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Nitrogen enrichment differentially regulates the response of ecosystem stability to extreme dry versus wet events

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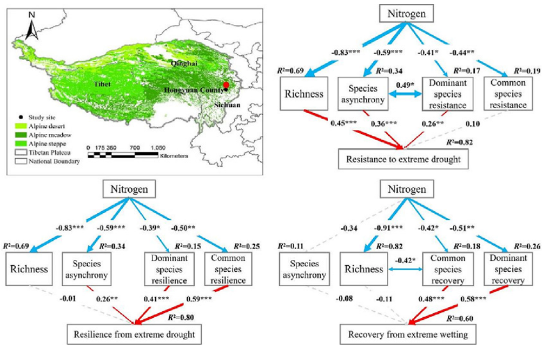
HIGHLIGHTS

- N regulates ecosystem stability in responses to extreme dry vs. wet events.
- Relative importance of main mechanisms varies with extreme dry vs. wet events.
- N addition interacts with discrete extreme rainfall events to affect ANPP stability.

GRAPHICAL ABSTRACT



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ABSTRACT

Extreme climate events, such as severe droughts and heavy rainfall, have profound impacts on the sustainable provision of ecosystem functions and services. However, how N enrichment interacts with discrete extreme climate events to affect ecosystem functions is largely unknown. Here, we investigated the responses of the temporal stability (i.e., resistance, recovery, and resilience) of aboveground net primary productivity (ANPP) in an alpine meadow to extreme dry and wet events under six N addition treatments (0, 2, 4, 8, 16, 32 g N m^{-2} $year^{-1}$). We found that N addition had contrasting effects on the responses of ANPP to the extreme dry versus wet events, which resulted in no overall significant effects on ANPP stability across 2015–2019. Specifically, high N addition rates reduced the stability, resistance, and resilience of ANPP in response to extreme drought, whereas medium N addition rates increased ANPP stability and recovery in response to the extreme wet event. The main mechanisms underlying the response of ANPP to extreme drought and wet events were discrepant. Species richness, asynchrony, and dominant species resistance contributed most to the reduction of ANPP resistance to extreme drought, while species asynchrony and dominant and common species resilience contributed most to the decrease of ANPP resilience from extreme drought with N enrichment. The ANPP recovery from the extreme wet event was mainly explained by dominant and common species recovery. Our results provide strong evidence that N deposition mediates ecosystem stability in response to extreme dry and wet events in different ways and modulates the provisioning of grassland ecosystem functions under increasing extreme climate events.

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1. Introduction

As a fundamental attribute of an ecological system, stability is essential to the sustainable provision of ecosystem functions and services to humanity (Isbell et al., 2015; Ma et al., 2017). A growing number of studies have demonstrated that changes in ecosystem stability are mainly attributable to increasing levels of anthropogenic environmental change, especially extreme climate events (ECEs) (Xu et al., 2015; Zhang et al., 2019; Wilcox et al., 2020). Ongoing climate change is expected to dramatically increase the frequency, severity, and spatial extent of ECEs, including more intense droughts and heavy precipitation (Fischer et al., 2013; Reichstein et al., 2013). These ECEs are likely to impose increased stress on terrestrial ecosystems worldwide and significantly disrupt ecosystem functioning (Thomas et al., 2004; Hoover et al., 2014). Due to the high sensitivity of grassland ecosystem productivity to water availability (Wilcox et al., 2020), extreme precipitation events would threaten the temporal stability of aboveground net primary productivity (ANPP) (Ciais et al., 2005; Huang and Xia, 2019).

Three attributes have been proposed to describe ecosystem stability in response to ECEs, including (1) resistance, which is the ability of an ecosystem to persist its original state during an environmental perturbation (Van Ruijven and Berendse, 2010); (2) recovery, which is the capacity to return to the original state following an extreme event (Carter and Blair, 2012); and (3) resilience, or the capacity of ecosystem to resist change in the face of disturbance and return to the equilibrium state following disturbances. In other words, resilience involves two processes: resistance and recovery (Ingrisch and Bahn, 2018). Extreme drought affects different components of stability (Matos et al., 2019; Zhang et al., 2019). For example, some studies demonstrated that the stability of productivity in grasslands under extreme drought was characterized mainly by high resistance (Zhang et al., 2019; Huang and Xia, 2019), while other studies illustrated that rapid recovery, rather than resistance, stabilized ecosystem productivity in grasslands following extreme drought (Stuart-Haentjens et al., 2018; Matos et al., 2019). These different results may be due to the differences in ecosystem properties, such as nutrient availability and community composition, and the magnitude and duration of ECEs (Mitchell et al., 2016). Compared to the number of studies on extreme drought impacts (Knapp et al., 2015; Zhang et al., 2019), studies on extreme wet events are relatively scarce. Thus, it is unclear whether ecosystem stability and its attributes respond differently to extreme wet events as they do to extreme drought.

Multiple mechanisms have been proposed to explain changes in ecosystem stability caused by ECEs, such as species diversity that mainly involves sampling effect and complementary effect (Allison, 2004), and the stability of dominant species (Ma et al., 2017; Ma et al., 2020b). Previous results suggested that higher species diversity stabilizes ecosystem productivity by promoting resistance to ECEs for two reasons (Hautier et al., 2015; Isbell et al., 2015; O'Brien et al., 2017). First, high species diversity increases the likelihood that the community includes species that are resistant to environmental disturbance or better adapted to changing environments (i.e., the sampling effect) (Loreau and Hector, 2001; Polley et al., 2003). Second, high species diversity provides a stronger complementary effect against extreme precipitation conditions (Morin et al., 2014; Isbell et al., 2015), because species differ in their resistance and resilience to severe climatic disturbances (Sakschewski et al., 2016; O'Brien et al., 2017). As a crucial indicator of the complementary effect, species asynchrony refers to a scenario in which the reduction in the abundance of one species is more likely to be compensated by the increase in the abundance of other species (Loreau and de Mazancourt, 2008). Species asynchrony is expected to promote ecosystem stability (Grman et al., 2010). A growing body of research has also shown that the impact of extreme climates on stability is highly determined by dominant species independent of changes in species richness (Evans et al., 2011; Zhang et al., 2019). Subordinate species are likewise important, particularly for the maintenance of ecosystem functioning during periods of stress (Wang et al., 2007; Kardol et al., 2010). Thus, the resistance, recovery, and resilience of dominant and subordinate species contribute largely to ecosystem stability in response to ECEs (Ma et al., 2017; Yang et al., 2017b). Determining which of the above mechanisms dominate the resistance, recovery and resilience of ecosystem productivity in response to extreme precipitation events is crucial to predict ecosystem stability and provisioning of ecosystem services in the context of frequent ECEs.

