2019b). P addition levels were applied based on the application rates identified in our previous study (Chen et al., 2020). Calcium ammonium nitrate and triple superphosphate were used as the N and P fertilization sources. N and P fertilization were applied annually at the start of the growing season (late May to early June) from 2017 to 2022. The precipitation data from 2017 to 2022 were collected from the Zhifanggou watershed meteorological station (2 km away from the study sites). Annual precipitation and that during the growing season exhibited significant interannual fluctuations from 2017 to 2022 (Figure S2).

### 2.3. Plant sampling and analysis

From 2017 to 2022, community surveys were conducted annually at the end of August, coinciding with the peak biomass period. Within each subplot, a 1.0 m × 1.0 m quadrat was used to record species-level coverage, plant height, and abundance (Chen et al., 2020). Each species was harvested at ground level and oven-dried at 65 °C for 48 h to determine dry biomass. Community biomass was calculated as the sum of the biomass of all species. In each subplot, three soil samples (0–20 cm depth) were randomly collected using an auger with a diameter of 5 cm and depth of 20 cm, then combined into a single composite sample. Soil total N content was determined using an auto-Kjeldahl instrument (Kjeltec System 2300 Distilling Unit, Foss, Sweden). Soil total P content was measured using the molybdenum–antimony colorimetric method (Bai et al., 2019).

### 2.4. Community stability and decomposition

The temporal stability of the grassland community ( $S_{\text{com}}$ ) was defined as the inverse coefficient of variation of community biomass within each plot (Zhao et al., 2022).

$$\begin{aligned} S_{\text{com}} &= \mu_{\text{tot}} / \sigma_{\text{tot}} = \sum_i \mu_i / \sqrt{\sum_{ij} v_{ij}} \\ &= \sum_i \mu_i / \sqrt{\sum_{ij} \sigma_{ij}^2} \end{aligned} \quad (1)$$

where  $\mu_{\text{tot}}$  represents the temporal mean value of community biomass during 2017–2022, and  $\mu_i$  represents the temporal mean biomass value of species  $i$ .  $\sigma_{\text{tot}}$  represents the standard deviation of

community biomass, and  $v_{ij}$  ( $\sigma_{ij}^2$ ) represents the covariance of the temporal biomass variation of species  $i$  and  $j$  during 2017–2022.

$S_{\text{com}}$  can be decomposed into two components: species-averaged population stability ( $S_{\text{pop}}$ ) and species asynchrony ( $\Phi$ ) (Fig. 1) (Thibaut and Connolly, 2013).

**Population stability** ( $S_{\text{pop}}$ ) is defined as the inverse of weighted-average population variability during 2017–2022 (Thibaut and Connolly, 2013):

$$S_{\text{pop}} = \frac{1}{\sum_i \frac{\mu_i}{\mu_{\text{tot}}} \text{CV}_i} = \frac{1}{\sum_i \frac{\mu_i}{\mu_{\text{tot}}} \frac{\sigma_i}{\mu_i}} = \frac{\mu_{\text{tot}}}{\sum_i \sigma_i} \quad (2)$$

The relative contributions of dominant ( $S_{\text{dom}}$ ) and non-dominant species stability ( $S_{\text{non-dom}}$ ) to  $S_{\text{pop}}$  were evaluated separately. The calculation methods for  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$  were identical to those used for population stability. All species ranked in the top ten based on the relative biomass across all treatments were classified as dominant, and the remaining species were defined as non-dominant.

**Species asynchrony index** was the ratio of community stability ( $S_{\text{com}}$ ) over population stability ( $S_{\text{pop}}$ ) (Loreau and de Mazancourt, 2008):

$$\Phi = \frac{S_{\text{com}}}{S_{\text{pop}}} = \frac{\sum_i \sigma_i}{\sigma_{\text{tot}}} \quad (3)$$

$$S_{\text{com}} = \Phi S_{\text{pop}} \quad (4)$$

Species asynchrony ( $\Phi$ ) represents a combination of CPE and SAE (Fig. 1), and is expressed as  $\Phi = (\text{CPE})(\text{SAE})$  (Zhao et al., 2022). Thus,  $S_{\text{com}} = (\text{CPE})(\text{SAE})S_{\text{pop}}$ .

To calculate SAE, we hypothesized that grassland communities exhibited the same species variances over time and no temporal CPE (i.e., no species covariances). Species asynchrony over time depended solely on SAE. Therefore, community stability could be represented as  $S_{\text{com\_ip}} = (\text{SAE})S_{\text{pop}}$ , where  $S_{\text{com\_ip}}$  is the community stability in the case of independent populations (ip), namely,  $\sigma_{\text{tot}} = \sqrt{\sum_{ij} \sigma_{ij}^2}$  in Eq. (1).

$$\text{SAE} = \frac{S_{\text{com\_ip}}}{S_{\text{pop}}} = \frac{\mu_{\text{tot}}}{\sqrt{\sum_i \sigma_i^2}} / \frac{\mu_{\text{tot}}}{\sum_i \sigma_i} = \frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}} \quad (5)$$

CPE is the rest of  $\Phi$ , namely,

$$\text{CPE} = \frac{S_{\text{com}}}{S_{\text{pop}} \times \text{SAE}} = \frac{\sqrt{\sum_i \sigma_i^2}}{\sigma_{\text{tot}}} \quad (6)$$

CPE >1 or <1 indicates higher or lower community stability, respectively, than expected under the assumption of independent population dynamics among different taxa, reflecting compensatory or synchronous dynamics (Zhao et al., 2022).

## 2.5. Statistical analysis

Temporal diversity indices of the grassland communities include species turnover (total turnover, appearance, and disappearance), changes in species richness, and community compositional change distance during 2017–2022. The distance of community compositional changes was quantified using Euclidean distances, which were calculated between all pairwise community comparisons across the entire six-year time series (2017–2022). For each community, a six-year time series will yield distance values for five one-year intervals (e.g., 2017 vs. 2018, 2018 vs. 2019, 2019 vs. 2020, 2020 vs. 2021, and 2021 vs. 2022), four two-year intervals (e.g. 2017 vs. 2019, 2018 vs. 2020, 2019 vs. 2021, and 2020 vs. 2022), and so forth. Simple linear regression was used to assess the relationship between distance of community change and interval years. The slope of the relationship represents the rate and direction of community change over time. Temporal diversity indices were calculated using the “codiny” package in R version 4.4.2, as described by Hallett et al. (2016).

