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RESEARCH ARTICLE

Extreme Drought Decreases the Stability of Above- but Not Below-Ground Productivity Across Eurasian Steppes

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ABSTRACT

Ecological stability plays a crucial role in determining the sustainability of ecosystem functioning and nature's contribution to people. Although the disruptive effects of extreme drought on ecosystem structure and functions are widely recognized, their effect on the stability of above- and belowground productivity remains understudied. We assessed the effects of drought on ecosystem stability using a 3-year drought experiment established in six Eurasian steppe grasslands. The treatments imposed included ambient precipitation, chronic drought (66% reduction in precipitation throughout the growing season), and intense drought (complete exclusion of precipitation for two months during the growing season). We found that drought, irrespective of how it was imposed, reduced the stability of aboveground net primary productivity (ANPP) but had little impact on belowground net primary productivity (BNPP) stability. Reduced ANPP stability under drought was primarily attributed to changes in subordinate species stability, with mean annual precipitation (MAP) and its variability, historical drought frequency, and the aridity index (AI) also influencing responses to extreme drought. In contrast, BNPP stability was not related to any community factor investigated, but it was influenced by MAP variability and AI. Our findings that above- and belowground productivity stability in grasslands are differentially sensitive to multi-year extreme drought under both common (MAP and AI) as well as unique drivers (plant community changes) highlight the complexity of predicting carbon cycle dynamics as hydrological extremes become more severe.

1 | Introduction

The temporal stability of ecosystem functioning, quantified as the ratio of the mean of an ecosystem function (e.g., productivity) to its standard deviation over time, is pivotal for predicting the reliability of ecosystem functions and services vital for humanity despite environmental changes (Tilman and Downing 1994; Tilman et al. 2014; Wagg et al. 2017). Extreme drought events, known for their pervasive and detrimental effects on plant growth and ecosystem functions (Ciais et al. 2005; Hoover et al. 2014; Isbell et al. 2015), are expected to intensify in both frequency and duration due to climate change, potentially affecting ecosystem stability (Chiang et al. 2021; Dai 2013). As a result, understanding how extreme droughts impact ecosystem stability has become a key focus in ecological research (Kreyling et al. 2017; Van Meerbeek et al. 2021). Despite significant research, a consensus on how drought alters stability has not yet been reached. For example, the stability of aboveground productivity was reduced by an extreme drought event in an alpine meadow (He et al. 2022) but was not affected in an Inner Mongolia grassland (Gao et al. 2022). These contrasting responses could stem from differences in climatic factors, such as mean annual precipitation (MAP), which might explain the site-specific responses (Knapp et al. 2015; Wang et al. 2021; Yu et al. 2025). In particular, the ecological impact of drought may be amplified when the severity of drought represents a greater deviation from the long-term MAP, as is often the case in arid regions where baseline water availability is already low (Knapp et al. 2017; Wilcox et al. 2015). Thus, a comparative analysis across sites with varying MAP could provide deeper insights into the mechanisms underlying the observed variability, which is essential for advancing our knowledge of grassland ecosystem stability under extreme drought.

Emerging evidence suggests that shifts in ecosystem stability under extreme drought can be primarily attributed to variations in species richness (Hautier et al. 2015; Kreyling et al. 2017). For example, ecosystems with higher species richness are usually more stable under extreme drought (Isbell et al. 2015). This can be attributed to two main processes. First, the insurance effect, that is, ecosystems with higher richness are more likely to include species that can offset the reduction in biomass of other species, resulting in enhanced temporal stability of productivity (Chen et al. 2025; Loreau and Hector 2001; Tilman et al. 2006). Second, the sampling effect, that is, species-rich ecosystems are more likely to contain species with high resistance to a particular environmental change, thereby maintaining the temporal stability of productivity (Chen et al. 2025; Kreyling et al. 2017; Wagg et al. 2017). However, the stability of component populations is also expected to significantly impact ecosystem stability facing environmental perturbations, sometimes outweighing the influence of species richness (Yang et al. 2012; Zhang et al. 2016). Increasing empirical evidence suggests that ecosystems under extreme drought are strongly linked to dominant species stability rather than plant species richness (He et al. 2022; Smith et al. 2020). The mass ratio hypothesis also predicts that the exclusion of the dominant species would lead to substantial impacts on productivity, while the removal of rare or less common species, despite their influences on species richness, may yield relatively minor effects on productivity (Smith and Knapp 2003; Smith et al. 2020). Finally, there is evidence that subordinate species help to maintain ecosystem functions during extreme drought (Yu et al. 2025). Nevertheless, the relative contribution of dominant versus subordinate species to ecosystem stability remains highly elusive. Identifying the key processes underlying ecosystem stability is crucial for forecasting ecosystem functioning under increasingly frequent and intense drought scenarios.

Previous studies have primarily focused on extreme drought responses of aboveground net primary productivity (ANPP) (Sun et al. 2022; Wagg et al. 2017; Yu et al. 2025). As a consequence, the temporal stability of belowground NPP (BNPP) under extreme drought remains largely unexplored, hindering our understanding of how ecosystem stability responds to extreme drought. This is likely due to the technical challenges in observing or measuring BNPP (Xu et al. 2012; Yan et al. 2021). However, in grasslands, BNPP constitutes the majority of total NPP (Bai and Cotrufo 2022; Gherardi and Sala 2020; White 2000), and extreme drought can cause plants to allocate proportionately more photosynthate belowground to address soil water scarcity (Liu et al. 2018; Xu et al. 2013), potentially increasing BNPP relative to ANPP. Despite such enhanced belowground carbon allocation, drought may still lead to a decline in root productivity due to severe water limitation, ultimately resulting in a higher root-to-shoot ratio but reduced overall productivity (Song et al. 2019). This suggests that the responses of temporal stability of BNPP to extreme drought may be either similar to or differ from ANPP. To date, the few studies exploring BNPP responses have reported inconsistent findings. For example, long-term dynamics of ANPP and BNPP in response to interannual precipitation variability differed in desert grassland (Brown and Collins 2023). Extreme drought did not alter ANPP stability but reduced BNPP stability in a desert steppe (Li et al. 2023), while in an alpine meadow, the decrease in ANPP stability was greater than that in BNPP stability under extreme drought (Ma et al. 2024). Therefore, further understanding of the drivers of ANPP and BNPP stability is needed to develop better insights into the response of grassland structure and functioning under extreme drought.

