



Long-term evidence of differential resistance and resilience of grassland ecosystems to extreme climate events

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Abstract Grassland ecosystems are affected by the increasing frequency and intensity of extreme climate events (e.g., droughts). Understanding how grassland ecosystems maintain their functioning, resistance, and resilience under climatic perturbations is a topic of current concern. Resistance is the capacity of an ecosystem to withstand change against extreme climate, while resilience is the ability of an ecosystem to return to its original state after a perturbation. Using the growing season Normalized Difference Vegetation Index (NDVI_{gs}, an index of vegetation growth) and the Standardized Precipitation Evapotranspiration Index (a drought index), we evaluated the response, resistance, and resilience of vegetation to climatic conditions for alpine grassland, grass-dominated steppe, hay meadow, arid steppe, and semi-arid steppe in northern China for the period 1982–2012.

The results show that NDVI_{gs} varied significantly across these grasslands, with the highest (lowest) NDVI_{gs} values in alpine grassland (semi-arid steppe). We found increasing trends of greenness in alpine grassland, grass-dominated steppe, and hay meadow, while there were no detectable changes of NDVI_{gs} in arid and semi-arid steppes. NDVI_{gs} decreased with increasing dryness from extreme wet to extreme dry. Alpine and steppe grasslands exhibited higher resistance to and lower resilience after extreme wet, while lower resistance to and higher resilience after extreme dry conditions. No significant differences in resistance and resilience of hay meadow under climatic conditions suggest the stability of this grassland under climatic perturbations. This study concludes that highly resistant grasslands under conditions of water surplus are low resilient, but low resistant ecosystems under conditions of water shortage are highly resilient.

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Introduction

Understanding how plant communities respond to extreme climate events (e.g., heatwaves, periods of heavy rain, and droughts) is a global challenge (Jentsch & Beierkuhnlein, 2008; Seneviratne et al., 2012; Vicente-Serrano et al., 2013). Shifting precipitation patterns are of major concern (Cook et al., 2015). Extreme wet and dry events are becoming more intense and frequent due to climate change (Fischer et al., 2013; Singh et al., 2022; Sreeparvathy & Srinivas, 2022). This applies particularly to continental regions. The increase of extreme climate has recently been documented for China (Chen & Sun, 2021), where extreme climate is likely to become even more pronounced in the near future (Gao et al., 2020; Li et al., 2013; Meng et al., 2020; Zhu et al., 2017).

Extreme climate events are widely acknowledged to have an impact on the dynamics, functioning, and stability of terrestrial ecosystems (Beloïu et al., 2022; Hossain & Li, 2021a; Komatsu et al., 2019; Li et al., 2019). Numerous recent studies have provided convincing evidence that grasslands are particularly vulnerable to extreme dry and wet climatic conditions (Craven et al., 2016; Hossain & Li, 2021b; Liu et al., 2021; Zhang et al., 2017). The functioning and stability of grasslands in many regions, especially alpine, hay meadow, and steppe grasslands (Lu et al., 2019; Lei et al., 2020; Chen et al., 2022; Doležal et al., 2022), are likely to be impacted by the rising frequency and severity of extreme climate events (Bellard et al., 2012; Cardinale et al., 2012; Hossain et al., 2022; Loreau & de Mazancourt, 2013). In a global assessment of drought impacts, grasslands in Central Asia, Northeastern China, and the Mongolian Plateau are considered to represent ecosystems that are most susceptible to water stress (Liu et al., 2021). For large parts of China, there is clear evidence for changes in the frequency and intensity of climate extremes (Chen et al., 2019; Cui et al., 2017), and this is likely to become even more pronounced in the near future (Chen & Sun, 2015; Li et al., 2016, 2020a, b; Sui et al., 2018; Zhu et al., 2018). Specifically, the

number of consecutive dry and wet days is predicted to increase in the coming decades (Meng et al., 2021). Considering the emerging threats to ecosystem functioning through climate extremes, our current understanding of how the vegetation of different grassland types is responding to different intensities of extreme climate remains unsatisfactory.