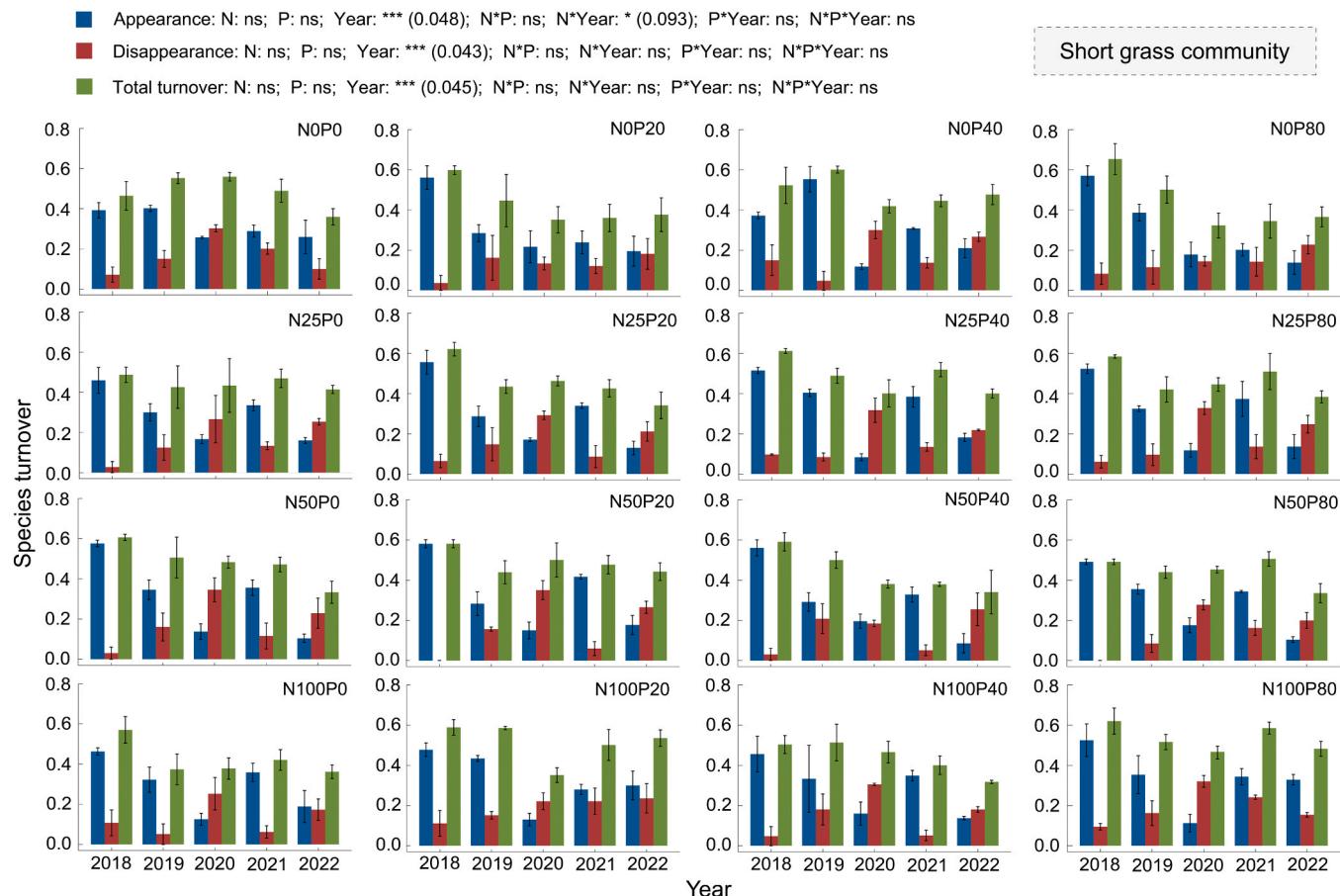
Interannual variations and changes under N and P addition treatments were analyzed using analysis of variance (ANOVA) of the split-plot design in GenStat (24th edition). The least significant difference (LSD) criterion was used to examine significant differences for interannual variations and changes in different N and P treatments. The relationship heat map between indices of community stability and its

components was generated in R version 4.4.2 using the “corrplot” package. The independent effects of the relative contributions of  $S_{\text{pop}}$  and  $\Phi$  to community stability, that of  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$  to  $S_{\text{pop}}$ , and that of CPE and SAE to  $\Phi$  were estimated through hierarchical partitioning analysis using the “rdacca.hp” package in R version 4.4.2 (Lai et al., 2022). Structural equation modeling (SEM) indicated the relative effects of population stability ( $S_{\text{pop}}$ ), dominant ( $S_{\text{dom}}$ ) and non-dominant ( $S_{\text{non-dom}}$ ) species stability, asynchrony, CPE, and SAE on community stability in relation to N and P addition using the “piecewise SEM” package in R version 4.4.2. The model’s goodness-of-fit was assessed using the chi-square ( $\chi^2$ ) test, with the fit considered satisfactory if  $0 \leq \chi^2/\text{df} \leq 2$  and non-significant  $\chi^2$  ( $p > 0.05$ ).

## 3. Results

### 3.1. Species turnover

In the SG community, appearance, disappearance, and total turnover rate exhibited significant variation among different years ( $p < 0.05$ ). N × year interaction showed significant effects on the appearance rate ( $p < 0.05$ ). Furthermore, species appearance rates demonstrated a declining trend from 2018 to 2020, with significantly lower values in 2020 compared to 2018 across all treatments ( $p < 0.05$ ). In contrast, disappearance rates exhibited an increasing trend, with significantly higher values in the SG community in 2020 than in 2018 under all combined N and P addition treatments ( $p < 0.05$ ). From 2020–2022, appearance and disappearance rates exhibited inverse trends under all combined N and P treatments in the SG community—when one increased, the other decreased (Fig. 2; Table S2).



**Fig. 2.** Species turnover, appearance, and disappearance from 2017 to 2022 after N and P addition in the short grass (SG) community. Least significant difference (LSD) values in parentheses indicate significant differences across years and N and P treatments (ns: non-significant; \*:  $p \leq 0.05$ ; \*\*:  $p \leq 0.01$ ; \*\*\*:  $p \leq 0.001$ ).