Here, we assessed the impact of extreme drought on ecosystem stability across six representative grasslands in Northern China, which is part of the Extreme Drought in Grasslands Experiment (EDGE). Since the drought intensity and measured variables in most previous studies vary widely, quantifying and comparing how extreme drought affects ecosystem stability is a challenge (Knapp et al. 2024). Coordinated experiments can yield a deeper understanding of global change impacts on ecosystems (Borer et al. 2014; Yahdjian et al. 2021). Therefore, EDGE provides a unique opportunity to investigate how extreme drought affects grassland ecosystem stability across environmental gradients. Specifically, we tested three hypotheses. (1) The response of ANPP stability to extreme drought is more pronounced than that of BNPP, likely because belowground productivity declines less than aboveground productivity under drought conditions (Song et al. 2019). (2) Species richness governs the responses of both ANPP and BNPP stability to extreme drought through mechanisms similar to the insurance and sampling effects (Kreyling et al. 2017; Loreau and Hector 2001; Tilman et al. 2006; Wagg et al. 2017). (3) The responses of ANPP and BNPP stability to extreme drought are mediated by site-specific precipitation regimes, with stronger responses in ecosystems where drought represents a greater departure from historical norms. Although all sites are located in dryland regions, those with especially low baseline MAP may be more sensitive to extreme drought due to their inherently limited water availability and reduced buffering capacity, whereas relatively higher MAP systems may show greater resistance (Knapp et al. 2015, 2024; Schlaepfer et al. 2017; Wilcox et al. 2017; Yu et al. 2025).

2 | Methods

2.1 | Study Site

EDGE encompasses six typical grassland sites across Northern China (Table S1). The six sites span a broad precipitation range, from 174 to 366 mm, and all are dominated by C_3 species. More site details can be found in Yu et al. (2025).

2.2 | Experimental Design

A randomized block design incorporating three drought treatments with six replicates was conducted at each of the six grassland sites. Within each of six blocks, three 6 × 6 m plots were randomly assigned to one of three treatments simulating different drought scenarios: ambient precipitation (control), chronic drought (CHR—a 66% reduction in precipitation throughout the growing season), and intense drought (INT—a complete exclusion of precipitation for two months during the growing season) Rainout shelters were employed to create both drought treatments, with a 66% interception for CHR and 100% interception for INT. A 1 m buffer was maintained around each plot to minimize edge effects of the rainout shelters, and aluminum flashing was buried around the plot perimeter to a depth of 1 m to prevent surface and subsurface water flow.

2.3 | Measurements of ANPP and BNPP

Aboveground net primary productivity (ANPP) was assessed annually from 2016 to 2018 by harvesting all live plant biomass at ground level at peak biomass within two 0.5 × 0.5 m quadrat frames, which were randomly placed in each plot. Subsequently, all living plant material was sorted by species and oven-dried (65°C for 48 h) to a constant weight. ANPP was defined as the total oven-dried biomass of all species per plot.

Belowground net primary productivity (BNPP) was also evaluated annually from 2016 to 2018 using the ingrowth-core method (Chen et al. 2012). In each plot, soil cores (5 cm diameter by 20 cm deep) were extracted using a root auger at the beginning of the growing season (May) to obtain soil samples from two different depths: 0–10 and 10–20 cm. These soil samples were sieved through a 2-mm mesh sieve. Then, the root-free soil samples were placed into nylon mesh bags (0.5 mm) and refilled into their original soil cores and depths. At the end of the growing season (September), the nylon mesh bags were retrieved from the different soil depths, and soil samples were sifted through a 0.5-mm mesh sieve. All root samples were oven-dried at 65°C for 48 h to a constant weight to evaluate BNPP for each year at the two soil depths, and total BNPP was calculated by summing the BNPP values from different soil depths. Given that root growth outside the growing season is minimal in these ecosystems, the growing-season BNPP was considered representative of annual BNPP.

2.4 | Stability Calculation

We calculated the temporal stability of ANPP and BNPP as μ/σ, where μ is the mean and σ is the standard deviation of ANPP or BNPP at plot level over 3 years (2016–2018) following previous studies (Hautier et al. 2014; Yan et al. 2023). We used the same method to quantify BNPP stability across soil depths and for stability of dominant and subordinate species. Community-level population stability was defined as the mean temporal stability of species-level biomass. In this case, dominant species were defined as those exhibiting a relative frequency and cover exceeding 0.8% and 12% (Mariotte 2014), respectively, while subordinate species included all remaining species. Details of the identities of dominant and subordinate species are available in Yu et al. (2025).

2.5 | Community Variables

Species richness was quantified as the total number of species recorded during the ANPP assessment within each plot. Dominance was calculated as:

$$\text{Simpson} = \sum_{i=1}^{n} \left(\frac{\text{bi}}{B}\right)^2 \quad (1)$$

where bi represents the biomass of species i, and B denotes the total community biomass in a plot containing n species.