Cumulative alterations in N availability induced by chronic N deposition (Ma et al., 2020a), usually accompanied by discrete extreme climate, may largely influence ecosystem productivity (Fay et al., 2015; Ma et al., 2020a). A hierarchical-response framework (HRF) has been proposed to explain the sensitivity of ecosystem to extreme events (Smith et al., 2009). For instance, an increase in N availability could reduce species diversity (Xu et al., 2015) and change community composition and structure (Grman et al., 2010; Evans et al., 2011; Carlsson et al., 2017) by reordering of species or species asynchrony (Ma et al., 2020b; Xu et al., 2015). These N-induced changes in community properties will in turn influence ecosystem resistance to and recovery from extreme precipitation events (Isbell et al., 2015; Bharath et al., 2020). However, there is no consensus about N-induced changes in community properties (i.e., diversity loss) and their effects on ecosystem responses to extreme precipitation events. For example, it was suggested that N-induced diversity loss would weaken the resistance and recovery of grassland productivity to a severe drought (Tilman and Downing, 1994). Nevertheless, Bharath et al. (2020) showed that diversity loss induced by nutrient additions was not associated with drought resistance or recovery rates in naturally assembled grasslands. Compared to drought studies, studies of N regulation on grassland response to extreme wet events are relatively scarce. Previous studies indicated that ANPP responded to N addition more strongly in wet than dry years (Bai et al., 2008), and that N addition had stronger impacts on primary production at mesic sites than in arid areas (Yahdjian et al., 2011). The increase in growing season precipitation has been predicted to increase species diversity (Xu et al., 2015; Yang et al., 2017a) and promote the temporal stability of aboveground biomass (Xu et al., 2015), mainly due to positive biodiversity-stability relationships (Hautier et al., 2015). That is to say, the projected increase in short-term heavy rainfall may potentially offset negative impacts of increased atmospheric N deposition on ecosystem stability (Xu et al., 2015; Liu et al., 2019), but conversely high nutrient availability would exacerbate drought stress (Gessler et al., 2017). Therefore, we hypothesized that (1) N enrichment will interact with discrete extreme precipitation events to affect ecosystem stability; (2) ecosystem stability and its attributes would respond differently to extreme dry and wet events under N enrichment; and (3) the mechanisms underlying N impacts on ecosystem stability in responses to extreme dry and wet events would differ. For example, N may impact different attributes (e.g., resistance, recovery, or resilience), or different pathways (e.g., species richness, asynchrony or dominant/common/rare species resistance, recovery, and resilience).

We tested the above hypotheses by taking advantage of an experiment with six N treatments in an alpine meadow on the Tibetan Plateau over 2015–2019. During this period, the alpine meadow naturally experienced one extreme dry event and one extreme wet event, which provided an opportunity for us to evaluate the regulatory effect of N on alpine meadow ecosystem ANPP stability and its characteristics in response to extreme precipitation events and to explore the underlying mechanisms. Being the largest plateau in the world and known as the Earth's "Third Pole" (Ma et al., 2020a, 2020b), the Tibetan Plateau (> 4000 m a.s.l., ca. 700,000 km^2) is larger than countries such as Afghanistan, France, and Somalia, and is characterized by alpine meadow, steppe, and desert (Fig. 1A). Observations from Tibetan meteorological stations have shown that the occurrence of ECEs has generally increased over the last several decades (Zhang et al., 2023). The Tibetan Plateau has also been undergoing an intense increase in the N deposition rate from 0.87 to 1.38 g N m^{-2} $year^{-1}$ (Shen et al., 2019). However, little attention has been paid to the impact of frequent extreme precipitation events on the stability of the alpine meadow ecosystem on the Tibetan Plateau, especially in the context of rapid increase in global N deposition. The Tibetan Plateau has high biodiversity and is important for livestock production (Chen et al., 2020; Ma et al., 2020b). Changes in vegetation can influence the carbon cycle, energy balances, and the ecosystem services provided to human society (Chen et al., 2020). The sustainable management and provision of these services requires a deeper understanding of how the alpine meadow ecosystem responds to extreme precipitation events under increasing N addition rates.

2. Materials and methods

2.1. Study site

The field experiment was conducted at the Qinghai-Tibetan Plateau (QTP) Research Base of Southwest Minzu University in Hongyuan County (32°48′N, 102°33′E) in a relatively flat alpine meadow on the eastern edge of QTP at an elevation of approximately 3500 m (Fig. 1A). Long-term (1961–2013) mean annual temperature and mean annual precipitation are 1.5 °C and 747 mm, respectively. According to the World Reference Base for Soil Resources, soils at this study area are classified as Mat Crygelic Cambisol (Li and Sun, 2011) with loamy sand texture (14.5 % fine sand, 0.1 % coarse sand, and 85.4 % clay silt). Top soil (0–20 cm) organic C content is 37 g/kg, and the total N content is 3.5 g/kg. Plant species can be divided into different functional groups, including the *Deschampsia*