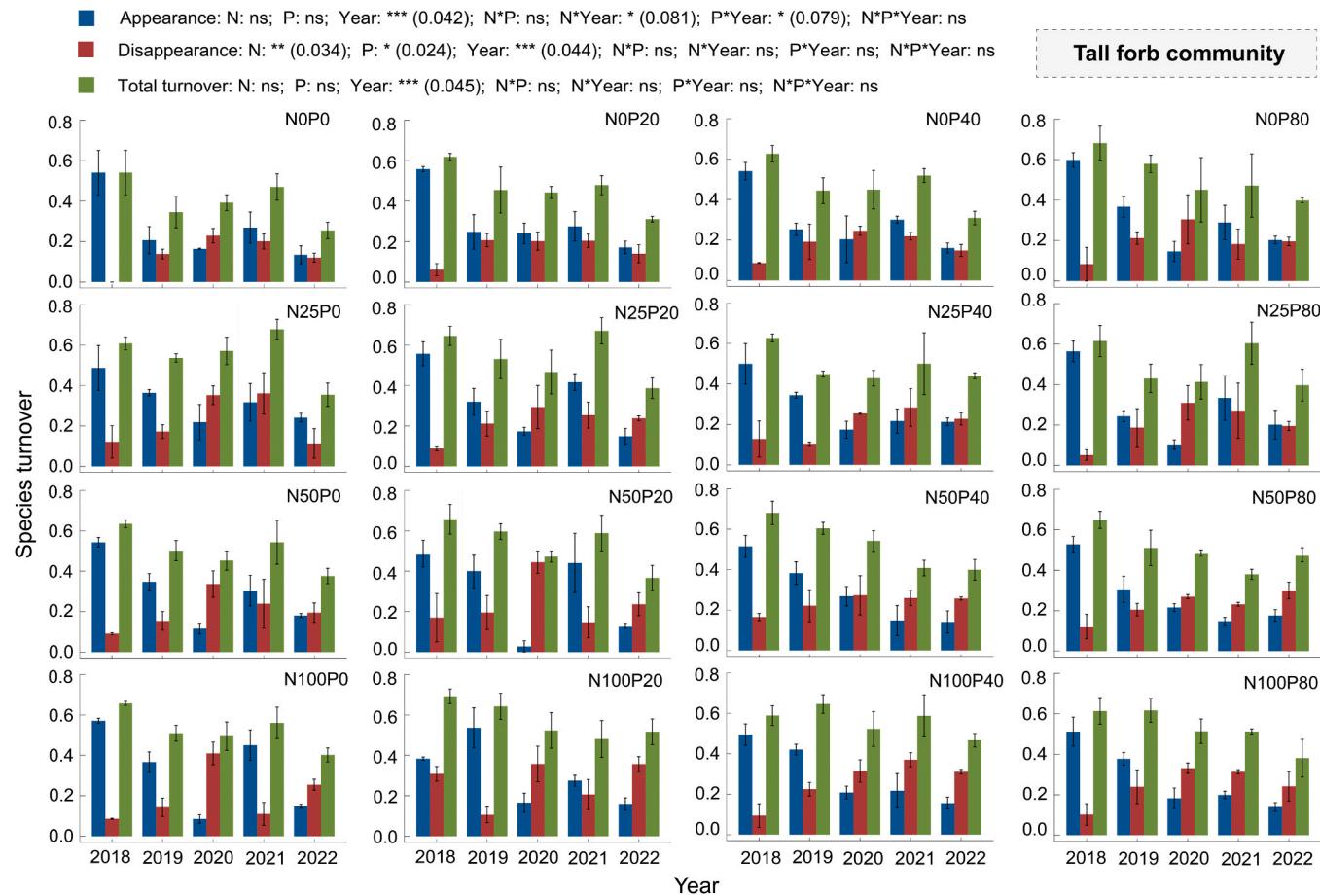
In the TF community, appearance, disappearance, and total turnover rate displayed significant variation among different years ( $p < 0.05$ ). N × year and P × year interactions exhibited significant effects on the appearance rate. Moreover, N and P showed significant effects on the disappearance rate ( $p < 0.05$ ). From 2018 to 2022, disappearance rates were significantly higher under N25 and N50 addition alone compared to NOP0. From 2020–2022, disappearance rates under N100 combined with P addition were significantly higher than those under P addition alone (2020–2022). Additionally, from 2021 to 2022, N100 combined with P addition resulted in notably higher disappearance rates compared to N100 alone. In 2022, disappearance rates under N25 and N50 combined with P addition showed a significant increase compared to P addition alone and N25 and N50 addition alone. Under low levels of N and P addition, appearance and total turnover rates decreased significantly from 2018 to 2020, with both being significantly lower in 2020 than in 2018 ( $p < 0.05$ ). The disappearance rate significantly increased from 2018 to 2020, and was significantly higher in 2020 than in 2018 (excluding N100P20) ( $p < 0.05$ ). From 2020–2022, appearance and disappearance rates under low levels of N and P addition exhibited opposing trends, with increases in one corresponding to decreases in the other. From 2018 to 2022, under moderate and high levels of N and P combined additions (N50P40, N50P80, N100P40, and N100P80), disappearance rates increased consistently, while appearance and total turnover rates exhibited a consistent decrease. Consequently, the TF community exhibited significantly lower appearance and total turnover rates but significantly higher disappearance rates in 2021 and 2022 than that in 2018 ( $p < 0.05$ ; Fig. 3; Table S3).