Species asynchrony was used to quantify species compensatory dynamics, and calculated as:

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

where φ_y represents species asynchrony, φ_x is species synchrony, σ^2 stands for the variance of plant community biomass and σ_i indicates the standard deviation of biomass for species i within a plot comprising n species.

2.6 | Climatic Variables

Climate data for all grassland sites were sourced from the China Meteorological Administration (http://data.cma.cn/). To characterize historical precipitation regimes, we analyzed long-term observational data (1982–2018), deriving both mean annual precipitation (MAP) and site-specific probability density functions (PDFs) to quantify precipitation variability for each site. The PDFs were then employed to classify years into categories: extreme drought (precipitation below the 5th percentile), nominal precipitation (within the 5th to 95th percentiles), and extreme precipitation (above the 95th percentile). In addition, the interannual coefficient of variation (CV) of MAP and number of years with extreme drought (historic drought frequency) were obtained. The annual aridity index (AI) for each site was calculated as the ratio of mean annual precipitation (MAP) to mean annual potential evapotranspiration (PET), with PET estimates obtained from WorldClim v2.5 at 2.5-arcminute resolution.

2.7 | Soil Moisture

Soil moisture (SM) was monitored continuously at a depth interval of 0–20 cm using Time-Domain Reflectometer probes (CS616, Campbell Scientific, Logan, UT, USA) inserted diagonally (at a 45° angle) within the center of each plot, with half-hourly recordings logged by a datalogger (CR1000X, Campbell Scientific).

2.8 | Statistical Analyses

Linear mixed-effects models with drought treatments as the fixed factor and study site as a random factor were used to assess the effect of drought treatments on the mean of ANPP and BNPP, SD of ANPP and BNPP, stability of ANPP and BNPP, species richness, dominance, asynchrony, population stability, dominant species stability, and subordinate species stability using the R package *lme4* across six sites. Statistical differences among drought treatments were assessed using Fisher's Least Significant Difference (LSD) post hoc test at $p < 0.05$. The treatment effect size of CHR and INT was quantified using the log response ratio, calculated as LNRR = ln (X_T/X_C), where X_T and X_C represent the values of drought treatments (CHR and INT) and control groups, respectively. Next, we evaluated relationships between ecosystem productivity components (mean, SD, and stability of ANPP and BNPP) and species richness, dominance, asynchrony, population stability, dominant species stability, and subordinate species stability using simple linear regression analysis.

We used structural equation modelling (SEM) to estimate the direct and indirect pathways by which drought influenced the response ratio of ANPP and BNPP stability using R package *lavaan*. Model parameters were estimated using maximum likelihood estimation. Model fit was evaluated using the chi-squared test (λ^2) and the root mean square error of approximation (RMSEA). We employed multiple regression analysis to assess the integrated effects of species richness, dominance, asynchrony, population stability, dominant species stability, and subordinate species stability on the temporal stability of both ANPP and BNPP.

Finally, linear and non-linear regressions were employed to examine the relationships between ANPP and BNPP stability responses and key climatic factors, including MAP, CV of MAP, historic drought frequency, AI, and SM. All statistical analyses were performed using R version 4.0.2.

3 | Results

3.1 | Drought Effects on ANPP and BNPP Stability

We found that both CHR and INT decreased mean and SD of ANPP as well as ANPP stability, but had limited impacts on mean and SD of BNPP and BNPP stability across the six grassland ecosystems (Table S2 and Figures 1a–f and S1a,b). Consistent with the drought response of total BNPP, both drought treatments had only a minor effect on mean and SD of BNPP and BNPP stability in the 0–10 and 10–20 cm soil depths (Figure S2a–f). Specifically, mean BNPP decreased under both drought treatments and BNPP stability decreased under INT in the 10–20 cm soil depth (Figure S2b,f).

3.2 | Relationships Between Stability and Community Structure

Both CHR and INT decreased species richness and increased species dominance (Table S3 and Figure 2a,b). Moreover, CHR had minimal effects on asynchrony, population stability, and the stability of both dominant and subordinate species, whereas INT reduced asynchrony and subordinate species stability but enhanced the stability of dominant species (Figure 2c–f). Linear regressions revealed a positive relationship between changes in ANPP stability in response to the drought treatments and the corresponding changes in dominant and subordinate species stability, and a negative relationship between changes in ANPP stability and asynchrony (Figure S3c). Both drought treatments altered the mean and SD of ANPP, and these changes were negatively correlated with asynchrony (Figure S4c) and dominance (Figure S4h), as well as dominant and subordinate species stability (Figure S4k,l). Changes in the mean and SD of total BNPP and BNPP stability under drought were not related to the drought-induced changes in species richness, dominance, asynchrony, population stability, dominant species stability, or subordinate species stability (Figure S5a–r). The same was true for BNPP stability in the two soil depths, except for the relationships between BNPP stability at 0–10 cm and species richness and at 10–20 cm and dominance (Figure S6a,b).

3.3 | Processes Through Which Drought Influences ANPP and BNPP Stability

The final SEM model explained 37% and 4% of the variation in ANPP and BNPP stability, respectively, under the two types of experimental drought (Figure 3). The SEM analysis provided support for the observation that drought decreased ANPP stability but had a limited effect on BNPP stability (Figure 3). The drought treatments negatively affected ANPP stability by impacting species richness, dominance, asynchrony, dominant species stability, and subordinate species stability, while BNPP stability was not influenced by any other community variables investigated (Figure 3). Consistently, the multiple regression models showed that the stability of ANPP was primarily controlled by dominant and subordinate species stability (Figure 4a).