There has been a dispute in ecological studies about the effect of extreme climate on the functioning of ecosystems (Hegerl et al., 2011; Isbell et al., 2015). For instance, some researchers have demonstrated increased grassland productivity during drought (Quan et al., 2020) and wet conditions (Hossain & Li, 2021c; Wilcox et al., 2017). While some other studies reported that the productivity of grasslands was negatively impacted by drought and wet periods (Lei et al., 2020; Padilla et al., 2019). Other studies revealed that grassland performance was unexpectedly steady during extreme climate conditions (Jentsch et al., 2011; Kreyling et al., 2008; Zhang et al., 2019). These divergent findings may be due to variations in the classification and intensity of extreme climate events (Barnes et al., 2016; Isbell et al., 2015; Kreyling et al., 2017; Lei et al., 2020; Li et al., 2021). Instead of using an experimentally controlled climatic condition classification (e.g., Kreyling et al., 2017; Li et al., 2021), the application of a drought index classification, which explains the natural climatic conditions (Isbell et al., 2015) to evaluate the effects of extreme climate on grassland productivity is of great significance given the non-consistent classifications of drought to characterize extreme climate events. This approach will help shed light on how to manage grassland ecosystems sustainably and ensure a steady flow of ecosystem goods and services (Fraser et al., 2015).

Ecosystem stability refers to the capacity of an ecosystem to maintain a balanced and functional state, which is necessary for the steady supply of an ecosystem's services (Pimm, 1984). No agreement has been reached on whether an ecosystem's stability is related to its resilience after perturbations, its resistance to disturbances, or both (Bai et al., 2004; Hossain et al., 2022; Isbell et al., 2015). Ecological resistance and resilience are two crucial components that are used to assess and track an ecosystem's functionality and changes in response to shifting climatic conditions (Biggs et al., 2012). The ability of an ecosystem to tolerate change in a harsh environment is known as ecosystem resistance

(Pimm, 1984). Resilience is the ecosystem's ability to bounce back to its original state after a disturbance (Tilman & Downing, 1994).

Despite extensive research on ecosystem resistance and resilience, earlier attempts yielded varied results (Hossain, 2022; Hossain et al., 2022; Isbell et al., 2015). For instance, many studies have shown that species-rich communities are more resistant to and resilient towards extreme climate than species-poor communities (Craine et al., 2013; Kreyling et al., 2017; Vogel et al., 2012); in contrast, other studies have shown the opposite (Pennekamp et al., 2018; Pfisterer & Schmid, 2002). According to a recent study across three ecoregions (temperate dry steppe, humid temperate, and cold steppe), productive ecosystems exhibit lower resistance to but higher resilience towards dry events and higher resistance to but lower resilience towards wet events (Hossain & Li, 2021c). Although this study (Hossain & Li, 2021c) offered evidence of an inverse pattern of resistance and resilience of vegetation encompassing forests, shrubs, and grasslands, much of the current ambiguity surrounding ecosystem stability may be caused by variability in ecosystem types (e.g., forests, shrubs, and grasslands), differences in grassland types (e.g., alpine and steppe grasslands), and disparities in the spatial and temporal scales of the experiments (Piao et al., 2006; Wang et al., 2021). For example, using the Normalized Difference Vegetation Index (NDVI) values of four grassland types, Tong et al. (2017) reported a higher NDVI value in grass-dominated steppe than that of hay meadow, arid steppe, and semi-arid steppe in Inner Mongolia. Likewise, the spatial heterogeneity of NDVI values was reported by Piao et al. (2006), which showed a higher NDVI value in hay meadows, compared to arid and semi-arid steppes. We may have the best chance to increase our understanding of the resistance and resilience of grassland ecosystems to the predicted rising frequency and magnitude of extreme climate events by applying satellite-based long-term climatic and distinct ecological data (Ding et al., 2020; Hossain & Li, 2021c; Lei et al., 2020; Lu et al., 2019).