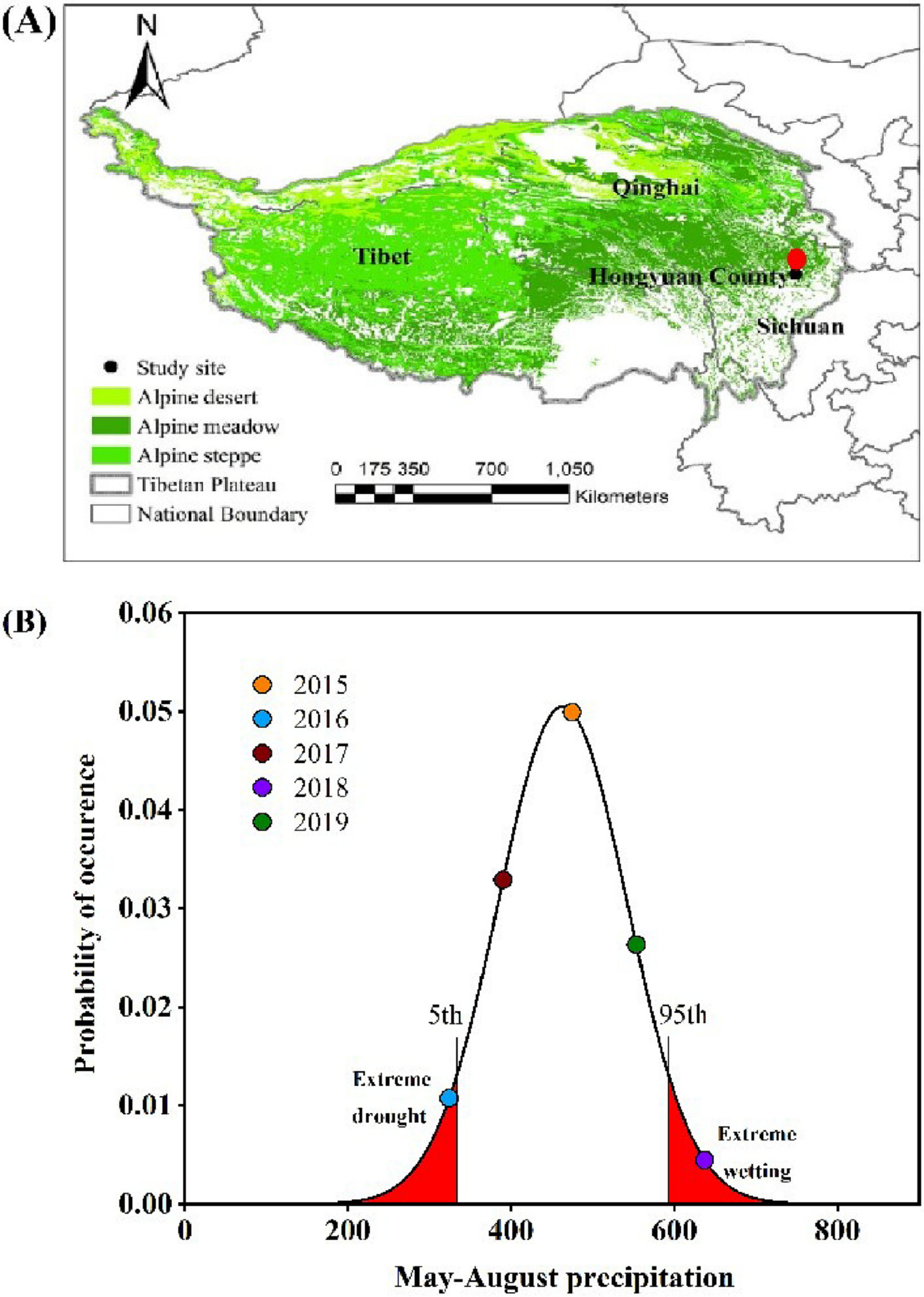

Fig. 1. (A) A map of our study area. Point indicates location. (B) Probability distribution diagram of total precipitation from May to August in the growing season from 1960 to 2019. The orange, blue, red, purple, and green circles represent 2015, 2016 (extreme dry year), 2017, 2018 (extreme wet year), and 2019, respectively.

caespitosa-dominant grass group, the *Carex*-dominant sedge group, and the forb group (dominated by *Euphorbia esula* Linn., *Polygonum viviparum* L., and *Anemonastrum coelestinum (*Franch.*) Mosyakin*) (Ma et al., 2020b). During the experiment, the cumulative precipitation from May to August (critical period for plant growth) during the growing season was 474.9 mm, 324.2 mm, 390.2 mm, 637.2 mm and 553.4 mm in 2015–2019 (Fig. S1), respectively.

2.2. Experimental design

A N addition experiment was established in early May 2014 using a complete random block design with six rates of N input (0, 2, 4, 8, 16, and 32 g N m^{-2} $year^{-1}$). The high N addition was intended to perturb the ecosystem to the extent that we can learn about the response of ecosystem processes and not just to mimic the real scenarios currently in the studied area. Hereafter, we denote these six N treatments as N0, N2, N4, N8, N16, and N32. Each treatment was repeated randomly five times, and a total of 30 plots of 8×8 m^2 were established with 3 m walkways between adjacent plots. During the growing season (May–September) of 2014–2019, N was added as NH_4NO_3 (>99 %) by hand every month before rainfall (Ma et al., 2020b). To distribute dry NH_4NO_3 evenly in the plots, we mixed dry NH_4NO_3 with soil. The N0 treatment was applied only to soil without NH_4NO_3. The concentration of soil inorganic nitrogen (SIN) increased gradually with increased N addition (Fig. S2), which indicated that the expected treatment effect had been achieved.

2.3. Extreme precipitation events

We collected 60 years (1960–2019) of monthly precipitation data for Hongyuan from nearby meteorological stations. We categorized extreme drought and extreme wet years as years with cumulative precipitation from May to August being lower than 5th percentile and greater than 95th percentile of the historical probability distribution, respectively (Hoover et al., 2014). Using frequency distribution of long-term precipitation from May to August in Hongyuan County (Fig. 1B), we determined the year 2016 to have been an extremely dry year (below the 5th percentile) and the year 2018 to have been an extremely wet year with 10 days of continuous flooding (beyond the 95th percentile; Fig. 1B).

2.4. ANPP measurement

ANPP was measured every year when biomass peaked (usually in the middle of August). All living plants were clipped at the ground level in a 0.50×0.50 m^2 quadrat frame, which was randomly placed in each plot while avoiding overlapping quadrats during the experiment. We separated all living plants into different species, oven-dried them at 65 °C for 48 h and weighed them. According to the average relative abundance, we further divided plants into three species groups, dominant (>5 %), common (1–5 %), and rare (<1 %) species (Ma et al., 2017). The specific classification of dominant, common and rare species was described by Ma et al. (2020b).

2.5. Statistical analysis

The temporal stability of ANPP was calculated as the ratio of temporal mean ANPP (μ) to its standard deviation (σ) across the years 2015–2019 (Ma et al., 2017). The temporal stability of ANPP in response to extreme dry and wet events were calculated using the same method across the years 2015–2017 and 2017–2019, respectively. We also calculated the ANPP stability of dominant, common, and rare species using the same method.

To directly compare sites under different N addition rates, we inferred dimensionless resistance, recovery, and resilience by employing relative measurement (Kreyling et al., 2017).

$$Resistance = \frac{\mathrm{ANPP}_{event}}{\mathrm{ANPP}_{pre-event}}$$

$$Recovery = \frac{\mathrm{ANPP}_{post-event}}{\mathrm{ANPP}_{event}}$$

$$Resilience = \frac{\mathrm{ANPP}_{post-event}}{\mathrm{ANPP}_{pre-event}}$$

where ANPP_{event} is the ANPP in years of extreme dry and wet events; $\mathrm{ANPP}_{pre\text{-}event}$ is the ANPP of the years preceding the extreme dry and wet events; and $\mathrm{ANPP}_{post\text{-}event}$ is the ANPP of the years following the extreme dry and wet events. A resistance index equal to or >1 means complete resistance, and a value of 0 indicates no resistance (no biomass production during extreme precipitation year) (Ruppert et al., 2015; Kreyling et al., 2017). A recovery index equal to 1 indicates complete recovery and <1 represents incomplete recovery. When the recovery and resilience indices are >1, then it indicates overcompensation.