In addition, we found that the response ratio of both ANPP and BNPP stability were closely linked to shifts in precipitation

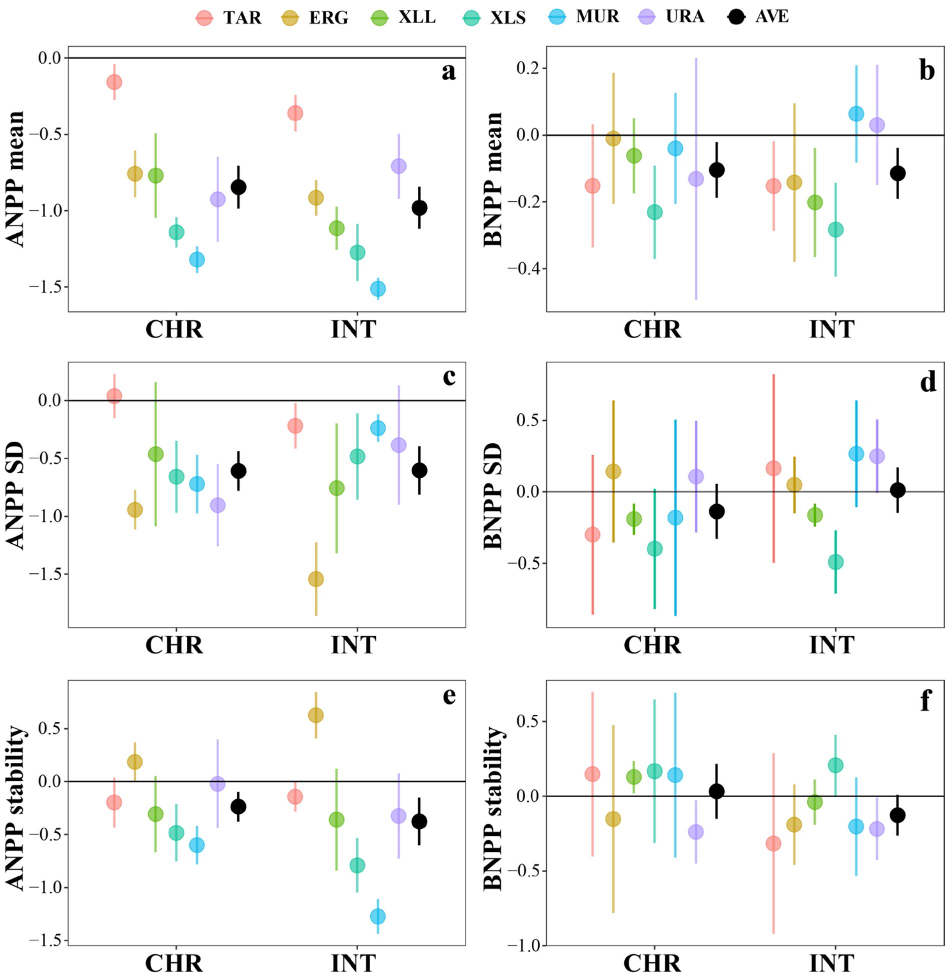

FIGURE 1 | The response ratio of (a) mean of aboveground net primary productivity (ANPP), (b) mean of belowground net primary productivity (BNPP), (c) temporal standard deviation (SD) of ANPP, (d) SD of BNPP, (e) stability of ANPP, and (f) stability of BNPP across six grassland sites in Northern China. Value is mean ±95% confidence interval. If the 95% confidence interval does not overlap zero, the drought effect is considered significant. CHR and INT represent chronic (season long) and intense (partial season) drought, respectively. TAR, ERG, XLL, XLS, MUR, and URA represent the experimental sites Sher Tara, Erguna, Xilingol-*Leymus chinensis*, Xilingol-*Stipa grandis*, Sheila Muren and Urat, respectively. Black points (AVE) represent the average value across six grassland sites in Northern China.

patterns. Specifically, drought responses of ANPP stability exhibited a concave-up relationship with MAP and AI, while demonstrating a concave-down association with CV of MAP and historic drought frequency (Figure 5a,c,e,g). In contrast, BNPP stability showed a negative correlation with CV of MAP and a concave-down relationship with AI under drought (Figure 5d,h).

4 | Discussion

We have shown that for a 3-year time frame across multiple grassland ecosystems, extreme drought caused a more pronounced response of ANPP to chronic and intense drought relative to BNPP, with ANPP stability decreasing and BNPP stability remaining unchanged (Figure 1e,f). Previous studies investigating the impact of drought on grassland ecosystems have primarily focused on ANPP stability, consistently concluding that drought decreases the temporal stability of grassland ecosystem productivity (Muraina et al. 2021; Wilcox et al. 2020). But our results, and those of others, suggest that BNPP stability may dominate the overall temporal stability of grassland ecosystem NPP to drought (Gherardi and Sala 2020; White 2000). The limited effect of the drought treatments on BNPP stability in our study suggests that previous studies may have overestimated the impacts of drought on grassland ecosystem productivity because BNPP stability could buffer responses of total NPP to drought. The positive correlation between drought-induced changes in BNPP stability and total NPP stability observed in this study supports this conclusion (Figure S7). It should be acknowledged that not all previous studies have focused on statistically extreme droughts, which may contribute to variations in observed ecosystem responses. For example, a global study found that extreme droughts (1-in-100-year events) led to a 60% greater reduction in ANPP compared to nominal drought (Smith et al. 2024), suggesting that extreme droughts have a disproportionately greater impact on aboveground productivity. The limited change in BNPP stability under our drought treatments emphasizes the importance of BNPP stability as a buffer for C cycling against extreme climatic events, ultimately sustaining grassland ecosystem productivity under increasing climate extremes.

