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Responses of plant community drought resistance and resilience to warming and nitrogen addition vary with recurrent droughts in a semi-arid grassland

Haidao Wang [a], Jian Song [a,b], Yongge Fan [a], Jianyang Xia [c], Lin Jiang [d], Qingshan Zhang [a], Heng Li [a], Jingyi Ru [a,b], Jiayin Feng [a,b], Lingjie Kong [a], Jiajun Zhang [a], Xueli Qiu [a], Guilin Zhou [e], Benqing Li [e], Jiaxin Zhou [a], Shiqiang Wan [a,b,*]

[a] *School of Life Sciences/Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding, Hebei 071002, China*
[b] *Engineering Research Center of Ecological Safety and Conservation in Beijing, Hebei University, Tianjin-Hebei (Xiong'an New Area) of MOE, Baoding 071002, China*
[c] *Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, Center for Global Change and Coastal Ecosystems, Institute of Eco, Chongming, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China*
[d] *School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA*
[e] *School of Life Sciences, Henan Normal University, Xinxiang, Henan 453007, China*

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ABSTRACT

Climate warming and atmospheric nitrogen (N) deposition can substantially influence the structure and functions of the terrestrial biosphere. Understanding how these factors affect community stability in the context of recurrent droughts is essential for maintaining the sustainability of ecosystem services. A five-year (2006–2010) manipulative experiment, during which two droughts occurred in 2007 and 2009, was designed to examine the influences of warming and N addition on community resistance and resilience and whether these effects vary with recurrent droughts in a semi-arid grassland. During the whole experimental period, warming enhanced community resilience by 8.4 %. Nitrogen addition decreased community resistance by 31.6 % but increased community resilience by 10.4 %. A shift of warming effects on community resistance from neutral during the first drought to negative during the second drought was observed, attributed to the suppressed rare species resistance. A substantial warming-induced reduction in rare species biomass contributed to decreased community resistance during the second drought. The influences of N addition on community resilience were reversed from positive during the first drought to negative during the second drought, driven by divergent responses among plant functional groups. In contrast to the positive N effect on dominant species resilience observed in first drought, N addition weakened dominant species resilience and the asynchrony of subordinate species, leading to declines in community resilience during the second drought. These findings highlight that interannual precipitation anomalies, particularly increasingly frequent droughts, should be incorporated when assessing the sustainability of grassland ecosystem service under future global change scenarios.

1. Introduction

Resistance and resilience represent important proxies for the capability of ecosystems to sustain stable productivity and deliver ongoing ecological services in the face of environmental changes (Pimm, 1984; Tilman and Downing, 1994). Greater resistance and resilience could enhance ecological functioning, with subsequent benefits for human well-being (Ives and Carpenter, 2007; Isbell et al., 2015). Under global change scenarios, climate warming and atmospheric nitrogen (N) deposition have profound impacts on the resistance and resilience of terrestrial ecosystems (Sun et al., 2022; Xu et al., 2022, 2023; Yan et al., 2023a). In addition, the frequency and intensity of extreme climate events are predicted to increase significantly (Dai, 2013; Hughes et al., 2018; IPCC, 2021). For example, droughts have been documented to suppress the land carbon sink and ecosystem stability (Ciais et al., 2005; Reichstein et al., 2013; Isbell et al., 2015; Yin et al., 2023). Previous studies have devoted to evaluating ecosystem productivity and stability response to a single drought event in one or several continuous years

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[*] Corresponding author at: School of Life Sciences/Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding, Hebei 071002, China.
E-mail address: swan@hbu.edu.cn (S. Wan).

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(Hoover et al., 2014, 2021; Kreyling et al., 2017; Griffin-Nolan et al., 2019; Xu et al., 2023). However, our comprehension of the resistance and resilience of plant communities response to recurrent droughts remains largely unclear (Vicente-Serrano et al., 2013; Müller and Bahn, 2022).

Climate warming could alter the composition and structure of plant communities (Bastazini et al., 2021; Jónsdóttir et al., 2023) and subsequently affect ecosystem productivity and stability (Fussmann et al., 2014; Ma et al., 2017; Feeley et al., 2020; Speißer et al., 2022). For example, given the crucial roles of dominant species in determining ecosystem stability proposed by the mass ratio hypothesis (Grime, 1998), it has been illustrated that warming increases community resistance through stimulating dominant species resistance (Yang et al., 2016; Yan et al., 2023a) but decreases community stability via reducing dominant species stability in grasslands (Yang et al., 2017; Wu et al., 2020; Li et al., 2021; Quan et al., 2021; Ma et al., 2024). In addition, previous studies have demonstrated both neutral and negative impacts of experimental warming on community resilience after a single extreme precipitation event (Yang et al., 2016; Sun et al., 2022; Yan et al., 2023a). There is no consensus on how climate warming affects ecosystem stability under more frequent extreme climate events, posing challenges for robust projections of future dynamics of terrestrial ecosystems (Müller and Bahn, 2022).

Concurrent with climate warming, atmospheric N deposition rates have been widely observed to increase across the world (Galloway et al., 2008; Yu et al., 2019). Although improved N availability under atmospheric N deposition can stimulate terrestrial ecosystem productivity (Xia and Wan, 2008), it may decrease plant species diversity and asynchrony, ultimately destabilizing ecosystems (Hautier et al., 2015; Zhang et al., 2016). For example, N addition weakens the capability of ecosystems to resist environmental fluctuations by reducing species asynchrony within community and/or plant functional groups, resulting in decreased ecosystem stability (Grman et al., 2010; Xu et al., 2014; Huang et al., 2020; He et al., 2022; Hou et al., 2023). In addition, N addition has been shown to reduce community resistance by suppressing the resistance of dominant species (Xu et al., 2022, 2023). By contrast, community resilience has been documented to increase with the enhanced resilience of dominant species under N addition (Xu et al., 2022). Moreover, the neutral effects of N addition on both the resistance and resilience of grassland ecosystems have also been observed (Yu et al., 2021; Hou et al., 2023; Xu et al., 2023). Therefore, the influences of N deposition on ecosystem stability are highly uncertain.

When droughts occur frequently, their cumulative effects on plant community composition and structure may alter ecosystem responses to climate warming and atmospheric N deposition (Müller and Bahn, 2022; Luo et al., 2023). For example, given the regulatory roles of temperature and water availability on plant growth (Thuiller et al., 2005; Song et al., 2019), warming and drought can interact to affect plant growth by intensifying soil water deficits and ultimately reduce the stability of ecosystem productivity (De Boeck et al., 2016; Wang and Wang, 2023). In addition, drought exacerbates N limitation by inhibiting soil N mineralization rates, resulting in suppressed plant growth and productivity (He and Dijkstra, 2014; Deng et al., 2021). Model simulation has shown that N enrichment could delay the threshold of terrestrial ecosystem productivity response to extreme drought by alleviating drought-induced reductions of N availability (Li et al., 2023). However, evidence from manipulation experiments has demonstrated that N addition may exacerbate the declines of plant productivity under drought by increasing plant community drought sensitivity (Bharath et al., 2020; Meng et al., 2021). The interactions of warming and/or N addition with drought may be more complex with increasing drought events. Capturing the dynamic nature of these interactions is crucial in accurately predicting ecosystem stability under future global change scenarios (Müller and Bahn, 2022).