Species diversity in each plot was estimated using species richness, which was defined as the total number of species present in the same frame that ANPP was sampled every year. Species asynchrony was quantified as:

$$\varphi_y = 1 - \varphi_x = 1 - \frac{\sigma^2}{\left(\Sigma_{i=1}^{n}\sigma_i\right)^2}$$

where φ_y is species asynchrony of each plot; φ_x is species synchrony of each plot; and σ^2 is the variance of plant community biomass. Specifically, during extreme dry and wet events, the value of σ^2 is equal to the variance of plant community biomass during 2015–2017 and 2017–2019, respectively. σ_i is the standard deviation of biomass of species i in a plot with n species (Loreau and de Mazancourt, 2008; Ma et al., 2017). This index is 1 when species fluctuations are perfectly asynchronized, and is 0 when species fluctuations are perfectly synchronized (Ma et al., 2017).

To test our first two hypotheses, we used linear mixed-effects models to evaluate N addition effects on ANPP temporal stability, species asynchrony, resistance to extreme dry and wet events, and recovery from and resilience to extreme dry and wet events, in which N addition and the block were treated as the fixed factor and random factor, respectively. The least significant difference (LSD) test ($P < 0.05$) was used for a posteriori comparisons. We also performed linear mixed-effects models to test the effects of N addition, year, and their interaction on ANPP and species richness, in which N addition and year were treated as fixed factors, and the block was treated as a random factor. We used linear regression to explore the relationships between resistance (recovery/resilience/ANPP stability) to extreme drought and resistance (recovery/resilience/ANPP stability) to extremely wet conditions. To test our third hypothesis, we used linear regression to explore community resistance (recovery and resilience) in relation to species richness, species asynchrony, and the resistance (recovery and resilience) of dominant, common, and rare species.

According to the regression results, structural equation modeling (SEM) was performed to investigate the dominant pathways through which N addition influenced the responses of resistance (recovery and resilience) to extreme dry and wet events. We first considered a full model that contained all possible pathways (Fig. S3), and used the χ^2 test, Akaike information criteria (AIC), and root square mean errors of approximation (RMSEA) to evaluate the fit of the final model. All statistical analyses were conducted using SPSS software package: SPSS 22.0 for windows, (SPSS Inc., Chicago, IL, USA). The SEM analyses were performed using AMOS 21.0 (Amos Development Corporation, Chicago, IL, USA). Origin 8.5 was used for plotting data.

3. Results

3.1. ANPP stability and its attributes in response to the extreme drought under N enrichment

We found that nitrogen addition under extreme drought significantly negatively affected ANPP stability, resistance, resilience, species richness, and species asynchrony, but did not significantly affect recovery (Fig. 2,

Table S1). Also, N enrichment under extreme drought significantly negatively affected common species resistance and resilience, but had no significant effects on (1) dominant species resistance, recovery, or resilience, (2) common species recovery, or (3) rare species resistance or resilience (Fig. 3).

Bivariate regressions showed that ANPP resistance and resilience from the drought significantly increased with species richness and species asynchrony under extreme drought. ANPP recovery had no relationship with species richness, but decreased with increasing species asynchrony (Fig. 4). Dominant species resistance and resilience significantly promoted community resistance and resilience from the drought. Dominant species recovery marginally stimulated community recovery from extreme drought (Fig. S4A-C). Common species resistance, recovery, and resilience also significantly improved community resistance, recovery and resilience (Fig. S4D-F). However, there were no significant relationships of community resistance, recovery, or resilience with the corresponding rare species resistance, recovery, or resilience (Fig. S4G-I).

3.2. ANPP stability and its attributes in response to the extreme wet event under N enrichment

We found that nitrogen addition significantly affected ANPP stability and recovery in response to the extreme wet event, which showed a unimodal trend along increasing N addition rates. Also, N enrichment significantly negatively affected species richness during the wet event, but did not affect resistance, resilience, or species asynchrony (Fig. 2, Table S1). Moreover, N enrichment during the wet event significantly affected dominant species resistance and recovery, and rare species recovery, but did not significantly affect (1) dominant species resilience, (2) common species resistance, recovery, or resilience, or (3) rare species resistance or resilience (Fig. 3).

Bivariate regressions showed that ANPP resistance to the extreme wet event marginally decreased with species richness, and no significant relationships were found between species richness and ANPP recovery or resilience from the extreme wet event (Fig. 5A-C). ANPP resilience had a negative and linear correlation with species asynchrony under the wet event. There was no relationship between ANPP resistance, recovery, or species asynchrony (Fig. 5D-F). Dominant species resistance and recovery significantly promoted ANPP resistance and recovery from the extreme wet event (Fig. S5AB). Common species recovery and resilience significantly improved the recovery and resilience from the extreme wet event (Fig. S5EF). There were no relationships between rare species resistance, recovery, and resilience and community resistance, recovery, and resilience from the wet event (Fig. S5G-I).

Considering both extreme dry and wet events over the 5 years, N addition did not significantly affect the temporal stability of ANPP (Fig. S6, Table S1). There was no significant difference in ANPP stability between the control (N0) and any of the N addition treatments (Fig. S6).

3.3. The pathways of N addition impacts on ANPP resistance, recovery, and resilience

Although N addition had significant negative effects on ANPP resistance to extreme drought, resilience from extreme drought, and recovery from the extreme wet event, the pathways of the impacts differed. The SEM analysis showed that the model explained 82 % of the variation in ANPP resistance to extreme drought. Nitrogen addition exerted a negative effect on the response of ANPP resistance to extreme drought mainly by negatively affecting species richness (path coefficients = −0.83), species asynchrony (path coefficients = −0.59), and dominant species resistance (path coefficients = −0.41) (Fig. 6A, Table S3, all $P < 0.05$). The SEM model explained 80 % of the ANPP resilience from extreme drought, in which N