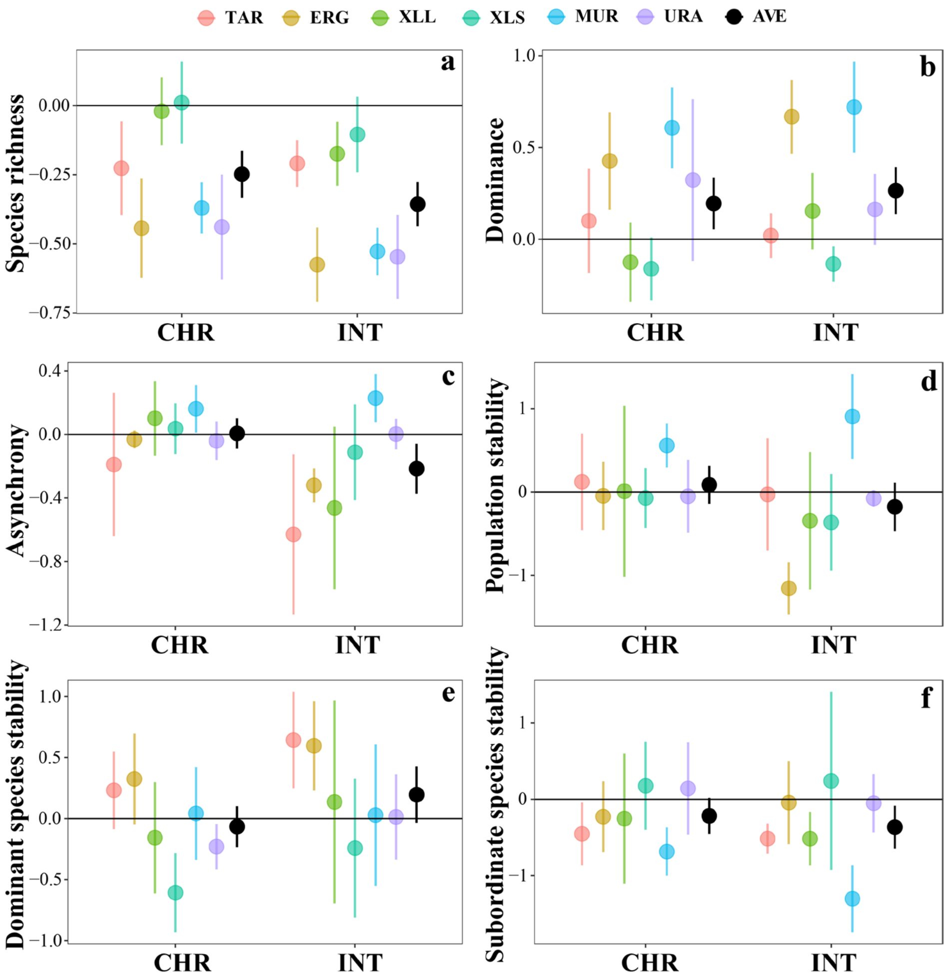

FIGURE 2 | The response ratio of (a) species richness, (b) dominance, (c) asynchrony, (d) population stability, (e) dominant species stability, and (f) subordinate species stability across six grassland sites in Northern China. Value is mean ±95% confidence interval. If the 95% confidence interval does not overlap zero, the drought effect on variables is considered significant. CHR and INT represent chronic (season long) and intense (partial season) drought, respectively. TAR, ERG, XLL, XLS, MUR, and URA represent the experimental sites Sher Tara, Erguna, Xilingol-*Leymus chinensis*, Xilingol-*Stipa grandis*, Sheila Muren and Urat, respectively. Black points (AVE) represent the average value across six grassland sites in Northern China.

The decoupled responses of ANPP and BNPP stability to chronic and intense seasonal droughts were mainly attributable to their dissimilar responses to the drought treatments (Figure S1a,b). In this study, the consecutive three years of drought led to a decrease both in the mean and SD of ANPP, with the mean of ANPP decreasing more than the SD across the six sites in Eurasian steppe grasslands (Figure 1a,c). A previous study conducted in an alpine meadow found that the impacts of drought on ANPP intensified over time (Zhang et al. 2019). However, there was no detectable difference in ANPP observed in either the control or drought treatments in different years in our study (Figure S1a). These differences may be because MAP in the alpine meadow (747 mm) is higher than the MAP in our study sites (174 to 366 mm). While extensive studies suggest that arid ecosystems are more sensitive to precipitation variability and drought than mesic ecosystems (Huang et al. 2017; Knapp et al. 2024; Wilcox et al. 2017), our findings suggest that arid ecosystems may exhibit greater resistance to drought over a 3-year timescale, potentially due to the dominance of drought-adapted species and conservative resource-use strategies (Huang et al. 2024; Liu et al. 2018). These contrasting results highlight the complexity of ecosystem responses to drought, which are influenced by factors such as regional climate, ecosystem characteristics, and historical exposure to drought events (Knapp et al. 2017; Sun et al. 2022; Yu et al. 2025). Beyond drought, recent research has also shown that while nitrogen addition can detrimentally impact the stability of ANPP, it may not similarly affect BNPP or total NPP (Yang et al. 2022). This suggests that the decoupling of ANPP and BNPP stability is not limited to drought as a global change driver in grasslands.