A two-factor field manipulative experiment was conducted in a semiarid grassland on the Mongolian Plateau for five years (2006–2010), during which two extreme droughts occurred in 2007 and 2009, providing a unique opportunity to explore the impacts of experimental warming and N addition on community resistance and resilience under recurrent droughts. Our study aimed to address two questions: 1) Do community resistance and resilience change under recurrent droughts? and 2) How do warming and N addition influence community resistance and resilience, and do their underlying mechanisms change with recurrent droughts?

2. Materials and methods

2.1. Study site

This study was conducted at the Duolun Restoration Ecology Research Station of the Institute of Botany, Chinese Academy of Sciences, in Duolun County, Inner Mongolia, China (42°02′ N, 116°17′ E, 1324 m a.s.l.). Long-term (1953–2021) mean annual temperature and precipitation are 2.4 °C and 384 mm, respectively (China Meteorological Data Sharing Service System). Approximately 90 % precipitation occurs during growing season (May−October). The soil in the study site is categorized as chestnut soil in the Chinese classification system and as Haplic Calcisols in the Food and Agriculture Organization (FAO) classification. The dominant plant species includes *Stipa krylovii*, *Agropyron cristatum*, *Artemisia frigida*, and *Potentilla acaulis*.

2.2. Experimental design and manipulations

A randomized complete block design was implemented, featuring four treatments including control, 24-hr continuous warming, N addition, and 24-hr continuous warming plus N addition (also see Xia et al., 2009; Song et al., 2021). Each treatment was replicated six times across 24 plots with an area of $3 \times 4\,m^2$ for each plot. These plots were organized in a 4×6 matrix, with 3 m buffer zone separating any two adjacent plots. The warmed plots were heated continuously for 24 h using MSR-2420 infrared radiators (Kalglo Electronics Inc), positioned 2.25 m above the ground. In each unwarmed plot, a ‘dummy’ heater matching the shape and size of the infrared radiators was also suspended at the same height to mitigate any shading effects. The daily soil temperature was raised by 0.90 °C due to 24-hr continuous warming. The warming treatment lasted from April 23 to November 15 in 2006, and from March 15 to November 15 during the years 2007–2010. Previous study has observed the saturation point of ecosystem responses to N deposition in this area at a rate of approximately $10.5\,g\,N\,m^{-2}\,yr^{-1}$ (Bai et al., 2010). Thus, ammonium nitrate was added into the enriched N plots in mid-July each year with the level of $10\,g\,N\,m^{-2}\,yr^{-1}$.

During the five experimental years, the growing season precipitation in 2007 and 2009 was 32 % and 40 % below the long-term mean (1953–2010), respectively (China Meteorological Data Sharing Service System). The precipitation of the two years was outside the 90 % confidence interval for the normal distribution of precipitation (Fig. S1). Therefore, the two overlapping stages of 2006–2008 and 2008–2010 were defined as the first and second drought, respectively.

2.3. Aboveground biomass and plant functional groups

In the semiarid grassland, plant communities are characterized by short-stature plants and relatively uniform plant height, making cover a reliable indicator of productivity (Fig. S2; Ji et al., 2009; Sanaei et al., 2018). Therefore, plant peak biomass in each plot was estimated through a non-destructive approach, utilizing regression equations that correlate biomass and cover for each species in August from 2006 to 2010. To achieve this, two permanent $1 \times 1\,m^2$ quadrats were set up at opposite corners of each plot in May 2006. In addition, 80 calibration plots ($1 \times 1\,m^2$) were established near our experimental plots at the same time. Half of the 80 calibration plots received N addition of $10\,g\,N\,m^{-2}\,yr^{-1}$ with ammonium nitrate on 19 July each year. In August each year, the percent cover of each plant species was visually assessed using a $1 \times 1\ \mathrm{m}^2$ frame divided into 100 evenly distributed grids ($10 \times 10\ \mathrm{cm}^2$) in each calibration plot. Simultaneously, the percent cover of each plant species was also visually monitored in two permanent quadrats in each experimental plot. After the cover estimates, all living aboveground biomass (AGB) of each species in each calibration plot was clipped, oven-dried at 65 °C to constant weight, and then weighed. To estimate the AGB of each plant species and address potential variations in plant height among treatments, separate empirical equations for ambient and N addition treatments were fitted to establish the cover-biomass relationships. This approach minimizes the influence of nitrogen-enriched effects on biomass estimation, thereby enhancing the reliability of our method.

Based on the relative AGB of each species in the control plots averaged across the five experimental years, plant species were categorized into three functional groups: dominant species ($> 5\,\%$), subordinate species ($1-5\,\%$), and rare species ($< 1\,\%$; Mariotte et al., 2013; Ma et al., 2021; Table S1). The average values of AGB were calculated by taking the mean value of the measurements from the two opposite corners of each plot.

2.4. *Community resistance and resilience, species asynchrony, and drought-induced changes in aboveground biomass*

Resistance represented the capability of ecosystems to maintain stable productivity under environmental perturbations (Pimm, 1984). Resistance was quantified as the ratio of AGB between drought and pre-drought year (Lloret et al., 2011). Resilience referred to the rate with which a community returns to its original state following environmental disturbances (Pimm, 1984). Resilience was quantified as the ratio of AGB between post-drought and pre-drought year (Lloret et al., 2011).

Species asynchrony during the first and second drought were calculated as (Loreau and de Mazancourt, 2008):

$$1 - \varphi_x = 1 - \sigma^2 \Big/ \left(\sum_{i=1}^{S} \sigma_i\right)^2, \tag{1}$$

where φ_x is species synchrony, σ^2 is the standard deviation of AGB, σ_i is the temporal standard deviation of biomass of species i in a community with S species. Species asynchrony ranges from $0-1$, with 0 and 1 referring to that species fluctuations are perfectly synchronized and asynchronized, respectively. Resistance, resilience, and species asynchrony were calculated at plant community and functional group levels in the first and second drought, respectively. In addition, averaged resistance, resilience, and species asynchrony of community and three functional groups across the two drought stages were used as the values of them over the whole experimental period.

The drought-induced changes in AGB of plant community and rare species during the first and second drought were calculated as:

$$\mathrm{Drought-induced\ changes\ in\ AGB} = \mathrm{AGB}_{\mathrm{drought\ year}} - \mathrm{AGB}_{\mathrm{normal\ year}}, \tag{2}$$

where $\mathrm{AGB}_{\mathrm{drought\ year}}$ and $\mathrm{AGB}_{\mathrm{normal\ year}}$ were AGB in the drought year and averaged across the two normal years during the first and second drought, respectively.

2.5. *Statistical analyses*

Prior to analysis, tests were performed to assess the homoscedasticity and normality of the data utilized in the mixed-effects models. To address questions 1 and 2, mixed-effects models for repeated measures analysis were performed to examine impacts of drought stage, warming, N addition, and their interactions on the resistance, resilience, and species asynchrony of plant community and three functional groups over the whole experimental period. Drought stage, warming, N addition, and their interactions were set as fixed factors. The random effect structure was specified as a random intercept and slope for drought stage within each block (for details, see Appendix S1), which accommodates the repeated measures design and minimizes the potential effects of interactions between two consecutive drought stages in our data analyses. If there were significant interactions between drought stage and warming/N addition, the responses of these variables to warming and N addition during the first and second drought were further explored using mixed-effects models. Warming, N addition, and their interactions were considered as fixed factors, and block as a random factor during both first and second drought. It is important to note the differences of structure of mixed-effects model between the first and second drought (for details, see Appendix S2). During the second drought, the variables of first drought as covariate factors were included in the mixed-effects models to control for differences in baseline values between the first and second drought. Mixed-effects models were also performed to investigate the influences of warming, N addition, and their interactions on the drought-induced changes in AGB of plant community and rare species during the first and second drought. The 'lme' in the '*nlme*' package in R was used in these analyses. In addition, Tukey's honestly significant difference test ($P < 0.10$) with blocks as random effects for multiple comparisons were used to examine the differences among the absolute value of changes in the resistance and resilience of community and three functional groups under recurrent droughts, warming, and N addition over the whole experiment period.