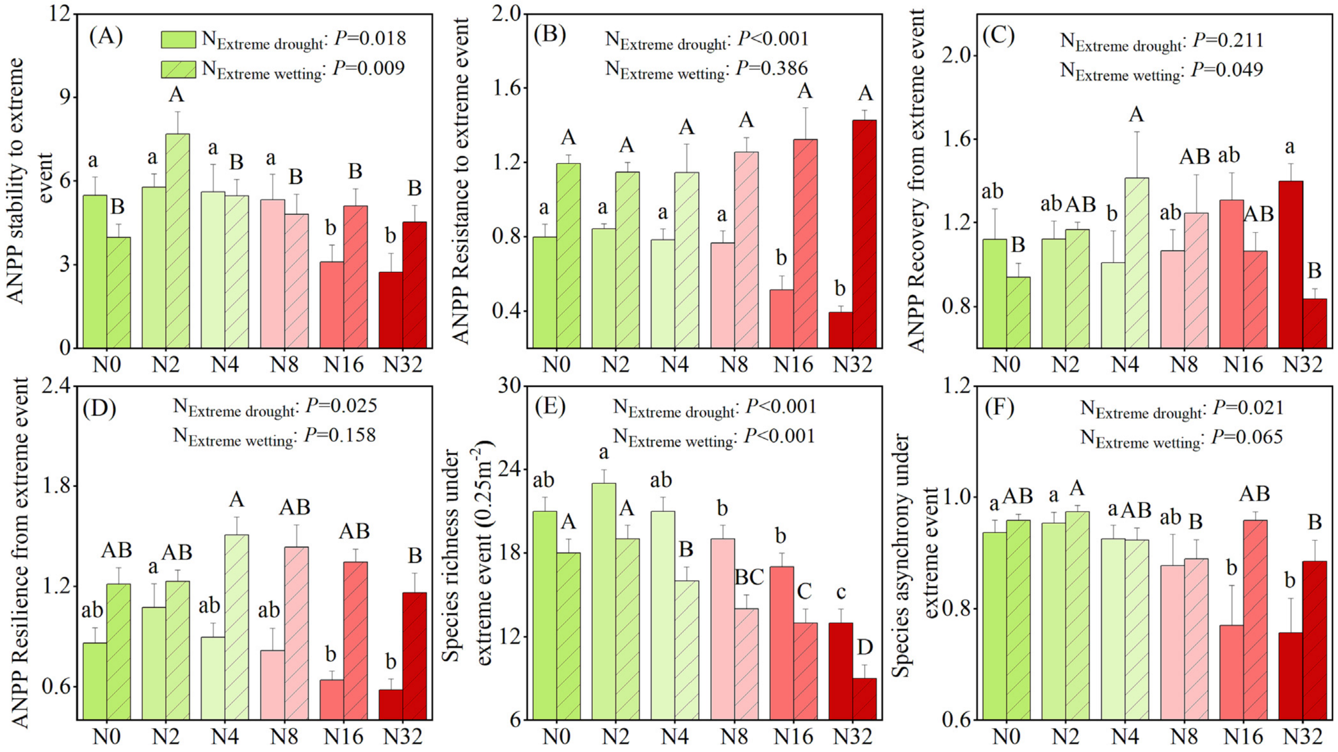

Fig. 2. Nitrogen effects on ANPP stability and resistance to extreme drought and the wet event (A, B); ANPP recovery and resilience from extreme drought and the wet event (C, D); and species richness and species asynchrony under extreme drought and the wet event (E, F). Means ± se. The values of all indices in response to extreme drought and the wet event under each N addition treatment are evaluated over 2015–2017 and 2017–2019, respectively. Bars of different colors represent different N addition treatments. Bars without and with diagonals represent extreme dry and wet events, respectively. Different lower-case and upper-case letters indicate a significant difference in how the indicators responded to extreme drought and the wet event among different N treatments at $P < 0.05$, respectively.

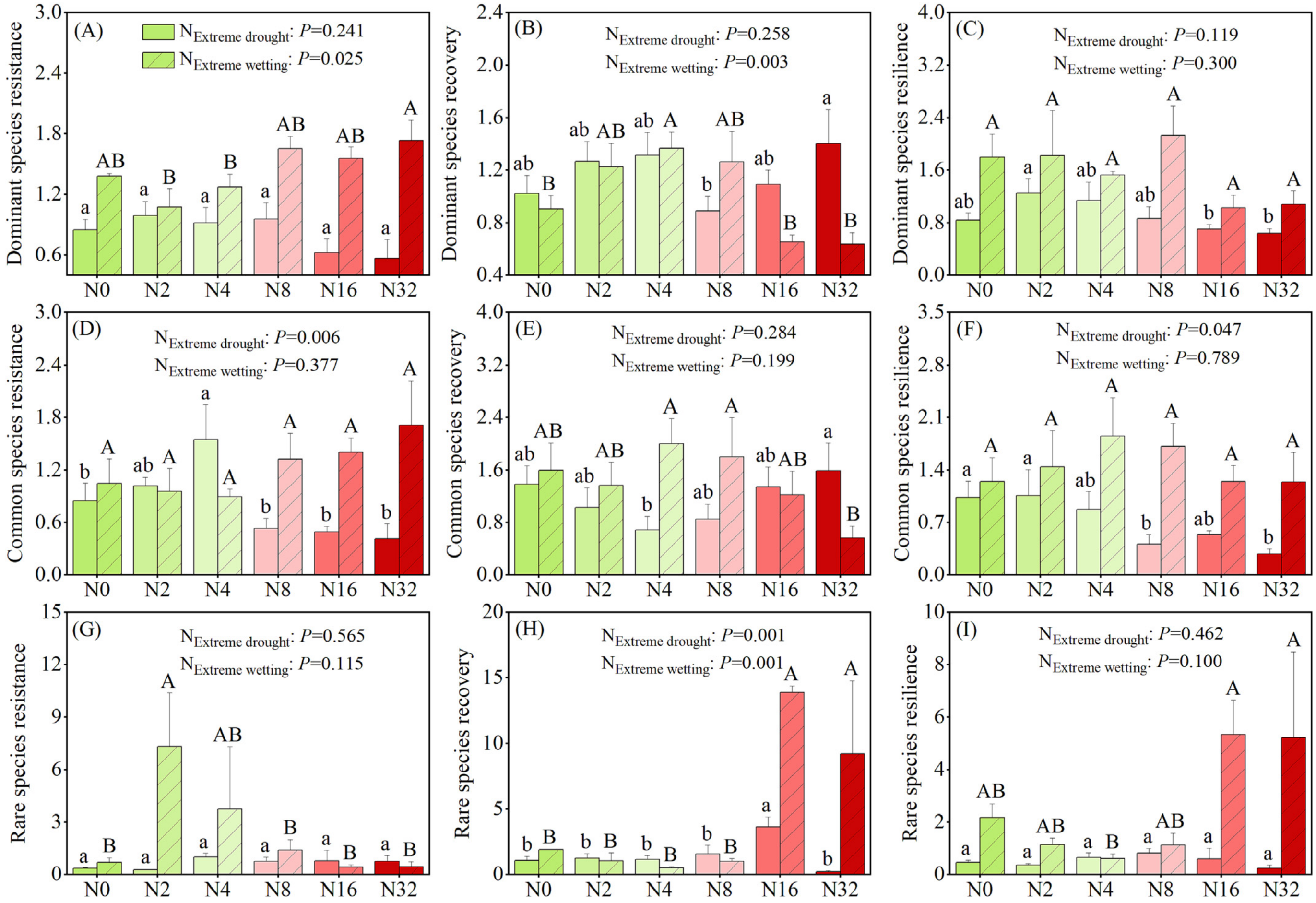

Fig. 3. Nitrogen effects on dominant, common, and rare species resistance to extreme drought and the wet event (A, D, G); dominant, common, and rare species recovery from extreme drought and the wet event (B, E, H); and dominant, common, and rare species resilience from extreme drought and the wet event (C, F, I). Means ± se. The values of all indices in response to extreme drought and the wet event under each N addition treatment are evaluated over 2015–2017 and 2017–2019, respectively. Different lower-case and upper-case letters indicate a significant difference in how the indicators respond to extreme drought and the wet event among different N treatments at $P < 0.05$, respectively.