### 3.2. Relationship between the distance of community compositional change and interval years

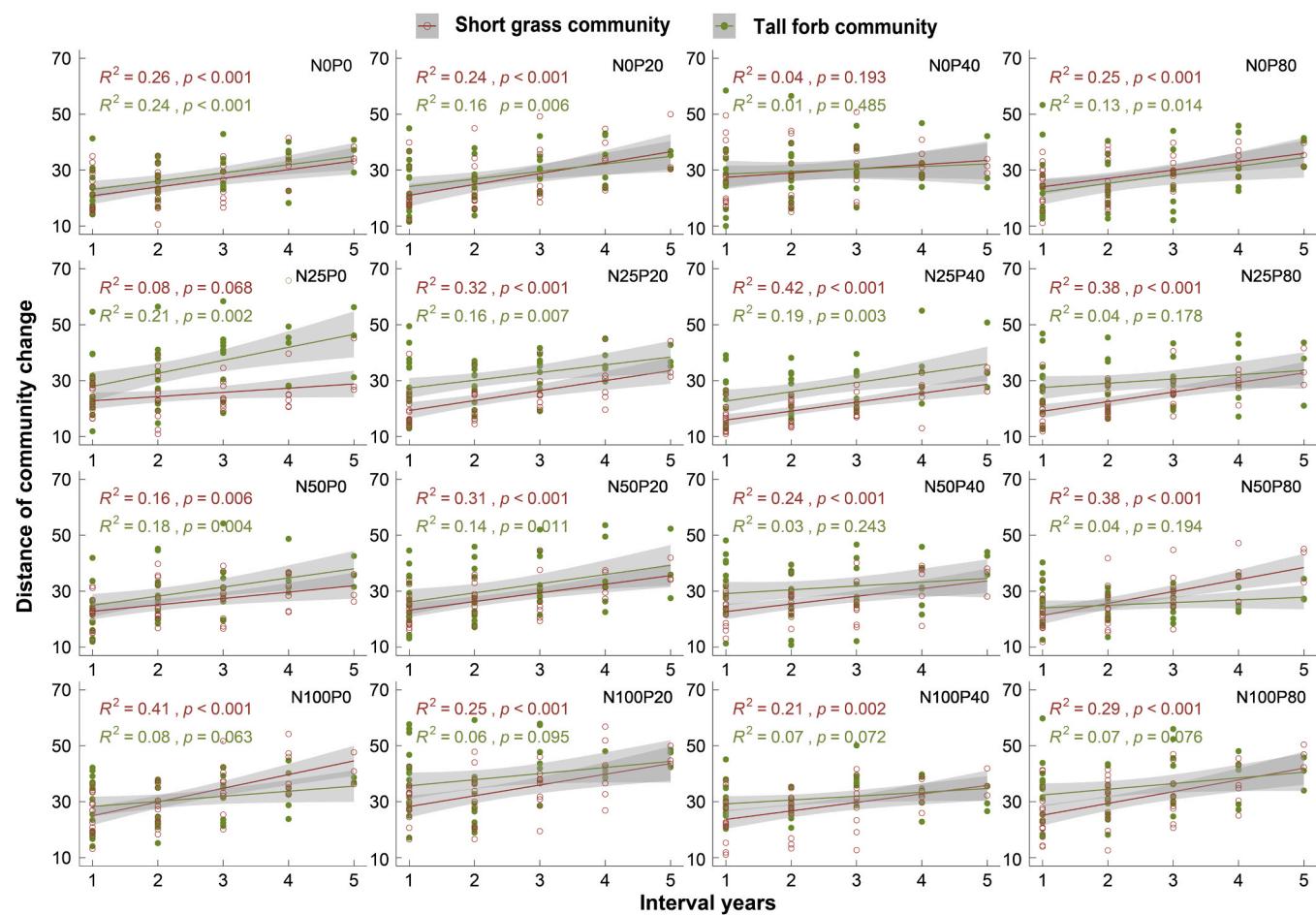
The TF community demonstrated a less pronounced increase in compositional change distance over time compared with the SG community. In the control treatment (NOP0), distance of community change was positively correlated with the interval years in both communities ( $p < 0.05$ ). Under N addition alone, the SG community displayed a strengthening positive relationship with increasing N levels. In contrast, this relationship gradually diminished in the TF community with increasing N levels. In the SG community, the distance of community changes exhibited significant positive relationships with interval years under all combined N and P addition treatments ( $p < 0.05$ ). In contrast, in the TF community, significant positive correlations were observed only under N0 and N25 treatments combined with P addition, excluding N0P40 and N25P80 ( $p < 0.05$ ). These correlations became non-significant under N50 and N100 treatments combined with P addition (Fig. 4).

### 3.3. Changes in species richness

In the SG community, species richness showed a significant increase only under the control and N100P0 treatments from 2017 to 2022 ( $p < 0.05$ ). However, these significantly increasing trends were not observed in the remaining treatments. In the TF community, species richness showed a significant increasing trend over time under the control, N0P20, and N0P40 treatments. In contrast, species richness in the TF community declined significantly from 2017 to 2022 under moderate and high levels of combined N and P additions (e.g., N50P80,



**Fig. 3.** Species turnover, appearance, and disappearance from 2017 to 2022 after N and P addition in the tall forb (TF) community (ns: non-significant; \*:  $p \leq 0.05$ ; \*\*:  $p \leq 0.01$ ; \*\*\*:  $p \leq 0.001$ ).



**Fig. 4.** Linear relationship between the distance of community change and interval years from 2017 to 2022 in the short grass (SG) and tall forb (TF) communities.

N100P40, and N100P80) ( $p < 0.05$ ; Fig. 5).

#### 3.4. Relationships between the community stability and different influencing factors

In the SG community,  $S_{\text{com}}$  exhibited significant positive relationships with  $S_{\text{com\_ip}}$ ,  $S_{\text{pop}}$ ,  $S_{\text{dom}}$ ,  $S_{\text{non-dom}}$ , asynchrony, and CPE ( $p < 0.05$ ). In contrast, significant positive relationships in the TF community were only observed between  $S_{\text{com}}$  and asynchrony, CPE, and  $\mu_{\text{ric}}$  ( $p < 0.05$ ). In the SG community,  $S_{\text{com\_ip}}$  exhibited significant positive relationships with  $S_{\text{pop}}$ ,  $S_{\text{dom}}$ , SAE, and  $\mu_{\text{ric}}$  ( $p < 0.05$ ). In the TF community, these correlations were positive but weaker compared to those observed in the SG community (Fig. 6).

In the SG community,  $S_{\text{pop}}$  showed a significant positive relationship with  $S_{\text{dom}}$  and a significant negative relationship with  $\sigma_{\text{ric}}$  ( $p < 0.05$ ). In the TF community,  $S_{\text{pop}}$  was significantly positively correlated with  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$ , and significantly negatively correlated with asynchrony and  $\sigma_{\text{ric}}$  ( $p < 0.05$ ). Asynchrony showed a significant positive relationship with CPE in both communities ( $p < 0.05$ ), but its relationship with SAE was not significant. CPE was significantly positively correlated with  $\mu_{\text{ric}}$  in the TF community. Meanwhile, SAE exhibited a significant positive relationship with  $\mu_{\text{ric}}$  in the SG and TF communities ( $p < 0.05$ ) (Fig. 6).