The differences between first and second drought of the resistance, resilience, and species asynchrony of community and three functional groups in each of the six blocks averaged across the four treatments (i.e., the effects of recurrent droughts) were calculated as:

$$\left((\mathrm{C}+\mathrm{W}+\mathrm{N}+\mathrm{WN})_{\mathrm{Second}} - (\mathrm{C}+\mathrm{W}+\mathrm{N}+\mathrm{WN})_{\mathrm{First}}\right)/(\mathrm{C}+\mathrm{W}+\mathrm{N}+\mathrm{WN})_{\mathrm{First}} \times 100\%, \tag{3}$$

where C, W, N, and WN refer to control, warming, N addition, and warming plus N addition.

In addition, the effects of warming and N addition on the resistance, resilience, and species asynchrony of community and three functional groups as well as the drought-induced changes in AGB of community and rare species in each of the six blocks were calculated as:

$$(\mathrm{W}+\mathrm{WN}-\mathrm{C}-\mathrm{N})/(\mathrm{C}+\mathrm{N}) \times 100\% \tag{4}$$

and

$$(\mathrm{N}+\mathrm{WN}-\mathrm{C}-\mathrm{W})/(\mathrm{C}+\mathrm{W}) \times 100\%, \tag{5}$$

respectively, over the whole experiment period, first and second drought.

Simple linear regressions were conducted to examine the relationships of community resistance/resilience with the resistance/resilience and asynchrony of three functional groups over the whole experimental period as well as in the first and second drought. Linear regression analyses were also conducted to explore the relationships of drought-induced changes in plant community AGB with that in rare species AGB across the two drought stages. In addition, the relationship of warming-induced changes in dominant species resilience with warming-induced changes in rare species asynchrony and the relationship between N-induced changes in community resilience and N-induced changes in subordinate species resilience over the whole experimental period were detected by linear regression analyses. Moreover, simple linear regression was used to investigate the relationship of rare species resilience with rare species asynchrony during the second drought. All statistical analyses were conducted using R version 4.2.2 (R Development Core Team, 2022).

Based on the results from linear regressions analysis and theoretical knowledge, structural equation models (SEMs) were used to identify causal linkages between community resistance/resilience and the resistance/resilience and asynchrony of three functional groups over the whole experimental period as well as in the first and second drought, respectively. The fit of each model was evaluated with the chi-square (χ^2) and root mean square error of approximation (RMSEA) tests (Grace and Bollen, 2005). The SEM analyses were performed in AMOS 21.0.1 (Amos Development Corporation, Greene, ME, USA).

3. Results

3.1. Resistance of plant community and functional groups

Averaged across the four treatments, the resistance of community and subordinate species during the second drought were 10.9 % (Fig. 1a; Table 1, $P < 0.10$) and 41.6 % (Fig. 1c; $P < 0.001$) lower than those during the first drought, respectively. Over the whole experimental period, N addition significantly reduced the resistance of community, dominant, subordinate, and rare species by 31.5 %, 31.8 %, 24.4 %, and 26.4 %, respectively (Fig. 1; all $P < 0.05$). Neither warming nor its interaction with N addition affected the resistance of community or three functional groups, whereas N addition interacted with drought stage to affect the resistance of rare species ($P < 0.05$). In addition, the decrease of community resistance under N addition was greater than that under recurrent droughts (Fig. 1a inset and S3a).

When the first and second drought were analyzed separately, warming and its interaction with N addition had no influence on the resistance of plant community or three functional groups during the first drought. However, N addition decreased the resistance of community, dominant species, subdominant species and rare species by 29.9 % ($P < 0.01$), 27.1 % ($P < 0.05$), 25.0 % ($P < 0.10$) and 48.4 % ($P < 0.05$), respectively (Fig. 1; Table 2). During the second drought, warming reduced the resistance of community, dominant species, and rare species by 13.0 % ($P < 0.05$), 11.9 % ($P < 0.10$) and 34.0 % ($P < 0.10$), respectively. Nitrogen addition suppressed the resistance of community, dominant species, and subordinate species by 33.5 %, 35.7 %, and 28.1 %, respectively (Fig. 1a, b, c; all $P < 0.01$). However, there was no interaction between warming and N addition on the resistance of community or three functional groups during either drought stage.

3.2. Resilience of plant community and functional groups

Averaged across the four treatments, the resilience of community, dominant, subordinate, and rare species during the second drought was 70.3 %, 73.0 %, 69.6 %, and 63.2 % lower than those during the first drought, respectively (Fig. 2; Table 1, all $P < 0.001$). Over the whole experimental period, warming increased community resilience by 8.38 % (Fig. 2a; $P < 0.05$). Nitrogen addition enhanced the resilience of community and subordinate species by 10.4 % and 44.7 % (Fig. 2c; both $P < 0.01$), respectively. Significant interactions between warming and N addition on the resilience of community and rare species were detected in the whole experimental period (both $P < 0.05$). In addition, warming interacted with drought stage to affect the resilience of community ($P < 0.05$) and dominant species ($P < 0.10$), and N addition interacted with drought stage to affect the resilience of community, dominant, and subordinate species (all $P < 0.05$). Moreover, the changes in community resilience under recurrent droughts were greater than those under