Although plant species richness significantly decreased under both drought treatments in our study (Figure 2a), we did not find that plant species richness increased the stability of ANPP (Figures 3 and S3a). This may occur because reduced water availability under drought can impede the growth of plants with high water requirements, but high water demanding species make a relatively small contribution to ecosystem productivity in our six study sites (Muraina et al. 2021). Consequently, the loss of these plant species may exert a notable influence on species richness with little effect on the stability of ANPP (Smith

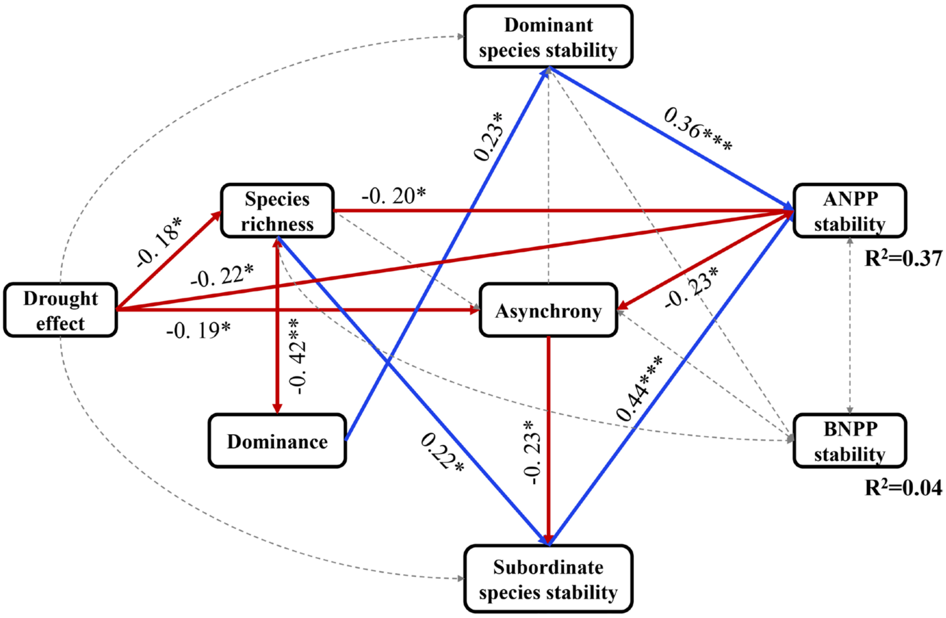

FIGURE 3 | Structural equation model (SEM) examining the direct and indirect effects of driving factors on the response ratio of the stability of above- and belowground net primary productivity (ANPP and BNPP, respectively) under two experimental drought treatments ($\chi^2 = 3.215$, $p = 0.955$, df = 9, AIC = 762.291, RMSEA = 0.000). Blue and red arrows indicate significant positive and negative relationships, respectively. The values along the lines represent the effect size. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$, respectively.

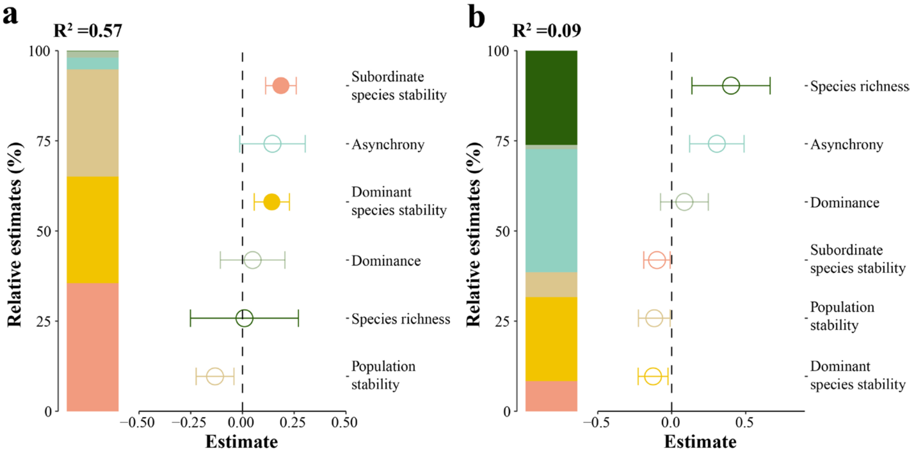

FIGURE 4 | Relative effects of multiple predictors on (a) aboveground net primary productivity (ANPP) stability and (b) belowground net primary productivity (BNPP) stability, respectively, showing the relative importance of each predictor, expressed as the percentage of explained variance, as well as the average parameter estimates (standardized regression coefficients) of the model's predictors and their 95% CIs. Solid points represent significant effects, while hollow points represent non-significant effects.

et al. 2020). The six sites of our study occur in dry ecoregions, and the dominant, drought tolerant species collectively contribute the majority of biomass to ANPP, increasing the stability of ANPP under the drought treatments. But our results revealed that subordinate species stability contributed strongly to the responses of ANPP stability to our drought treatments. These findings contrast with the mass ratio hypothesis, which suggests that uncommon or rare species have minor effects on productivity (Smith and Knapp 2003; Smith et al. 2020). With respect to NPP stability, the predominant role of subordinate species in controlling ANPP stability under our drought treatments suggests that although dominant species contribute most to ANPP, it is the subordinate species that drive ANPP changes in grasslands under drought (Yu et al. 2025). This highlights the important role of subordinate species in maintaining grassland ecosystem productivity in the face of extreme climatic events.