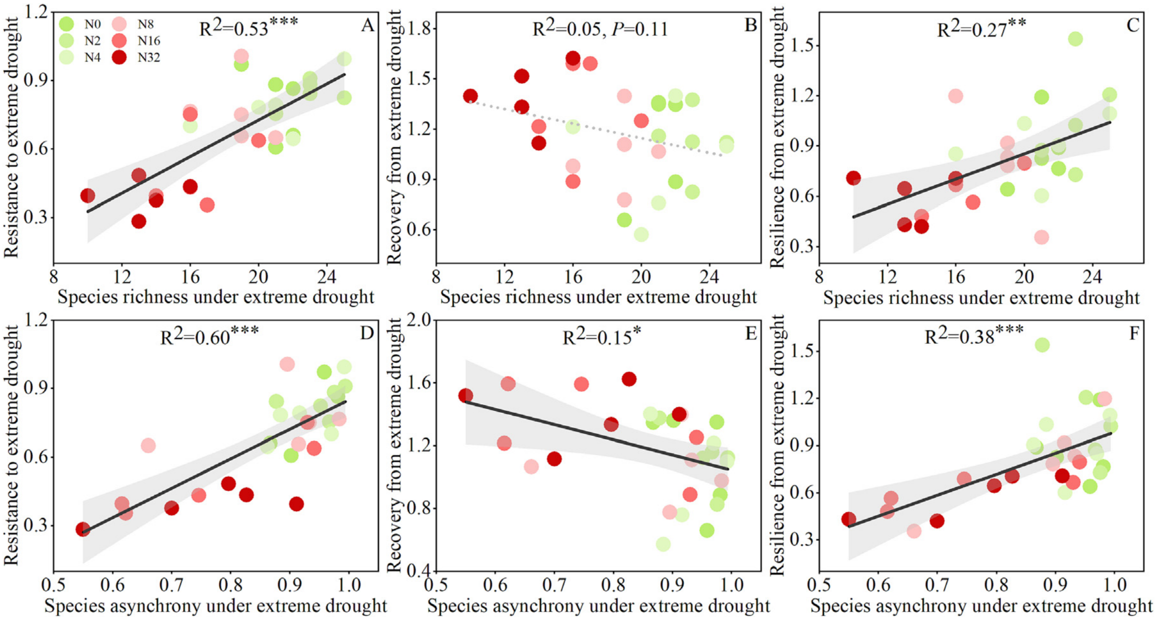

Fig. 4. Relationships between extreme drought resistance, recovery, and resilience and species richness and species asynchrony under extreme drought. The black solid lines are significant regression lines, and the gray dashed lines are non-significant regression lines. Each circle represents an experimental plot (n = 30). Shaded area represents 95 % confidence intervals. Level of significance: ***: $P < 0.001$; **: $0.001 \le P < 0.01$; *: $0.01 \le P < 0.05$.

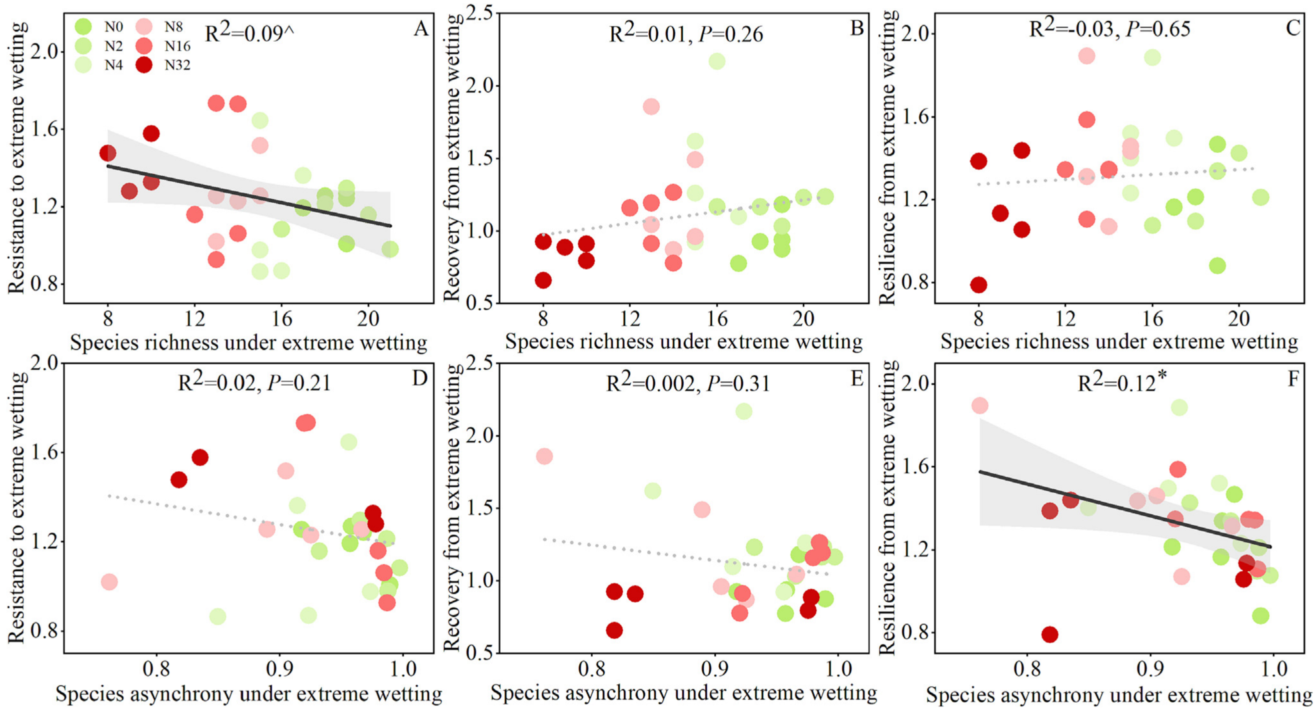

Fig. 5. Relationships between extreme drought resistance, recovery, and resilience and species richness and species asynchrony under the extreme wet event. The black solid lines are significant regression lines, and the gray dashed lines are non-significant regression lines. Each circle represents an experimental plot (n = 30). Shaded area represents 95 % confidence intervals.

addition negatively affected ANPP resilience from extreme drought mainly by negatively affecting species asynchrony (path coefficient = −0.59), dominant species resilience (path coefficient = −0.39), and common species resilience (path coefficient = −0.50) (Fig. 6B, all $P < 0.05$). The SEM model explained 60 % of the variation in recovery from the extreme wet event, in which N enrichment presented indirect effects on the recovery