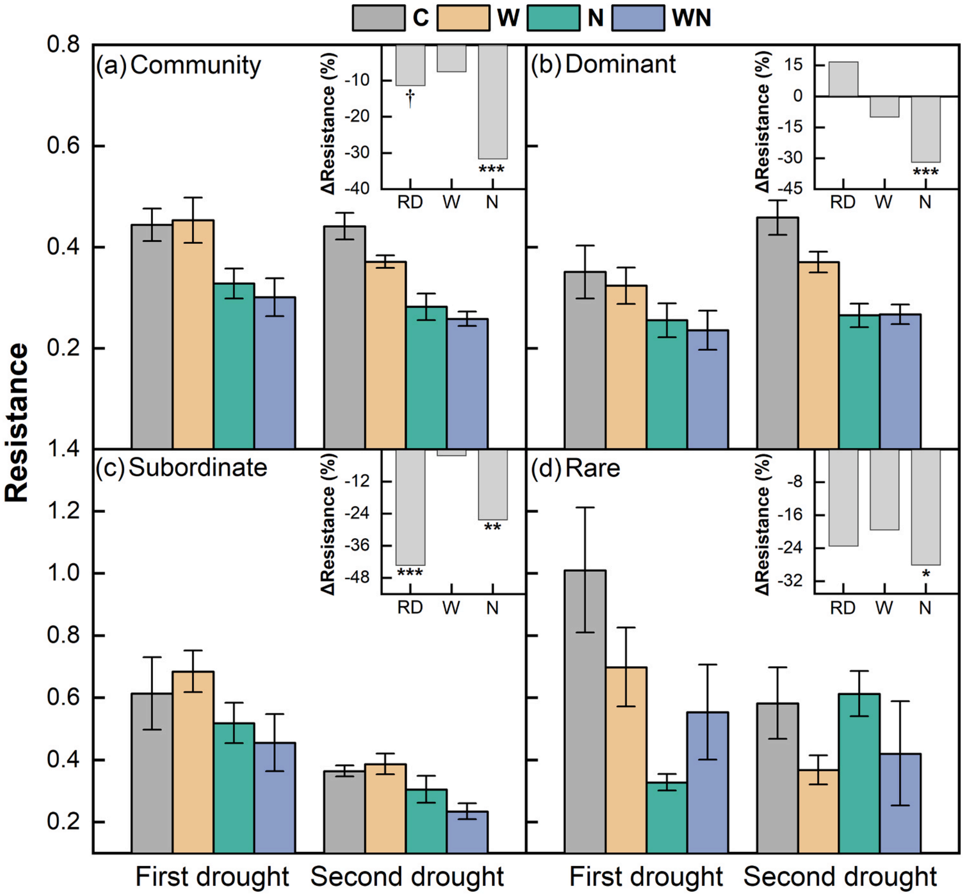

Fig. 1. Effects of warming and N addition on the resistance of community (a), dominant (b), subordinate (c), and rare species (d) during the first and second drought (means ± 1 SE, $n = 6$). Insets show the resistance changes of community and three functional groups induced by recurrent droughts, warming, and N addition over the whole experiment period. †$P < 0.10$, *$P < 0.05$, * *$P < 0.01$, and * **$P < 0.001$. C: control, W: warming, N: nitrogen addition, WN: W plus N, RD: recurrent droughts.

Table 1
Summary (*F* values) of mixed-effects models on the effects of drought stage (D), warming (W), nitrogen addition (N), and their interactions on the resistance, resilience, and species asynchrony of aboveground biomass of community and three plant functional groups (dominant, subordinate, and rare species) over the whole experimental period. *df* and *ddf* are the abbreviations of the degree of freedom and denominator degree of freedom, respectively. †$P < 0.10$, *$P < 0.05$, * *$P < 0.01$, and * **$P < 0.001$.

	Source of variation	*df, ddf*	Community	Dominant	Subordinate	Rare
Resistance	D	1, 35	4.11†	2.08	23.9 * **	2.85
	W	1, 35	1.83	2.40	0.05	1.88
	N	1, 35	41.5 * **	30.7 * **	9.31 * *	4.32 *
	W×N	1, 35	0.01	1.18	1.67	2.43
	D×W	1, 35	0.77	0.22	0.10	0.83
	D×N	1, 35	0.01	1.84	0.40	6.37 *
	D×W×N	1, 35	1.15	0.86	0.05	2.04
Resilience	D	1, 35	247 * **	103 * **	36.0 * **	15.5 * **
	W	1, 35	4.40 *	1.62	1.51	0.25
	N	1, 35	7.69 * *	0.03	12.5 * *	1.51
	W×N	1, 35	6.59 *	2.37	0.96	6.77 *
	D×W	1, 35	5.39 *	3.19†	1.47	0.09
	D×N	1, 35	33.9 * **	6.05 *	20.1 * **	2.22
	D×W×N	1, 35	2.65	0.25	1.54	4.93 *
Species asynchrony	D	1, 35	2.68	0.66	0.43	0.63
	W	1, 35	0.77	1.69	0.04	5.39 *
	N	1, 35	2.75	0.91	9.51 * *	0.01
	W×N	1, 35	0.42	0.01	1.73	0.97
	D×W	1, 35	1.49	0.86	0.48	1.63
	D×N	1, 35	1.08	10.1 * *	1.69	0.01
	D×W×N	1, 35	0.65	2.01	0.45	0.49

Table 2
Summary (*F* values) of mixed-effects models on the effects of warming (W), nitrogen addition (N), and their interactions on the resistance, resilience, and species asynchrony of aboveground biomass of community and the three plant functional groups during the first and second drought. *df* and *ddf* are the abbreviations of the degree of freedom and denominator degree of freedom, respectively. †$P < 0.10$, *$P < 0.05$, * *$P < 0.01$, and * **$P < 0.001$.

		Source of variation	*df, ddf*	Community	Dominant	Subordinate	Rare
Resistance	First drought	W	1, 15	0.06	0.39	0.00	0.09
		N	1, 15	13.6 * *	6.04 *	3.43†	8.49 *
		W×N	1, 15	0.24	0.01	0.58	3.58
	Second drought	W	1, 14	5.34 *	3.17†	0.56	3.85†
		N	1, 14	44.8 * **	37.6 * **	10.8 * *	0.16
		W×N	1, 14	0.94	3.60	2.17	0.65
Resilience	First drought	W	1, 15	4.57 *	2.63	1.53	0.01
		N	1, 15	17.3 * **	1.95	16.4 * *	1.79
		W×N	1, 15	4.21†	1.17	1.26	5.63
	Second drought	W	1, 14	0.17	0.34	0.00	1.91
		N	1, 14	38.8 * **	6.98 *	1.84	0.20
		W×N	1, 14	9.63 * *	0.64	0.59	1.55
Species asynchrony	First drought	W	1, 15	0.10	0.15	0.15	0.62
		N	1, 15	0.33	21.2 * **	9.00 * *	0.03
		W×N	1, 15	1.82	2.79	0.19	1.69
	Second drought	W	1, 14	1.50	1.52	0.40	5.63 *
		N	1, 14	2.62	1.66	1.46	0.00
		W×N	1, 14	0.02	0.33	1.73	0.00

warming and N addition (Fig. 2a inset and S3e).

During the first drought, warming significantly promoted community resilience by 10.7 % (Fig. 2a; Table 2, $P < 0.05$,). Nitrogen addition stimulated the resilience of community and subordinate species by 22.0 % and 72.6 %, respectively (Fig. 2a, c; both $P < 0.01$). There were interactions between warming and N addition on the resilience of community ($P < 0.10$) and rare species ($P < 0.05$) in the first drought. During the second drought, N addition, but not warming, decreased the resilience of community and dominant species by 21.4 % ($P < 0.001$) and 31.9 % (Fig. 2b; $P < 0.05$), respectively. In addition, the interactions of warming and N addition were detected on community resilience in the second drought ($P < 0.01$).

3.3. *Species asynchrony of plant community and functional groups*

Averaged across the four treatments, the asynchrony of community and three functional groups did not differ between the first and second drought (Fig. 3; Table 1). Over the whole experimental period, warming and N addition did not affect the asynchrony of either community or dominant species (Fig. 3a, b). The asynchrony of subordinate species was reduced by 37.3 % under N addition (Fig. 3c; $P < 0.01$). Warming suppressed the asynchrony of rare species by 22.1 % (Fig. 3d; $P < 0.05$). There was no interaction between warming and N addition on the asynchrony of plant community or three functional groups. However, N addition interacted with drought stage to affect the asynchrony of dominant species ($P < 0.01$).

When the first and second drought were analyzed separately, warming and its interaction with N addition had no effect on the asynchrony of community or three functional groups during the first drought. Nitrogen addition significantly increased the asynchrony of dominant species by 108 % (Fig. 3b; Table 2, $P < 0.01$), but inhibited that of subordinate species by 51.1 % (Fig. 3c; $P < 0.01$). During the second drought, warming decreased the asynchrony of rare species by 31.3 % (Fig. 3d; $P < 0.05$). Neither N addition nor its interaction with warming influenced the asynchrony of community or three functional groups.