Furthermore, our assessment of population-level temporal stability revealed that neither chronic nor intense drought altered population stability. Previous studies suggested that population stability is a critical determinant of ANPP stability (Quan et al. 2021; Zhang et al. 2016). For instance, the enrichment of nitrogen led to a reduction in community productivity stability via decreasing plant population stability (Zhang et al. 2016). In our study, however, drought had limited effects on plant population stability (Figure 2d), and population stability did not serve as a prominent pathway through which drought influenced the stability of ANPP (Figure S3d). This finding implies

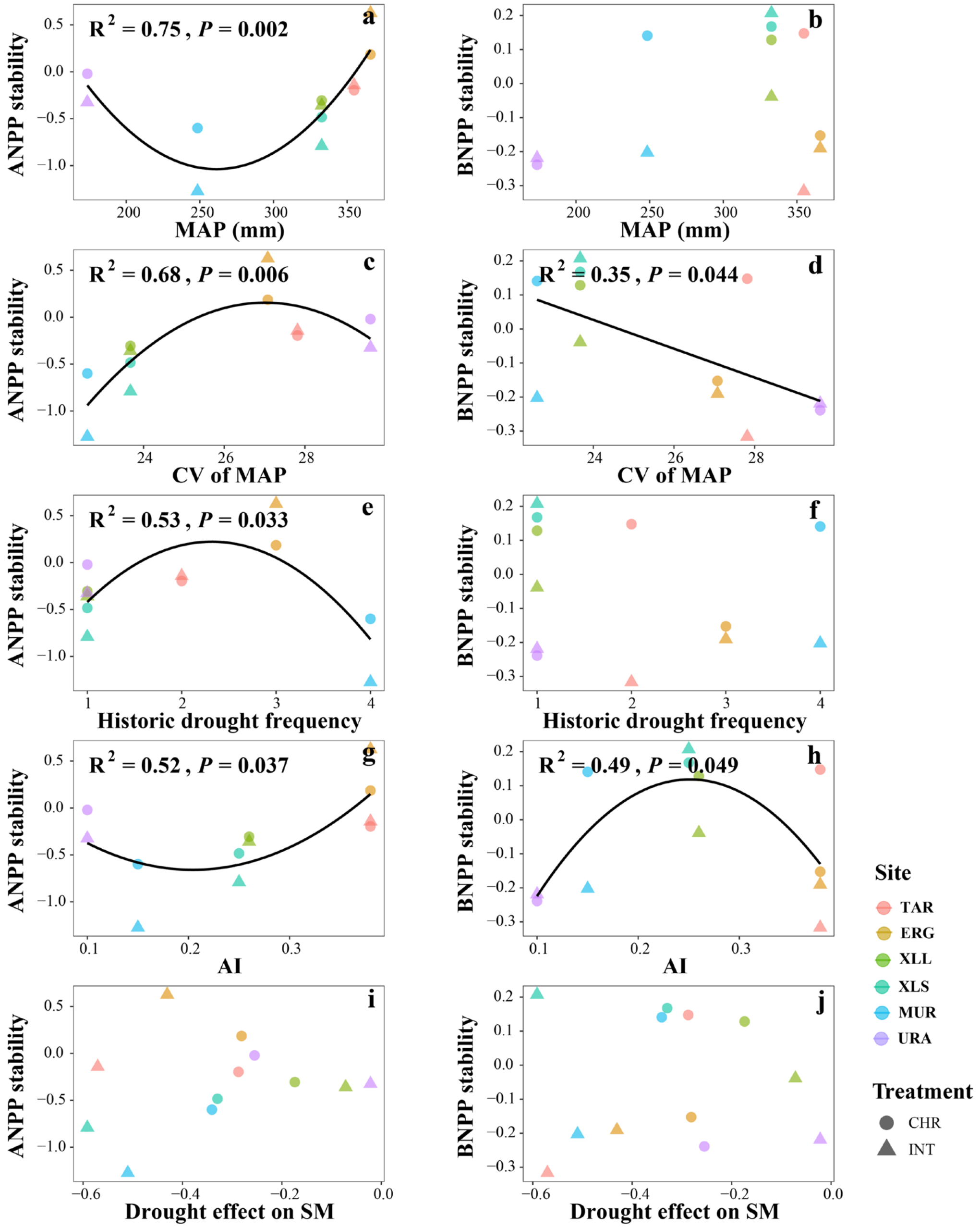

FIGURE 5 | Relationships between the response ratio of above- and below-ground net primary productivity (ANPP and BNPP, respectively) stability and (a and b) mean annual precipitation (MAP), (c and d) interannual percent coefficient of variation (CV) of MAP, (e and f) historic drought frequency, (g and h) aridity index (AI), and (i and j) the response ratio of soil moisture (SM). MAP, CV of MAP, and historic drought frequency were calculated based on 37-year historical climate data from 1982 to 2018 for each site. AI was calculated as MAP/mean annual potential evapotranspiration. TAR, ERG, XLL, XLS, MUR, and URA represent the experimental sites Sher Tara, Erguna, Xilingol-*Leymus chinensis*, Xilingol-*Stipa grandis*, Sheila Muren and Urat, respectively. CHR and INT represent chronic (season long) and intense (partial season) drought, respectively.

that alternative stabilizing processes may outweigh this effect in governing the stability of ANPP under drought, such as the stability of subordinate species observed in our study.