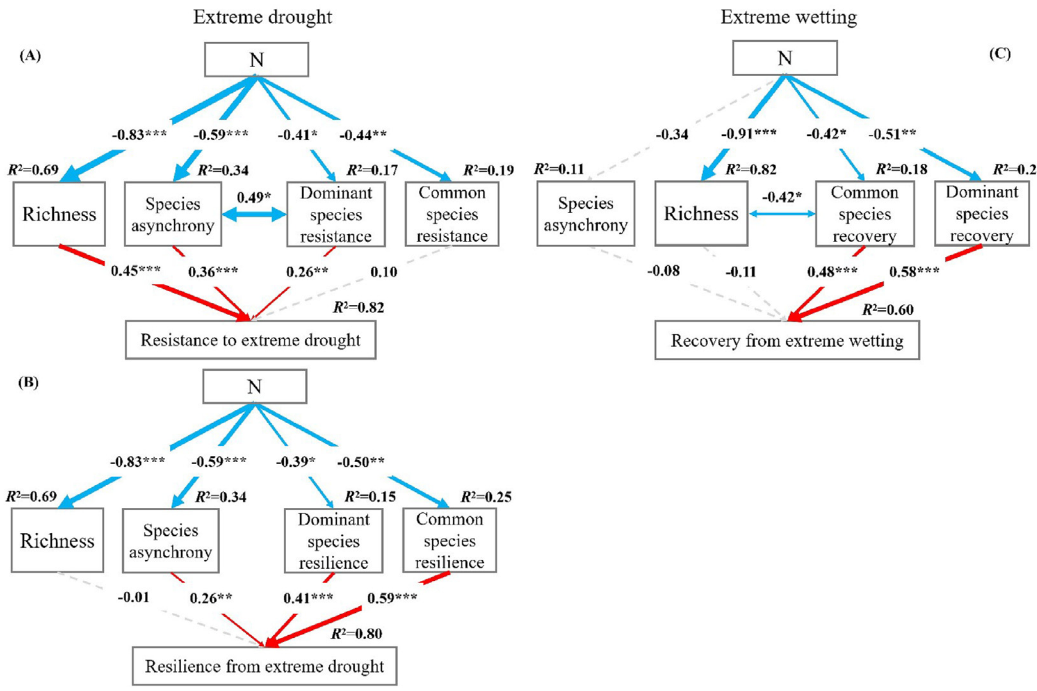

Fig. 6. The final structural equation modeling (SEM) shows the direct and indirect effect of N addition on (A) resistance to extreme drought, (B) resilience from extreme drought, and (C) recovery from the extreme wet event. Red and blue solid arrows indicate significant positive and negative pathways, respectively, and gray dashed arrows represent non-significant pathways. The R^2 values associated with variables suggest the proportion of variance explained by relationships with other variables. The values adjacent to arrows are standardized path coefficients. Arrow width is proportional to the strength of the relationship. Goodness-of-fit statistics for (A):χ^2 = 4.139, P = 0.658, d.f. = 6, root mean square error of approximation (RMSEA) < 0.001, AIC = 34.14; for (B): χ^2 = 4.039, P = 0.775, d.f. = 7, RMSEA<0.001, AIC = 32.04; for (C): χ^2 = 7.503, P = 0.277, d.f. = 6, RMSEA = 0.09, AIC = 37.50. Level of significance: ***: $P < 0.001$; **: $0.001 \le P < 0.01$; *: $0.01 \le P < 0.05$.

from the extreme wet event by negatively affecting dominant species recovery (path coefficient = −0.51) and common species recovery (path coefficient = −0.42, all $P < 0.05$, Fig. 6C).

4. Discussion

4.1. Nitrogen changes ecosystem ANPP stability in response to extreme precipitation events

We found that N enrichment interacted with discrete extreme precipitation events to affect ecosystem stability, which supported our first hypothesis. Nevertheless, our work can be distinguished from previous studies on ecosystem responses to extreme precipitation events by three aspects. First, most of the previous studies focused mainly on extreme drought (Carlsson et al., 2017; Zhang et al., 2019), but we examined the effects of both extreme drought and wet events on an ecosystem under six nitrogen treatments over time. Second, the extreme drought in 2016 and the extreme wet event in 2018 occurred naturally in our ongoing N addition experiment, which provided a unique opportunity to examine the interaction between N enrichment and discrete extreme precipitation events on ecosystem stability. Third, and most importantly, we demonstrated that N regulated ecosystem ANPP stability and that its attributes responded to extreme drought and wet events differently (Fig. S7AB), which supported our second hypothesis. The linear increase in ANPP with N addition rates at the beginning of experiment and the decrease of ANPP under drought stress (Fig. S8AB) suggested that the ANPP of this ecosystem was co-limited by N and water, which explained the sensitivity of ANPP to N enrichment and extreme precipitation events.

Nitrogen regulates the responses of ecosystem stability to different extreme precipitation events by changing resistance, recovery, and resilience. In the face of extreme drought, N addition significantly reduced the resistance of ANPP to drought, which can be explained in the following ways. First, N addition favors the allocation toward above-ground net primary production (Ladwig et al., 2012; Gessler et al., 2017) and has the potential to reduce below-ground productivity (Bai et al., 2015; Peng et al., 2017). The latter would limit the capability of plants to satisfy their water demands, increase their susceptibility to severe water shortage during drought (Meyer-Grünefeldt et al., 2015; Dziedek et al., 2016), and consequently decrease the resistance to drought. This explanation was supported by our findings that N significantly reduced BNPP (Table S2, Fig. S9) and that the resistance to drought was significantly positively correlated with BNPP in the drought year (Fig. S10). Second, N addition can affect plant hydraulic traits, such as by increasing stomatal conductance (Fangmeier et al., 1994), promote the risk of hydraulic failure (Gessler et al., 2004; Gessler et al., 2017), and thus reduce resistance to drought. Our finding that N enrichment reduced drought resistance significantly corroborated the results reported by Friedrich et al. (2011) and Xu et al. (2014) but contradicted those reported by Carlsson et al. (2017) and Evans et al. (2011). These divergent responses to drought are probably caused by differences in magnitude, severity, and/or the duration of drought across the various experiments (Evans et al., 2011; Zhang et al., 2019).

Resilience from drought also decreased significantly with N addition. A possible explanation for this could be the variation of the functional group composition under N addition treatments (Carlsson et al., 2017). Our previous work illustrated that N addition significantly decreased the biomass of forbs (Ma et al., 2020b), which would reduce resilience from drought (Mariotte et al., 2013). Other possible explanations might be that species richness and asynchrony were significantly reduced with higher N addition rates, which could also decrease resilience (Xu et al., 2014; Carlsson et al., 2017). In our study, the recovery from drought did not significantly change with N addition. However, the recovery values of all N addition treatments ranged from 1.00 to 1.39, which indicated that the alpine meadow ecosystem fully recovered from drought.