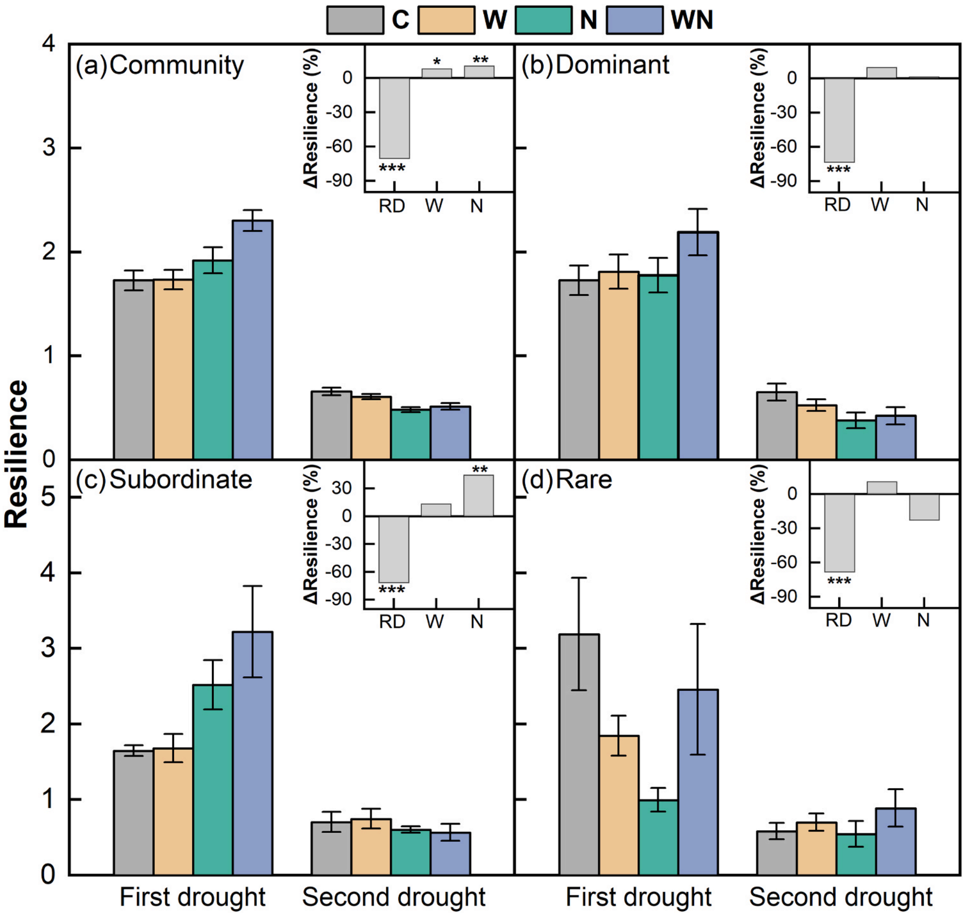

Fig. 2. Effects of warming and N addition on the resilience of community (a), dominant (b), subordinate (c), and rare species (d) during the first and second drought (means ± 1 SE, $n = 6$). Insets show the resilience changes of community and three functional groups induced by recurrent droughts, warming, and N addition over the whole experiment period. $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. See Fig. 1 for abbreviations.

3.4. Driving factors for community resistance and resilience under warming and N addition over the five years

Over the whole experimental period, community resistance increased linearly with the resistance of dominant, subordinate, and rare species as well as the asynchrony of subordinate species (Fig. S4a, b, c, e). Community resilience showed a positive linear dependence on the resilience of dominant species, but negative correlations with the asynchrony of subordinate and rare species (Fig. S4g, k, l). In addition, the warming-induced changes in resilience of dominant species showed a negative dependence on those in asynchrony of rare species (Fig. S5), whereas the N-induced changes in community resilience demonstrated a positive linear relationship with those in the resilience of subordinate species (Fig. S6). The optimal SEMs accounted for 98 % and 87 % of the variations in community resistance and resilience, respectively (Fig. 4). The inhibited resistance of dominant species (standardized directly coefficient (SDC) = 0.78, Fig. 4a) under N addition was mainly responsible for the N-induced suppression in community resistance. Moreover, the warming-induced decreases in asynchrony of rare species lead to the stimulated community resilience under warming (SDC = 0.43, Fig. 4b). The N-induced enhancements in community resilience could be attributed to the increased resilience of subordinate species under N addition (SDC = 0.54).

3.5. Driving factors for community resistance and resilience under warming and N addition vary with recurrent droughts

During the first drought, community resistance and resilience increased linearly with the resistance and resilience of dominant species (Fig. S7a, g) and subordinate species (Fig. S7b, h), respectively. However, community resistance decreased with the asynchrony of dominant species (Fig. S7d) but was negatively correlated with the asynchrony of rare species (Fig. S7l). In addition, community resistance showed a positive relationship with the asynchrony of subordinate species (Fig. S7e). Moreover, 96 % and 93 % of the variations in community resistance and resilience, respectively, could be explained by the optimal SEMs. The suppressed community resistance under N addition primarily resulted from the N-induced reduction in the resistance of dominant species (SDC = 0.58, Fig. 5a). The stimulated community resilience under N addition could be attributed to the N-induced enhancement in the resilience of subordinate species (SDC = 0.46, Fig. 5b).

During the second drought, community resistance showed positive linear relationships with the resistance and the asynchrony of both dominant and subordinate species (Fig. S7 a, b, d, e). Community resilience increased linearly with the resilience and asynchrony of dominant species (Fig. S7g, j). In addition, the resistance of rare species showed a positive linear dependence on the asynchrony of rare species (Fig. S8). The optimal SEMs explained 99 % and 91 % of the variations in community resistance and resilience, respectively. The warming-induced decreases in the resistance of rare species (SDC = 0.38, Fig. 5c) accounted for the suppressed community resistance under warming. The N-induced reductions in the resistance (SDC = 0.63) and resilience (SDC = 0.40, Fig. 5d) of dominant species was mainly responsible for the decreased community resistance and resilience under N addition, respectively.