#### 3.5. Relative contribution of different components to community stability

Hierarchical partitioning analysis in the SG community revealed that asynchrony and  $S_{\text{pop}}$  contributed 64.65 and 35.35 %, respectively, to community stability ( $R^2 = 0.89$ ). CPE and SAE contributed 77.94 and

22.06 %, respectively, to the variability in asynchrony ( $R^2 = 0.96$ ).  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$  contributed 91.84 and 8.16 %, respectively, to the variability in  $S_{\text{pop}}$  ( $R^2 = 0.78$ ; Fig. 7). Hierarchical partitioning analysis in the TF community revealed that asynchrony and  $S_{\text{pop}}$  contributed 84.40 and 15.60 %, respectively, to community stability ( $R^2 = 0.73$ ). CPE and SAE contributed 86.99 and 13.01 %, respectively, to the variability in asynchrony ( $R^2 = 0.65$ ).  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$  contributed 57.94 and 42.06 %, respectively, to the variability in  $S_{\text{pop}}$  ( $R^2 = 0.28$ ; Figure S3).

#### 3.6. Factors influencing community stability

SEM was further conducted to evaluate the distinct impact pathways of different components on the stability of SG and TF communities under different levels of N and P addition. N and P addition affected community stability by influencing population stability and asynchrony. These two components explained 84 % and 55 % of the variation in stability caused by N and P addition in the SG and TF communities, respectively. In both communities, N addition reduced population stability by reducing  $S_{\text{dom}}$  and  $S_{\text{non-dom}}$ , which further decreased community stability. Meanwhile, N and P addition directly reduced CPE in the SG community. In contrast, in the TF community, N addition indirectly reduced CPE by decreasing species richness. The reduction in CPE further resulted in declines in asynchrony and community stability in both communities. Moreover, the decline in species richness caused by N addition directly contributed to the reduction of community stability (Fig. 7).

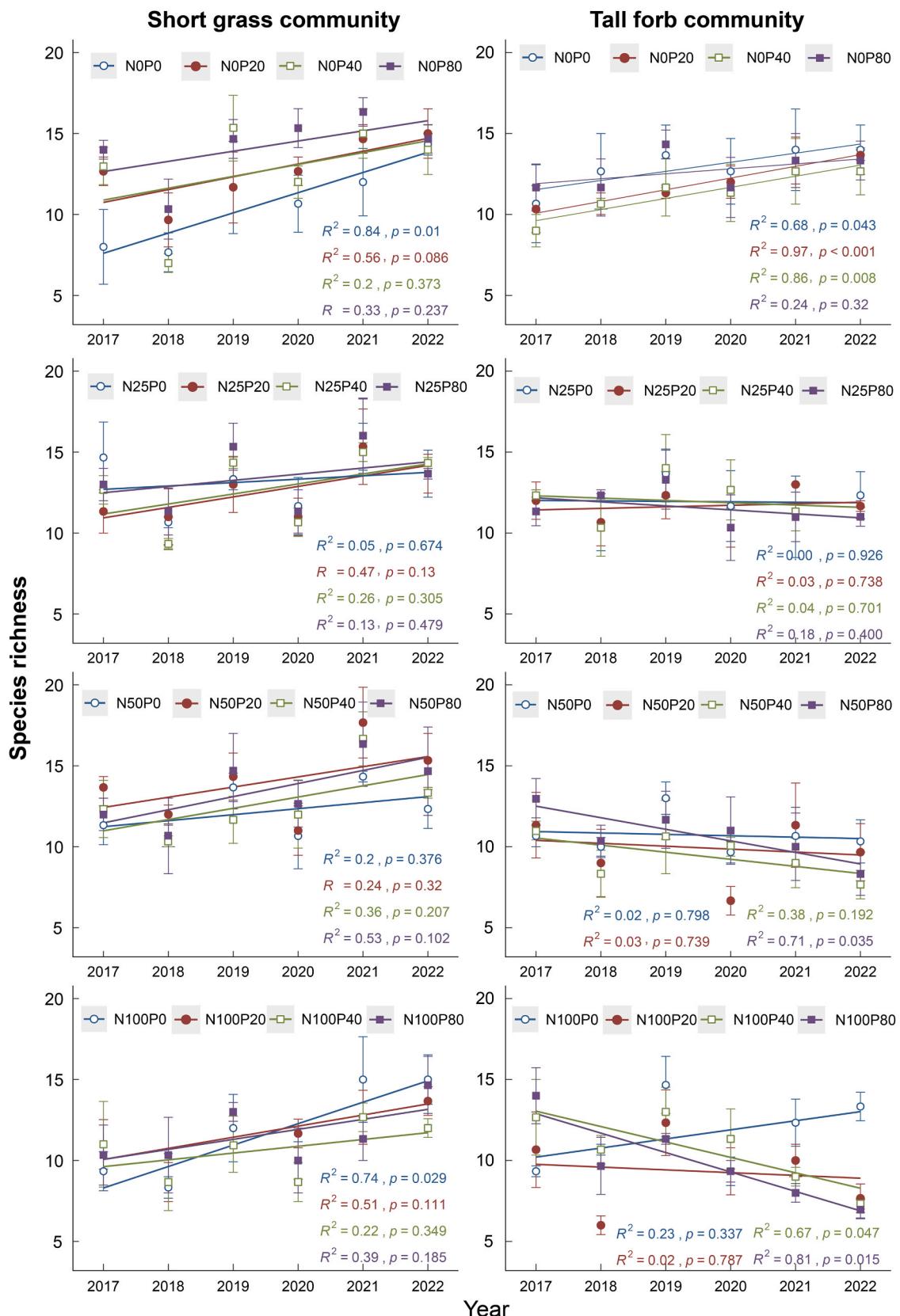
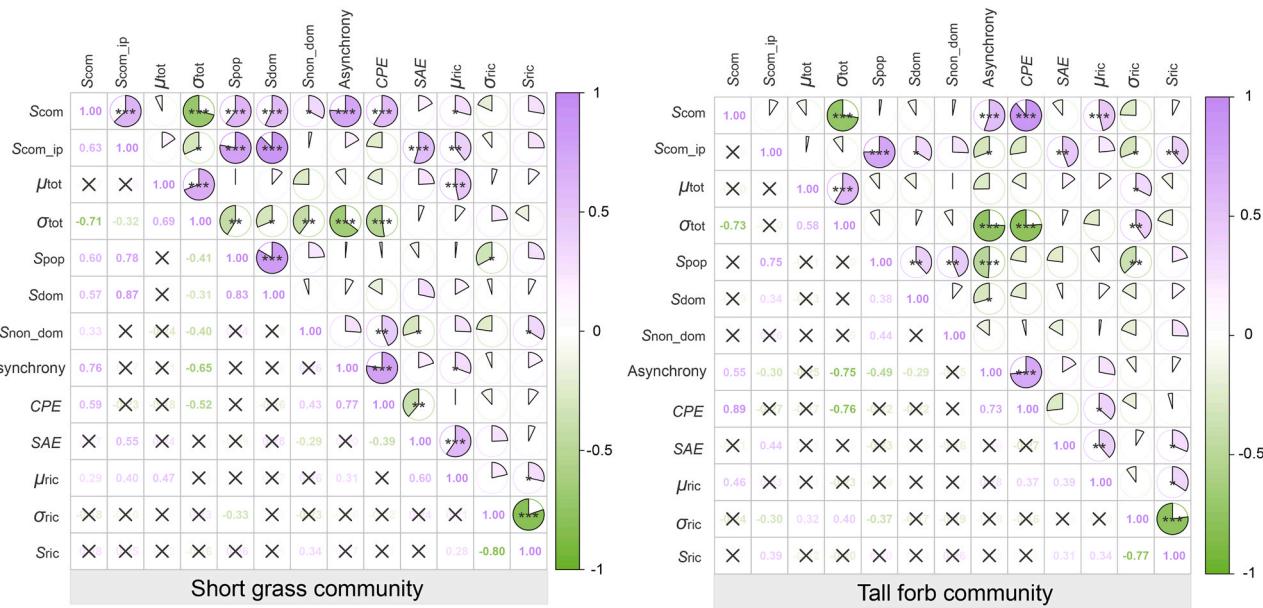
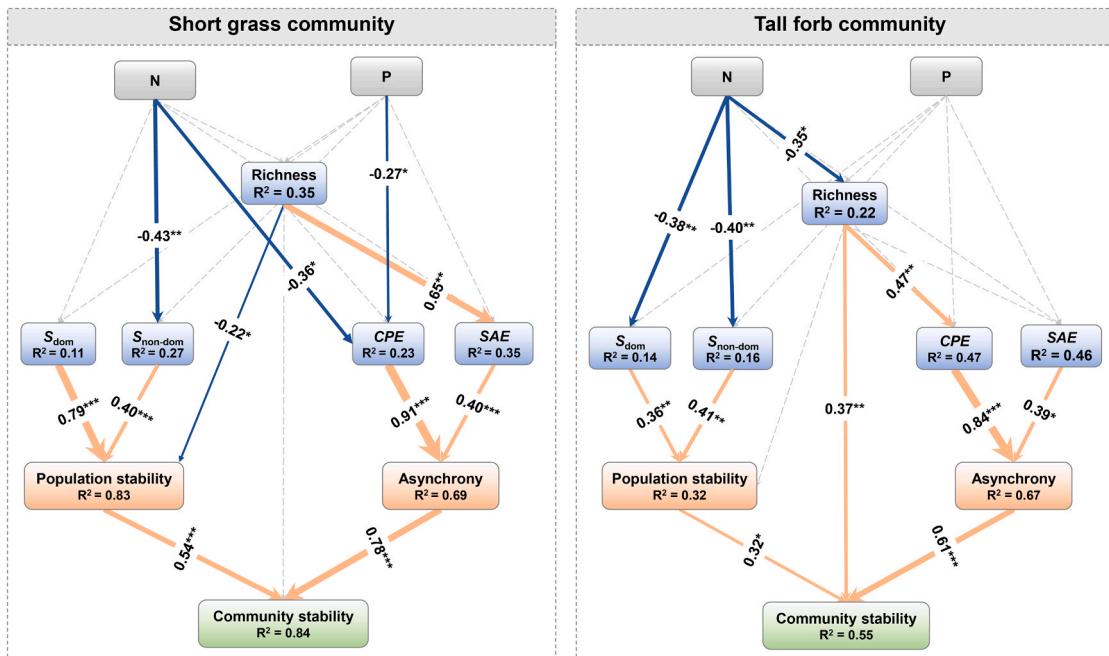