Contrary to ANPP stability, drought had little effect on the stability of BNPP across the six grassland ecosystems (Figure 1f), likely for the following reasons. First, the stability of productivity may be contingent on pre-disturbance community biomass (Wang et al. 2007). Since the majority of plant productivity in grasslands is allocated belowground (Gherardi and Sala 2020), changes in BNPP following three years of drought were relatively small, and thus impose a minor impact on overall BNPP stability. However, the cumulative effects of prolonged drought could potentially alter belowground allocation patterns and destabilize BNPP, which warrants further investigation in long-term experiments. Second, although drought exerted a small negative impact on BNPP under low soil water and nitrogen availability (Hoover et al. 2022; Sardans et al. 2008), it could instead increase BNPP due to changes in allocation strategies, such as increased root growth in search of soil resources (Liu et al. 2018; Slette et al. 2021). These dual effects could result in stable BNPP under drought. Third, trait-mediated responses may also contribute to the observed BNPP stability. Drought-induced shifts in root traits—toward more acquisitive or conservative strategies—may stabilize resource uptake and turnover, thereby buffering belowground productivity against environmental fluctuations and decoupling it from aboveground dynamics (Comas et al. 2013). The absence of correlations between BNPP stability and community variables indicates that drought-induced changes in aboveground community structure may not directly translate to belowground biomass reductions (Brown and Collins 2023). Furthermore, we also observed that the stability of BNPP at different soil depths under our drought treatments did not correlate with changes in community structure and composition (Figure S6a–l). One possible explanation lies in species-specific plasticity in carbon allocation strategies under drought. Different species may differentially adjust their root-to-shoot allocation in response to water stress, with some increasing and others decreasing root investment depending on their functional traits and ecological strategies (Liu et al. 2018). These divergent responses may offset one another at the community level, resulting in stable BNPP despite underlying changes in species composition or dominance. Overall, our study indicates that some aspects of grassland ecosystem functioning may be less susceptible to global changes compared to previous studies that only focused on aboveground responses.

We found strong support for the third hypothesis, which posited that the responses of ANPP and BNPP stability to drought are mediated by site-specific precipitation regimes. However, at some arid sites, ANPP stability under both chronic and intense drought was comparable to that in our relatively more mesic ecosystems. This suggests that some arid ecosystems may have a greater capacity to sustain aboveground productivity during seasonal drought than previously anticipated, challenging the assumption that these ecosystems are more sensitive to drought. Specifically, drought responses of ANPP stability exhibited a concave-up relationship with MAP and AI, indicating that sensitivity to our drought treatments was lowest under both low and high levels of MAP and AI. This indicates that under lower MAP and AI, ANPP stability was primarily driven by adaptation to water scarcity in communities dominated by drought-tolerant species (Knapp et al. 2015, 2024). Conversely, in ecoregions with higher MAP and AI, greater species richness allows compensation in which declines in the biomass of some species during drought are offset by increases by other species, thereby buffering the impacts of drought and maintaining ANPP stability (Chen et al. 2025; Isbell et al. 2015). The concave-down relationships between drought responses of ANPP stability and both CV of MAP and historic drought frequency indicate that ANPP is most stable under intermediate levels of historical variability and disturbance, consistent with the intermediate disturbance hypothesis (Connell 1979) and suggesting that moderate levels of climatic variability and disturbance foster conditions where stabilizing mechanisms can enhance ecosystem stability.

In contrast, the drought responses of BNPP stability exhibited a negative correlation with CV of MAP, indicating that increased precipitation variability destabilizes belowground productivity. This divergence between ANPP and BNPP stability responses suggests that in grassland ecosystems with historically stable precipitation patterns, ANPP is more vulnerable to sudden drought stress due to limited adaptive strategies or community shifts. In these environments, dominant aboveground species are unable to cope with abrupt water deficits, leading to decreased ANPP stability (Smith 2011). Conversely, the relatively consistent BNPP stability could be attributed to a counterbalance between drought-induced decrease in BNPP and shift in resource allocation, with plants investing in belowground biomass to access deeper soil moisture under drought (Liu et al. 2018). Furthermore, the concave-down relationship between drought responses of BNPP stability and AI indicates that drought strongly reduced BNPP stability in both arid and mesic ecosystems, while ecosystems with intermediate aridity exhibit greater BNPP stability. In arid ecosystems, severe water deficits limit root productivity, whereas in humid regions, excessive moisture variability disrupts BNPP stability (Guasconi et al. 2023). Conversely, ecosystems with moderate aridity likely support plant communities with root traits better adapted to variable conditions (Kano et al. 2011), sustaining more stable belowground productivity. The contrasting relationships of drought responses of ANPP and BNPP stability with AI underscore distinct above- and belowground responses to aridity gradients, and highlights how differences in compensatory dynamics above and belowground can be critical for sustaining total productivity and functioning under climatic extremes.

In summary, we provide empirical evidence that an increase in multi-year growing season droughts will have divergent effects on above- and belowground productivity stability across Eurasian steppe grasslands. We observed a decrease in ANPP stability, while BNPP remained relatively stable under these drought treatments, suggesting that some aspects of grassland ecosystem functioning may not be as susceptible as previously indicated by studies that focused only on aboveground responses. We also provide empirical evidence that subordinate species are an important determinant of ecosystem functioning under global change (Yu et al. 2025). Finally, our results reveal that the stability of ANPP and BNPP under drought is related to site-specific historic precipitation regimes, with ANPP stability showing stronger sensitivity to shifts in mean precipitation and aridity, while BNPP stability is more vulnerable to increased precipitation variability. We conclude that integrating the role of subordinate species and site-level precipitation regimes into grassland management and restoration strategies is necessary, particularly under the influence of intensifying climatic extremes.

Author Contributions

Yingjie Yan: formal analysis, funding acquisition, writing – original draft, writing – review and editing. **Chong Xu:** investigation. **Yann Hautier:** methodology, writing – review and editing. **Hongqiang Wang:** investigation. **Yuguang Ke:** investigation. **Honghui Wu:** writing – review and editing. **Jinsong Wang:** writing – review and editing. **Changjin Cheng:** writing – review and editing. **Xiaoan Zuo:** investigation, methodology. **Wentao Luo:** investigation, methodology. **Melinda D. Smith:** methodology, supervision, writing – review and editing. **Alan K. Knapp:** methodology, writing – review and editing. **Scott L. Collins:** funding acquisition, methodology, writing – review and editing. **Qiang Yu:** conceptualization, methodology, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.29107070. Meteorological observation data were obtained from the China Meteorological Administration at http://data.cma.cn/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.