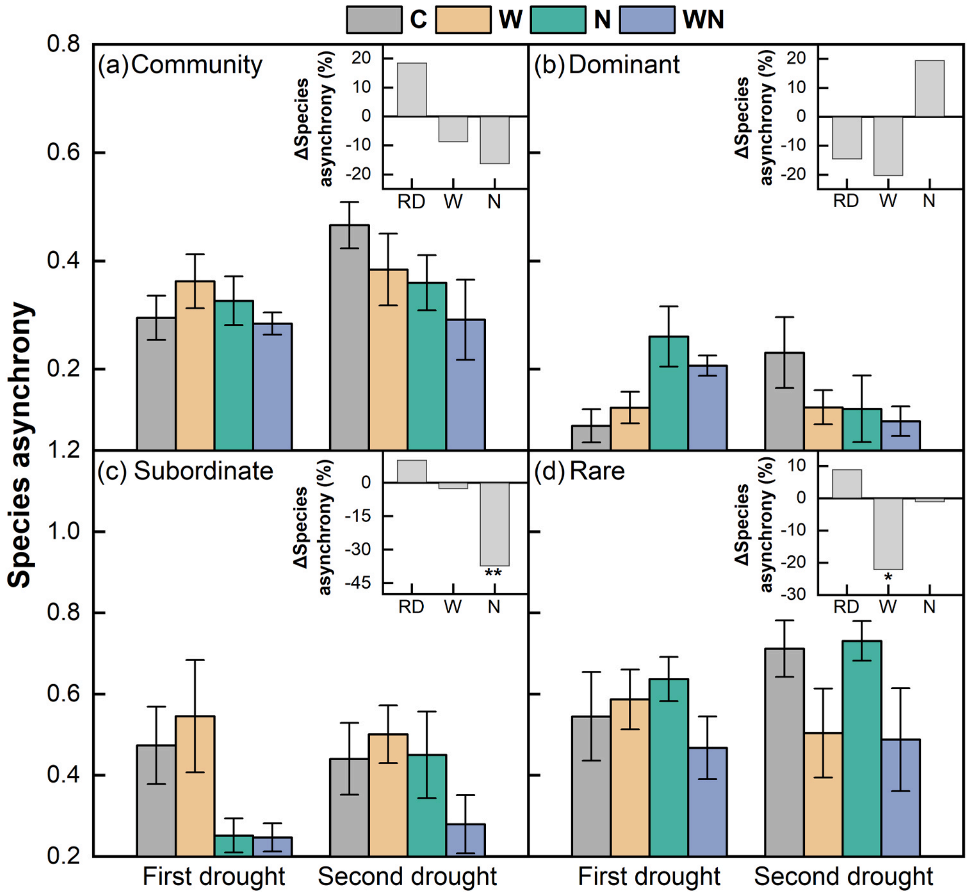

Fig. 3. Effects of warming and N addition on the asynchrony of community (a), dominant (b), subordinate (c), and rare species (d) during the first and second drought (means ± 1 SE, $n = 6$). Insets show the species asynchrony changes of community and three functional groups induced by recurrent droughts, warming, and N addition over the whole experiment period. $^{*}P < 0.05$ and $^{**}P < 0.01$. See Fig. 1 for abbreviations.

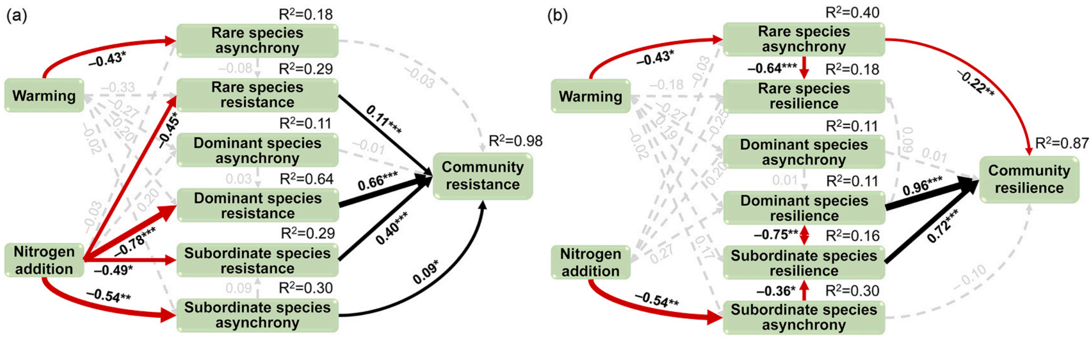

Fig. 4. The results of structural equation models showed the pathways through which warming and nitrogen addition affected community resistance (a) and resilience (b) over the whole experimental period. Solid and dashed arrows represent significant and non-significant paths, respectively. Black and red arrows indicate positive and negative pathways, respectively. Numbers adjacent to the arrows are standardized path coefficients with different significance levels: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Arrow width is proportional to the strength of the relationship. R^2 value for each dependent variable refers to the proportion of variance explained by the model. The final models fit the data well based on the results of the chi-square (χ^2) and RMSEA tests (a, $\chi^2 = 10.68$, $df = 16$, $P = 0.83$, RMSEA = 0; b, $\chi^2 = 13.46$, $df = 15$, $P = 0.57$, RMSEA = 0).

3.6. *Drought-induced changes in aboveground biomass of community and rare species*

During the first drought, N addition, but not warming, significantly intensified the drought-induced changes in AGB of community and rare species by 61.8 and 4.23 g m^{-2}, respectively (Fig. 6a, b; both $P < 0.05$). During the second drought, warming and N addition stimulated the drought-induced changes in community AGB by 13.8 ($P < 0.05$) and 53.9 g m^{-2} ($P < 0.001$), respectively. In addition, warming, but not N addition, enhanced the drought-induced changes in rare species AGB by 6.22 g m^{-2} ($P < 0.01$). There was no interaction between warming and N addition on the drought-induced changes in AGB of community and rare species. Moreover, the drought-induced changes in community AGB increased linearly with the drought-induced changes in rare species AGB across the two drought stages (Fig. 6c; $R^2 = 0.17$, $P < 0.01$).

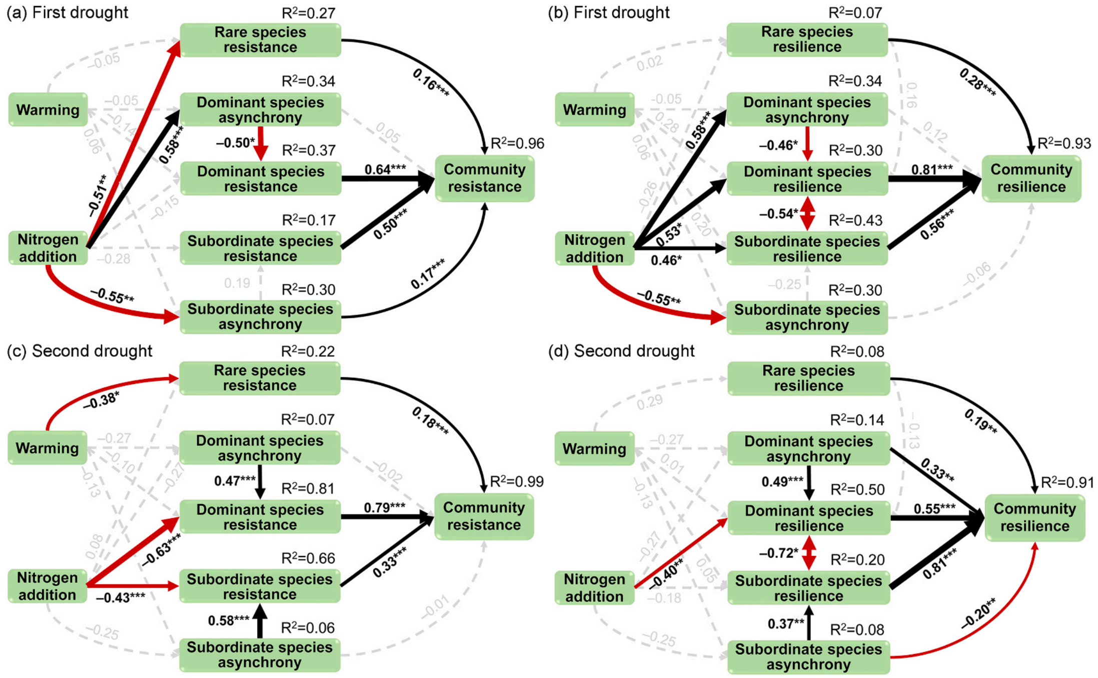

Fig. 5. The results of structural equation models showed the pathways through which warming and nitrogen addition on community resistance and resilience during the first (a-b) and second drought (c-d). Solid and dashed arrows represent significant and non-significant paths, respectively. Black and red arrows indicate positive and negative pathways, respectively. Numbers adjacent to the arrows are standardized path coefficients with different significance levels: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Arrow width is proportional to the strength of the relationship. R^2 value for each dependent variable refers to the proportion of variance explained by the model. The final models fit the data well based on the results of the chi-square and RMSEA tests (a, $\chi^2 = 11.86$, $df = 12$, $P = 0.46$, RMSEA = 0; b, $\chi^2 = 6.35$, $df = 9$, $P = 0.68$, RMSEA = 0; c, $\chi^2 = 4.45$, $df = 12$, $P = 0.97$, RMSEA = 0; d, $\chi^2 = 13.72$, $df = 10$, $P = 0.19$, RMSEA = 0.13).