Fig. 5. Species richness changes from 2017 to 2022 after N and P addition in the short grass (SG) and tall forb (TF) communities.



**Fig. 6.** Relationship heat map between community stability ( $S_{com}$ ), community stability in the case of an independent population ( $S_{com\_ip}$ ), mean ( $\mu_{tot}$ ) and standard deviation ( $\sigma_{tot}$ ) of the total community biomass, population stability ( $S_{pop}$ ), dominant ( $S_{dom}$ ) and non-dominant ( $S_{non\_dom}$ ) species stability, asynchrony, compensatory (CPE) and statistical-averaging effects (SAE), and mean ( $\mu_{ric}$ ) and standard deviation ( $\sigma_{ric}$ ) of richness and richness stability ( $S_{ric}$ ) in the short grass (SG) and tall forb (TF) communities (\*:  $p \leq 0.05$ ; \*\*:  $p \leq 0.01$ ; \*\*\*:  $p \leq 0.001$ ).



**Fig. 7.** Structural equation model depicting the relative effect of population stability ( $S_{pop}$ ), dominant ( $S_{dom}$ ) and non-dominant ( $S_{non\_dom}$ ) species stability, asynchrony, and compensatory (CPE) and statistical-averaging effects (SAE) on community stability under N and P addition in the short grass (SG) and tall forb (TF) communities. The width of arrows is equivalent to the strength of the standardized pathway coefficients, which are displayed over the arrows. Orange and blue arrows represent significant positive and negative pathways, respectively; \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , and \*\*\* $p \leq 0.001$ . Model fitting for the SG community:  $\chi^2 = 13.118$ ;  $p = 0.975$ , and  $df = 32$ ; TF community:  $\chi^2 = 20.101$ ,  $p = 0.949$ , and  $df = 32$  (\*:  $p \leq 0.05$ ; \*\*:  $p \leq 0.01$ ; \*\*\*:  $p \leq 0.001$ ).

#### 4. Discussion

This study investigated the stabilizing effects of population stability and species asynchrony in two typical grassland communities on the Loess Plateau. The results clearly demonstrated that N and P addition induced distinct patterns of species turnover and community dynamics in the SG and TF communities. These changes influenced community

stability in different ways based on the relative contributions of species asynchrony and population stability. In SG community, stability was primarily maintained through CPE and dominant species stability. In contrast, the stability of the TF community predominantly relied on CPE. The divergent responses of the SG and TF communities to nutrient addition underscore the importance of community-specific mechanisms in shaping ecosystem stability. These findings highlight the need for

tailored fertilization strategies to promote sustainable grassland restoration and management in semiarid regions.