In juxtaposition to the regulating effects of N on ANPP responses to extreme drought, N addition had no significant effects on the resistance or resilience of ANPP to the extreme wet event. However, it significantly affected ANPP recovery from the wet event, which was mainly attributed to the N effects on the recovery of dominant and common species (Fig. S5BE). With increasing N addition rates, the recovery from the extreme wet event tended to first increase and then decrease, which was mainly because high N addition stimulates the growth of functional species with high stature, e.g. *Deschampsia caespitosa* (Linn.) *Beauv.* or *Elymus nutans Griseb.* (Fig. S11F-J) (Ma et al., 2020b), which in turn causes light limitation, inhibits the recruitment of short seedlings (Ma et al., 2020a), and reduces the recovery from the extreme wet event.

We recognized that the two extreme events that occurred during our study might not be completely independent. However, the impact of the first event on the second one should be very weak because the recovery values from drought were >1 and the resilience values were similar to 1 in 2017, which indicated that the ecosystem had recovered from drought. Also, the non-significant difference in the species asynchrony of the control during the extreme dry and wet events suggested that the complementary effects among the species had also recovered one year after the drought. So, overall we believe that the extreme dry event did not influence our results.

4.2. Mechanisms underlying the different responses of ecosystem ANPP stability to extreme dry and wet events under N enrichment

Our results support the third hypothesis that the key drivers affecting the responses of ANPP stability to the extreme drought and wet events were different. The positive relationship between species richness and resistance but not with recovery from drought indicated that plant diversity played contrasting roles in regulating resistance and recovery. The ANPP changes further suggested that plant diversity, particularly plant species richness, played a major role in stabilizing ecosystem productivity by increasing resistance to drought rather than recovery (Tilman and Downing, 1994; Isbell et al., 2015). Similar to several previous studies (Shafran-Nathan et al., 2012; Klimeš et al., 2013), we also found a significant positive relationship between species richness and resilience from drought. Nevertheless, species richness was not retained in the SEM as a significant predictor of resilience from drought, probably because of the stronger effects of species asynchrony and because the resilience of dominant and common species overrode the significant effect of species richness on resilience from drought.

Species asynchrony buffers community productivity change under environmental fluctuations as decreased biomass of vulnerable species is compensated for by the growth of other species (Loreau and de Mazancourt, 2008; Hautier et al., 2014). The significant reduction of species asynchrony induced by N enrichment can make ecosystems more vulnerable to ECEs (Wilcox et al., 2017; Zhang et al., 2019). The large reduction in species asynchrony contributed considerably to the decrease of ANPP resistance and resilience, and thus the ANPP stability to drought. This effect may be explained as follows. First, N addition usually stimulates the growth of grasses and sedges with the same functional traits, like being higher in height (Niu et al., 2010; Ma et al., 2020b), which inhibits the growth of other functional groups like legumes (Table S2, Fig. S11A-E). The decline in the abundance of legumes and consequent reduction in N fixation rates further reduced the effect of legumes on the nutrient supply (Suding et al., 2005). This reduction signified that N enrichment decreased resource-based niche partitioning, e.g., differing nutrient and light foraging strategies, which resulted in a lower resistance and resilience to extreme environmental fluctuations (Xu et al., 2014). Second, grasses are more sensitive to water availability than other functional groups, as indicated by the decreased biomass during drought and post-drought years, but higher biomass during the wet event and the subsequent years. The biomass of other functional groups did not change significantly during extreme and non-extreme precipitation years (Fig. S11A-E). Therefore, the significant decrease in species asynchrony and associated increase in grass biomass caused by N enrichment combined to make the ecosystem more susceptible to extreme precipitation events.

As supported by Grime's mass ratio hypotheses (Grime, 1998), a growing body of evidence highlights the control of dominant species in ecosystem functioning (Sasaki and Lauenroth, 2011; Ma et al., 2017). In our study, we found that dominant species resistance and resilience significantly promoted ANPP resistance and resilience to drought, and that dominant species recovery significantly improved ANPP recovery from the extreme wet event (Figs. S4AC & S5B). These findings reinforced the importance of dominant species characteristics in governing the response of ANPP to extreme precipitation events (Hoover et al., 2014). Furthermore, common species resilience and recovery were considered to be one of the main contributors that affect drought resilience and recovery from extreme wet events. The regulatory effects of common species during extreme precipitation events may from the N-enrichment induced changes to the dominance hierarchy of this alpine meadow and increased the abundance of common species (Ma et al., 2020b). Previous studies showed that common species regrow more after stress (Kohyani et al., 2009; Mariotte et al., 2013), which benefits ecosystem recovery after ECEs.

Our results indicate that N addition regulates the sensitivity of alpine meadow ANPP stability and its attributes (i.e., resistance, recovery, and resilience) to extreme dry and wet events through different mechanisms. Our findings provide new empirical evidence that the relative importance of these mechanisms (i.e., species richness, asynchrony or resistance, recovery and resilience of species groups) vary with extreme dry and wet events.

5. Conclusions

Based on a field experiment with six N addition treatments, we investigated how N enrichment interacted with discrete extreme dry and wet events to affect ecosystem ANPP stability and its attributes (i.e., resistance, recovery, and resilience). We found that despite experiencing these two extreme events, the alpine meadow ecosystem under N enrichment remained relatively stable. This stability is mainly because N regulated ANPP in response to extreme dry and wet events differentially by changing resistance, recovery, and resilience. When experiencing the extreme drought event, N addition significantly reduced resistance and resilience. The reduction in the resistance to drought was caused by the decrease in species richness, asynchrony, and dominant species resistance. The reduction in resilience from drought was mainly due to the decrease in species asynchrony, and dominant and common species resilience. In comparison, medium N addition significantly increased ANPP recovery from the extreme wet event, which was mostly attributed to the effects of dominant and common species recovery. In conclusion, our results suggested that N enrichment regulated the responses of alpine meadow ANPP to the extreme climate events. Our findings also highlight the importance of multiple-factor studies in fostering an integrated understanding of how N addition and extreme climate events affect ANPP, and inform models that project ecosystem productivity in response to global change drivers. Our study is among the first to provide direct field evidence on how chronic global-change drivers interact with discrete natural disturbances to affect ecosystem productivity and stability.

CRediT authorship contribution statement

S.N. and F.M. conceived the ideas and designed the study; F.M., J.W., Y.H., R.Z., D.T. and Q.Z. collected the data; F.M. and S.N. analyzed the data and led the writing of the manuscript draft. F.M., J.W., Y.H., Y.L., R.Z., D.T., Q.Z., and S.N. contributed critically to the drafts and gave final approval for publication.

Data availability

Data will be made available on request.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.164152.

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