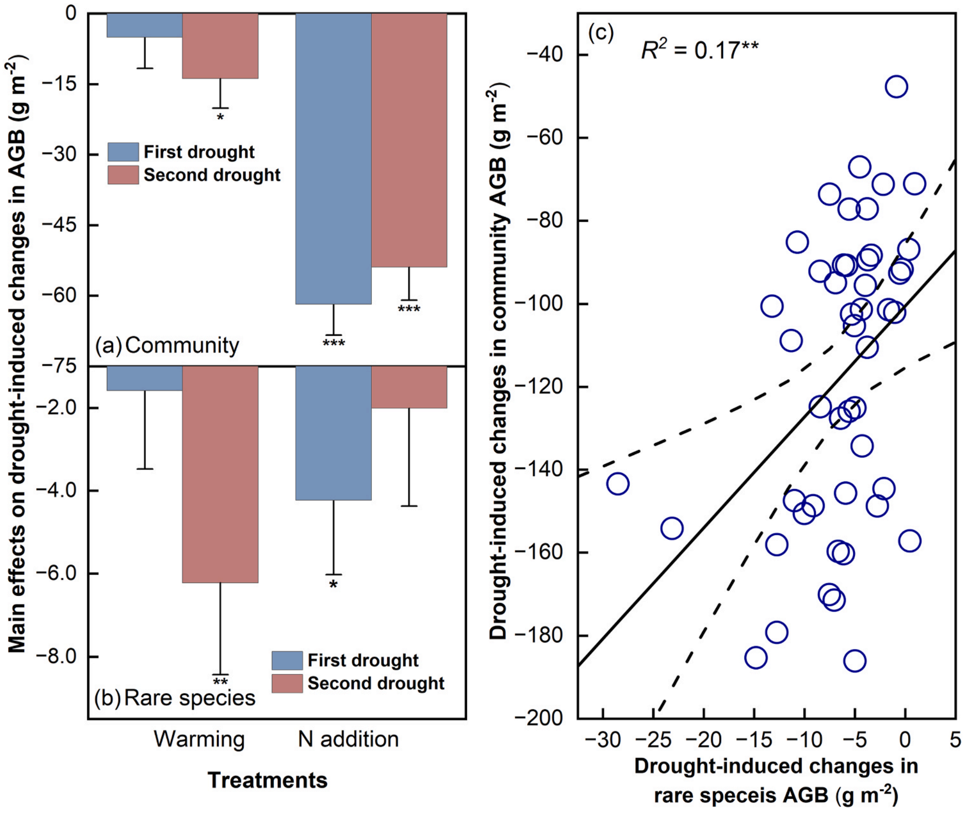

Fig. 6. The effects of warming and nitrogen (N) addition on drought-induced changes in aboveground biomass (AGB) of community (a) and rare species (b) during the first and second drought (Means ± 1 SE, $n = 12$). Dependence of the drought-induced changes in AGB of community on that in rare species across the two drought stages (c). Each data point represents the value of each plot across the two drought stages. The solid and dotted lines represent regression line and 95 % confidence interval, respectively. $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

4. Discussion

4.1. *Effects of recurrent droughts, warming, and N addition on community resistance and resilience over the whole experimental period*

Our results of the decreased community resistance and resilience under recurrent droughts are consistent with the observations from a previous experimental study conducted in a temperate grassland (Luo et al., 2023) and a meta-analysis (Liu et al., 2024). The lower community stability during the second drought may be attributed to the asymmetry of recovery between plant biomass and community composition after the first drought (Müller and Bahn, 2022; Luo et al., 2023). These findings suggest that drought has legacy effects on grassland ecosystems, which may affect plant community response to recurrent droughts (Hughes et al., 2018). In addition, the decreased resistance of subordinate species may explain the reductions in community resistance under recurrent droughts (Fig. 1 inset and S4b). Our results are consistent with the observations of a species removal study, which has revealed that the presence of drought-tolerant subordinate species could sustain community resistance (Mariotte et al., 2013). Although subordinate species has greater survival advantage under water stress due to their deeper roots in the semi-arid grassland (Yang et al., 2011), the cumulative negative impacts of recurrent droughts may exceed the drought tolerance thresholds of subordinate species, resulting in a suppressed resistance of subordinate species. These findings highlight the importance of subordinate species in maintaining the stability of ecosystem productivity under frequent extreme droughts and provide empirical evidence for the subordinate insurance hypothesis (Mariotte, 2014). The hypothesis suggests that subordinate species can compensate for the losses of ecosystem functions provided by other species under natural perturbations.

The neutral effects of warming on community resistance over the whole experimental period are inconsistent with the results of several previous grassland studies which have demonstrated that warming could stimulate community resistance (Yang et al., 2016; Yan et al., 2023a). Consistent community resistance under ambient and elevated temperature observed in our study may be ascribed to the unchanged resistance of three functional groups under warming. In addition, the increased community resilience under warming contradicts the neutral influences of warming on community resilience reported by previous studies (Yang et al., 2016; Yan et al., 2023a). The warming-induced decreases in rare species asynchrony could explain the enhanced community resilience under warming (Fig. 4b). Reduced rare species asynchrony may result in fewer ecological niches and nutrients being utilized by rare species during recovery, leaving a larger pool of available resources for other species. Given that dominant species play a pivotal role in driving community recovery, the shifts in resource allocation could accelerate dominant species resilience and consequently enhance community resilience (Figs. S4g and S5). The findings highlight that rare species are crucial for ecosystem recovery after extreme drought in the context of climate warming and provide new insights into the ecological functions of rare species under future climate change scenarios (Sutherland et al., 2013).

Over the whole experimental period, the reduced community resistance under N addition is consistent with the results of several previous studies conducted in temperate grasslands (Xu et al., 2014, 2022). Our results from the optimal structural equation model suggest that the N-induced reductions in dominant species resistance could mainly explain the decreased community resistance under N addition (Fig. 4a). It is supported by the mass ratio hypothesis (Grime, 1998), namely that ecosystem function is largely determined by the multifunctionality of dominant species. In addition, the asynchrony of subordinate species modulates the response of community resistance to N addition, providing more evidence for the insurance hypothesis, which has proposed that the decreased biomass of one or more species could be complemented by the increased production of other species (Yachi and Loreau, 1999). In contrast with the observations of several previous studies (Isbell et al., 2015; Wagg et al., 2017, 2022; Craven et al., 2018; Xu et al., 2021; Yan et al., 2023b), increasing evidence has demonstrated that species asynchrony, rather than species richness, may be more important in determining ecosystem stability (Zhang et al., 2016; Gilbert et al., 2020; Valencia et al., 2020; Muraina et al., 2021). Moreover, the increased community resilience under N addition observed in this work is consistent with the results of model simulations (DeAngelis, 1980; Harwell et al., 1981; DeAngelis et al., 1989) and field experiments (Bharath et al., 2020; Xu et al., 2022, 2023). Although community resilience is positively correlated with the resilience of dominant species, the evidence from our optimal structural equation model indicates that N-induced increases in community resilience can be accounted for by the enhanced resilience of subordinate species (Fig. 4b and S6). Subordinate species may have greater competitive advantages in resource access due to their deeper roots (e.g., water and N; Yang et al., 2011), which leads to them rapid recovery after drought. Therefore, elevated N availability might accelerate the recovery of subordinate species after drought, which could compensate for the loss of other species' biomass and ultimately increase community resilience. These findings imply that subordinate species may play vital roles in regulating community resilience following recurrent droughts under N addition and are supported by the subordinate insurance hypothesis (Mariotte, 2014).