#### 4.1. Species turnover and community composition change

The differences in species composition, especially dominant functional groups, drove distinct patterns of species turnover and community dynamics between SG and TF communities under N and P addition. Although N and P addition significantly increased soil N and P availability, the community-weighted height and cover in the SG community remained relatively low (30–50 cm and 50–70 %, respectively), even under high levels of N and P addition (Tables S4, S6). The limited light limitation resulting from the present canopy height and coverage was insufficient to cause the loss of short-stature species (Chen et al., 2020; Xiao et al., 2021). In the absence of strong light limitation, species appearance and disappearance rates exhibited a reciprocal and balanced pattern from 2017 to 2022, maintaining relatively stable total species turnover across all treatments in the SG community (Fig. 2). As a result, species richness in SG community did not exhibit significant decreases even under high levels of N and P addition (Fig. 5). However, the distance of SG community change increased significantly over time, indicating notable temporal shifts in species composition and dominance (Fig. 4). Under N or P addition alone, perennial and clonal grasses or legumes typically maintained their competitive advantage and exhibited increased dominance (Figure S4; Table S1). However, the combined addition of N and P favored annual and non-clonal forbs that are capable of efficiently exploiting increased nutrient availability, resulting in their greater dominance (Avolio et al., 2014; Bai et al., 2010) (Figure S4; Table S1). Therefore, nutrient addition gradually affected the structure of the SG community by shifting the species composition and dominance without altering species richness.

In the TF community, tall forbs were the dominant species and showed strong responsiveness to nutrient addition due to their higher growth rates and superior competitive ability (Avolio et al., 2014; Dickson et al., 2014). Combined N and P addition significantly enhanced soil N and P availability, further increasing the dominance of tall forbs, particularly tall annual and non-clonal species (Figure S5; Tables S1 and S7). Under moderate and high levels of combined N and P addition (N50 and N100 with P), community-weighted height and coverage increased substantially, reaching 60–90 cm and 70–90 %, respectively (Table S5). The dense canopy formed by tall forbs imposed severe light limitation, which suppressed and excluded non-dominant species, particularly those with conservative resource-use strategies and short stature (DeMalach et al., 2017; Xiao et al., 2021). The TF community experienced a progressive increase in species disappearance over time under moderate and high levels of N and P addition (Fig. 3). Moreover, the intense light competition limited the availability of ecological niches for new species establishment, leading to a progressive decline in species appearance (Fig. 3). The compounded effects of increased species disappearance and reduced appearance significantly reduced species richness from 2017 to 2022 (Fig. 5). Consequently, community composition became increasingly homogeneous, with the increased abundance of tall forbs masking the turnover of non-dominant species. The overall extent of community compositional change did not vary significantly over time. Therefore, nutrient addition reshaped the structure of TF community by enhancing the dominance of tall forbs and reducing species richness.

#### 4.2. Species asynchrony and population stability

Divergent patterns of species turnover and community compositional shifts fundamentally drove the distinct stabilization mechanisms in the SG and TF communities by regulating population stability and species asynchrony (Xu et al., 2022; Zhang et al., 2016). Species asynchrony and population stability play distinct roles in stabilizing SG and TF communities under N and P addition. In the SG communities,

stability was jointly regulated by species asynchrony (64.65 %) and population stability (35.35 %). The compensatory effect accounted for 78 % of the variation in species asynchrony contributing to the stability of the SG community (Figure S3). SEM demonstrated that N and P addition reduced species asynchrony primarily by directly reducing CPE (Fig. 7).

Under low-to-moderate levels of N and P addition (N25 and N50 combined with P), the SG community showed strong CPE among different functional groups (e.g., C<sub>4</sub> grasses, legumes, C<sub>3</sub> grasses, perennial forbs, and annual forbs; Table S1) (Chen et al., 2020, 2021). Thus, CPE stabilized community biomass by allowing different functional groups to exploit distinct resource-use strategies and exhibit asynchronous growth under environmental fluctuations. However, high levels of N and P addition (N100 combined with P) disrupted this balance by significantly increasing the dominance of tall forbs at the expense of other functional groups (Figure S4; Table S1). This shift synchronized population fluctuations, reduced interspecific CPE, and further weakened species asynchrony and overall community stability (Song and Yu, 2015).

Population stability also played an important role (35.35 %) in regulating SG community stability. Notably, the stability of dominant species contributed 91.84 % to population stability (Figure S3), emphasizing that population stability was principally maintained by the stable biomass production of dominant species (Hou et al., 2023; Liu et al., 2019; Zhang and Wang, 2023). Our previous study demonstrated that different functional groups exhibited significant differences in stability under N and P addition, largely associated with their functional traits (Chen et al., 2021). Perennial and clonal grasses generally displayed higher stability than non-clonal and annual forbs (Chen et al., 2021; Lv et al., 2023). This higher stability was attributed to key traits of perennial and clonal grasses, including conservative resource-use strategies, deep root systems, and clonal integration (Dickson et al., 2014; Lv et al., 2023). These traits enhanced drought tolerance, enabled efficient resource redistribution, and stabilized interannual population variability in semiarid regions under variable rainfall and frequent droughts (Liu et al., 2019; Lv et al., 2023). In contrast, annual and non-clonal forbs, which lack the stabilizing traits, were susceptible to environmental fluctuations (Lv et al., 2023). Under high levels of N and P addition, dominant species shifted from perennial and clonal grasses and legumes to annual and non-clonal forbs (Figure S4; Table S1), disrupting population stability (Bai et al., 2010; Chen et al., 2021). Overall, our findings indicate that the stability of the SG community under N and P addition was jointly governed by changes in CPE and the stability of dominant species, rather than by changes in species richness.

In contrast to SG communities, stability of TF communities almost entirely relied on species asynchrony (84.40 %), with minimal contribution from population stability (15.60 %; Figure S3). Furthermore, CPE accounted for 86.99 % of the variability in species asynchrony in driving TF community stability, contributing to an even higher proportion than that in SG communities (Figure S3). SEM demonstrated that N and P addition reduced species asynchrony by indirectly diminishing CPE through decreases in species richness (Fig. 7). Under low or moderate nutrient levels, high species richness in TF communities supported strong CPE, and the fluctuations in dominant species could be buffered by compensatory growth among non-dominant species. However, under high levels of N and P addition, intensified light competition excluded non-dominant species and reduced species richness. This species loss destabilized CPE and species asynchrony, as the remaining species responded more synchronously to environmental fluctuations (Hautier et al., 2014). Additionally, N and P addition amplified the dominance of tall annual forbs (a low-stability functional group), further undermining the population stability in the TF community (Figure S5; Table S1) (Chen et al., 2021).

Our findings highlight that distinct diversity dynamics play a crucial role in mediating community stability during grassland restoration under nutrient addition, with divergent mechanisms operating in SG and

TF communities (Lisner et al., 2024; Zhang et al., 2025). In the SG community, species diversity did not exhibit significant decline even under high levels of N and P addition. This was largely because the short canopy height was insufficient to generate strong light limitation and cause species loss. Community stability and CPE in the SG community were primarily influenced by species turnover rather than by diversity decline. In contrast, TF communities exhibited a significant decline in species diversity under high nutrient addition, where increased canopy height intensified light competition and accelerated species loss (Lisner et al., 2024). Therefore, in the TF community, both species turnover and diversity decline jointly shaped CPE and community stability. These contrasting responses highlight the importance of community-specific nutrient management strategies in maintaining balanced species composition and promoting biodiversity conservation in grassland restoration.

#### 4.3. Community stability mechanisms in the SG and TF grasslands under N and P addition

N and P addition differentially regulated the stability of SG and TF communities through distinct mechanisms. Species asynchrony served as the primary stabilizing mechanism under nutrient addition, however, its underlying drivers differed markedly between different community types (Valencia et al., 2020; Gan et al., 2025). Contrary to previous findings from natural vegetation surveys and biodiversity-manipulated experiments (Zhao et al., 2022), which indicated that SAE were the primary drivers of stability, our study revealed that CPE was the predominant driver of community stability under N and P addition. This was due to two synergistic factors: (1) higher diversification of functional groups enhanced interspecific CPE through niche complementarity, and (2) altered nutrient availability promoted species compensatory dynamics and amplified CPE (Hou et al., 2023; Song and Yu, 2015). Thus, preserving a higher CPE was key to maintaining community stability and promoting semiarid grassland restoration through fertilization on the Loess Plateau.

In the SG community, stability was maintained through a dual mechanism: the CPE among species, which stabilized community productivity by promoting species asynchrony, and the stability of dominant species, which reduced population-level fluctuations. In contrast, the stability of the TF community was almost entirely reliant on CPE, with minimal contributions from population stability. The distinct stabilization mechanisms observed in the SG and TF communities were primarily driven by differences in species interactions, turnover, and contrasting patterns of species diversity change under N and P addition. These findings demonstrated how species turnover and compensatory dynamics regulate community stability under nutrient addition. However, this study did not include functional traits or resource use strategies to explain the underlying interspecific interactions. Future research should adopt trait-based approaches to clarify how functional diversity mediates niche complementarity and stability. Furthermore, SG and TF communities exhibited contrasting patterns of diversity change under nutrient addition, with light competition hypothesized as a key driver of diversity loss. Although increased canopy height and coverage implied increased light limitation under N and P addition, direct measurements of light asymmetry or species-specific shade tolerance were lacking. Future studies should incorporate shading or light supplementation experiments to explicitly clarify the role of light competition in driving diversity declines.

The synergistic enhancement of multiple ecosystem functions is essential for ensuring sustainable grassland restoration through fertilization. Ideally, the knowledge acquired from long-term fertilization experiments must be incorporated in ecological studies before implementing nutrient addition (Melts et al., 2018). Based on our six-year fertilization experiment, we proposed a community-specific fertilization strategy framework for SG and TF communities to support sustainable semiarid grassland restoration on the Loess Plateau (Chen et al.,

2020, 2021). In the SG community, moderate levels of N combined with P addition are recommended to maintain high productivity and community stability while avoiding diversity loss. In contrast, high levels of N combined with P addition reduced community stability by disrupting both CPE and population stability. For the TF community, low levels of N combined with P addition are optimal for stabilizing CPE, maintaining community stability, and preventing diversity loss. However, moderate and high levels of N and P addition diminished CPE and community stability, accompanied by a substantial decline in species diversity.

Our study revealed that sustainable grassland restoration for different community types was highly dependent on the N enrichment level. These findings provide insights into the impacts of N deposition on the stability and sustainability of grassland restoration on the Loess Plateau. In the future, persistent N deposition is likely to induce ecological effects similar to those of the moderate and high N treatments. Given the unpredictable and variable trends in future N deposition patterns in China (Liu et al., 2024), regional N deposition dynamics should be integrated into community-specific fertilization strategies for future grassland restoration. By adopting such an adaptive approach, sustainable restoration efforts in semiarid grasslands can be optimized by simultaneously enhancing productivity, ensuring biodiversity conservation, and promoting ecosystem stability on the Loess Plateau.

#### 5. Conclusion

Species asynchrony emerged as the fundamental regulator of grassland community stability under N and P addition on the semiarid Loess Plateau. Compensatory effects, rather than statistical-averaging effects, served as the dominant stabilizing mechanism, even when species richness declined significantly. The two grassland communities displayed contrasting responses to nutrient enrichment and relied on different mechanisms to maintain stability. In SG communities, stability was mediated by a dual mechanism: compensatory effects among species and the stability of dominant species. Moderate nutrient addition was necessary in SG communities to preserve dominant species stability and promote compensatory effect and community stability. In contrast, stability of TF community relied almost entirely on compensatory effect, with minimal contributions from population stability. TF communities required careful conservation of species diversity to sustain compensatory interactions. Low levels of N and P addition are recommended to prevent competitive exclusion and species loss that further diminish the compensatory effect and stability. Therefore, the sustainability of grassland restoration efforts for different community types was highly dependent on the N enrichment level, highlighting the need to integrate regional N deposition dynamics into the community-specific fertilization strategy for future grassland restoration practices. This adaptive fertilization strategy offers a pathway to optimize the sustainability of semiarid grassland restoration by simultaneously enhancing productivity, ensuring biodiversity conservation, and promoting ecosystem stability on the Loess Plateau.

#### CRediT authorship contribution statement

**Yuting Yang:** Writing – review & editing, Writing – original draft, Software, Investigation, Formal analysis. **Junjie Zhou:** Methodology, Investigation. **Zhifei Chen:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Yingkun Mou:** Methodology, Investigation, Formal analysis. **Lingbin Yan:** Writing – review & editing, Software, Formal analysis. **Bingcheng Xu:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization. **Yuan Liu:** Writing – review & editing, Formal analysis.

## Declaration of Competing Interest

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

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.109852](https://doi.org/10.1016/j.agee.2025.109852).

## Data availability

Data will be made available on request.

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