The relative effect sizes of recurrent droughts, warming, and N addition on community resistance and resilience are further compared. The greater decreases of community resistance under N addition than under recurrent droughts suggest that the drought threshold of plant biomass may be lower under N enrichment in this semi-arid grassland (Fig. 1a), which is consistent with the results that N addition could exacerbate the negative impacts of drought on plant community productivity (Bharath et al., 2020; Meng et al., 2021). On the one hand, N addition may reduce ecosystem stability by decreasing species diversity and asynchrony (Hautier et al., 2015; Xu et al., 2022, 2023). On the other hand, soil acidification under long-term N addition, which may be exacerbated by recurrent droughts, can inhibit plant growth and exacerbate the instability of productivity (Yang et al., 2023). In addition, the greater changes in community resilience under recurrent droughts than those under warming and N addition indicate that frequent extreme climate events are more likely to breach ecosystem adaptation thresholds (Fig. 2a), which agrees with the results from a meta-analysis (Langley et al., 2018). Water availability is known to govern the structure and function of terrestrial ecosystems (Berdugo et al., 2020; Zhang et al., 2023), especially in the semi-arid grasslands. Thus, recurrent droughts may cause irreversible damage to the ecosystems by exacerbating water stress and subsequently suppress the recovery of plant community.

4.2. *Effects of warming on community resistance and resilience change with recurrent droughts*

Compared with the neutral effect of warming during the first drought, the decreased community resistance under warming during the second drought, which are consistent with the results of a previous study (Ma et al., 2024), can be attributed to the warming-induced reductions in rare species resistance (Fig. 5c). Our observations are contrary to those of several previous studies, which have emphasized the key roles of dominant species in maintaining ecosystem stability under warming (Yang et al., 2017; Wu et al., 2020; Quan et al., 2021; Yan et al., 2023a; Ma et al., 2024). Two possible reasons could help to explain the negative impacts of warming on grassland resistance under recurrent droughts. First, greater species asynchrony enhances the ability of plants to cope with environmental fluctuations, thereby improving community resistance (Yachi and Loreau, 1999; Loreau and de Mazancourt, 2013; He et al., 2022). Previous studies have demonstrated that warming can advance plant phenology, leading to increased synchrony among species

(Wang et al., 2016; Stuble et al., 2021). Thus, the warming-induced decreases in the asynchrony of rare species may lead to the reduced resistance of rare species during the second drought and consequently reduce community resistance (Fig. S8). Second, given that rare species (e.g., annual and/or biennial species) are characterized by resource-acquisitive traits (Jónsdóttir et al., 2023; Jing et al., 2024), warming may greater largely decrease rare species biomass by exacerbating water stress in topsoil (Fig. 6b). Although the biomass of rare species accounts for 6.97 % of the community biomass, the drought-induced changes in rare species biomass is a critical driving factor of the drought-induced changes in community biomass (Fig. 6c).

By contrast, the effects of warming on community resilience shift from positive during the first drought to neutral during the second drought. The results may be due to the trade-off between the positive and negative impacts of warming on plant growth. Warming-induced extension in the length of growing season could directly stimulate plant community recovery during the first drought. However, the intensified water stress caused by long-term warming during the second drought may exceed the drought tolerance threshold of plants, leading to limited growth or even premature death. These findings suggest that rare species can play a critical role in assessing community stability in the face of recurrent droughts under climate warming.

4.3. Effects of N addition on community resistance and resilience change with recurrent droughts

The impacts of N addition on community resistance have no difference between the first and second drought, but the mechanisms underlying community resistance response to N addition vary with recurrent droughts. Compared with the first drought, the influences of asynchrony of dominant and subordinate species are weakened during the second drought, which is similar with the results from a study established in an alpine meadow (Hou et al., 2023). It can be attributed to stress gradient hypothesis, which has proposed that organisms can resist increasing environmental stress by shifting their interspecific interactions from competition to facilitation (Callaway et al., 2002). Therefore, interspecific competition may turn into interspecific facilitation in the face of second drought in the semi-arid grassland, resulting in more synchronized dynamic of plant functional groups in resisting drought. In addition, dominant species represents an important component of community resistance response to N addition in both the first and second drought, supported by the mass ratio hypothesis (Grime, 1998). These findings highlight that the underlying mechanisms of community resistance response to N addition may shift from the complementary effects among species and/or functional groups to the dominance effect with increasing extreme drought events.

The influences of N addition on community resilience are reversed from positive during the first drought to negative during the second drought by reducing the resilience of dominant species during the second drought (Fig. 5d). These results are consistent with empirical evidence that N addition can exacerbate the negative impacts of second drought on plant community productivity (Bharath et al., 2020; Meng et al., 2021). First, with increasing occurrences of drought, the N-induced aggravation in biomass variation may cause irreversible damage to plant communities under recurrent droughts, subsequently restricting community recovery (Fig. 6a; Meng et al., 2021). Second, low water availability can indirectly inhibit plant growth by exacerbating soil acidification induced by N addition, ultimately reduce community resilience during the second drought (Yang et al., 2023). These findings highlight that dominant species may be crucial in controlling community resilience under N addition in the face of more frequent droughts.

In this study, the limitation of the nondestructive method for biomass estimation is the omission of plant height, which is a critical determinant of aboveground biomass (Quan et al., 2024). This may have resulted in an underestimation of biomass in the enriched N plots. However, the study was conducted in a semi-arid grassland, which is typically characterized by short-stature vegetation and relatively uniform height of plant communities. In these systems, productivity is more strongly driven by community cover rather than height (Fig. S2; Ji et al., 2009; Sanaei et al., 2018). Therefore, the conclusions drawn from this study remain robust and reliable.

5. Conclusion

The varied effects of warming and N addition on community resistance and resilience with recurrent droughts indicate the necessity to consider the predicted intensification of interannual precipitation anomalies when assessing ecosystem stability under future global change scenarios. In-depth investigation into the impacts of single and recurrent drought events on grassland ecosystems are beneficial to better understanding of the complex effects of external stresses, such as climate warming and atmospheric N deposition, on ecosystem functioning. By elucidating the changes of underlying mechanisms under recurrent droughts, more flexible and effective ecological management strategies can be developed to address the ongoing challenges of global change.

CRediT authorship contribution statement

Fan Yongge: Investigation, Data curation. **Zhang Jiajun:** Investigation, Data curation. **Kong Lingjie:** Investigation, Data curation. **Zhou Guilin:** Investigation, Data curation. **Song Jian:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Qiu Xueli:** Investigation, Data curation. **Wang Haidao:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Li Heng:** Investigation, Data curation. **Zhang Qingshan:** Investigation, Data curation. **Feng Jiayin:** Writing – review & editing, Data curation. **Ru Jingyi:** Writing – review & editing, Data curation. **Li Benqing:** Investigation, Data curation. **Wan Shiqiang:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Jiang Lin:** Writing – review & editing, Data curation. **Zhou Jiaxin:** Investigation, Data curation. **Xia Jianyang:** Writing – review & editing, Investigation, Data curation.

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.2025.109712.

Data availability

Data will be made available on request.

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