Remote sensing data enables the monitoring of ecosystem performance at varying spatial and temporal scales (Hossain et al., 2021; Huete, 2016; Tarantino et al., 2021). The successful utilization of satellite-derived NDVI data has enabled the assessment of vegetation dynamics in response to climatic

conditions across various ecosystems (Chu et al., 2019; Cui et al., 2021; Hossain & Li, 2021c; Huang et al., 2021; Xu et al., 2017). Because different grassland types have specific properties, early attempts showed that the relationships between NDVI and climate variability are complex (Bao et al., 2015; Hossain & Li, 2021c; Li et al., 2019; Piao et al., 2011).

Grasslands comprise one-third of China's land area (Zhou et al., 2014). In particular, grasslands in Inner Mongolia, Gansu, and Qinghai provinces are of great importance because of their high biodiversity and related ecosystem services. Maintaining these grasslands is a substantial contribution towards fulfilling the requirements of the Convention on Biological Diversity (CBD). The large area that is covered by grasslands in these regions and the outstanding economic role (food and fiber production) that grasslands play for the population living in these areas require in-depth knowledge about grassland functioning and threats. Here, we develop a research approach that is based on the current state of knowledge (Chen et al., 2022; Lu et al., 2019; Wang et al., 2019a, 2020) that considers varying degrees of human land use intensity in grasslands, from hay meadows to natural steppe and alpine grasslands, across a broad range of climatic conditions (Hossain et al., 2021; Lei et al., 2020; Wang et al., 2019a).

In this study, using both NDVI and SPEI data, we assessed the functioning and stability of the selected sites within five distinct grassland types (alpine grassland, grass-dominated steppe, hay meadow, arid steppe, and semi-arid steppe) in northern China to extreme climate events over the period 1982–2012. Accordingly, the objectives of this study are (i) to assess the differences and temporal patterns of NDVI of five grassland types, (ii) to examine the responses, resistance, and resilience of grasslands to different types of climatic extremes, and (iii) to conclude on the resistance and resilience of grassland ecosystems to extreme climate events.

Materials and methods

Study area

The study area encompasses 5 grassland types (alpine grassland, grass-dominated steppe, hay meadow, arid steppe, and semi-arid steppe), comprising 50 sites (10

sites in each grassland type) in grassland ecosystems in northern China (Fig. 1, Table S1). We selected these study sites from the previously published works (Wang et al., 2019b; Yang et al., 2021) to cover the large gradient in climatic conditions as well as in vegetation structures of Chinese grasslands.

The climate in alpine grassland is extremely cold and dry. The mean annual temperature ranges from -1.8 to 4.2 °C, and annual precipitation varies between 70 and 750 mm, with 90% of annual precipitation occurring from May to September (Zhang et al., 2020). Vegetation in alpine grassland on the Qinghai-Tibet Plateau in northern China is composed of highly productive perennial forbs, compared to grass-dominated meadow and steppes in northern China (Dai et al., 2019). Grasslands in the grass-dominated steppe, hay meadow, semi-arid steppe, and arid steppe are located in central Inner Mongolia in northern China (Hang et al., 2014). Annual precipitation ranges from 300 to 380 mm, and the annual average temperature varies between 0 and 3 °C. Precipitation decreases while temperature increases from

the east (hay meadow, grass-dominated steppe) to the west (semi-arid steppe and arid steppe) (Tong et al., 2017). Vegetation in hay meadow and grass-dominated steppe is highly productive, while grasslands in arid and semi-arid steppe are restricted by seasonal climate and less productive than the grass-dominated steppe.

Data sources

In this study, the growing season NDVI of the selected sites in five grassland types and SPEI data were obtained from two sources (Guay et al., 2015 for growing season NDVI and Vicente-Serrano et al., 2010 for SPEI). Over a long time, NDVI has been extensively employed to examine the dynamics, stability, and functioning of ecosystems (Chu et al., 2019; Hossain & Li, 2021c). The Oak Ridge National Laboratory Distributed Active Archive Center provided the growing season NDVI data from 1982 to 2012 used in this investigation (Guay et al., 2015). Growing season

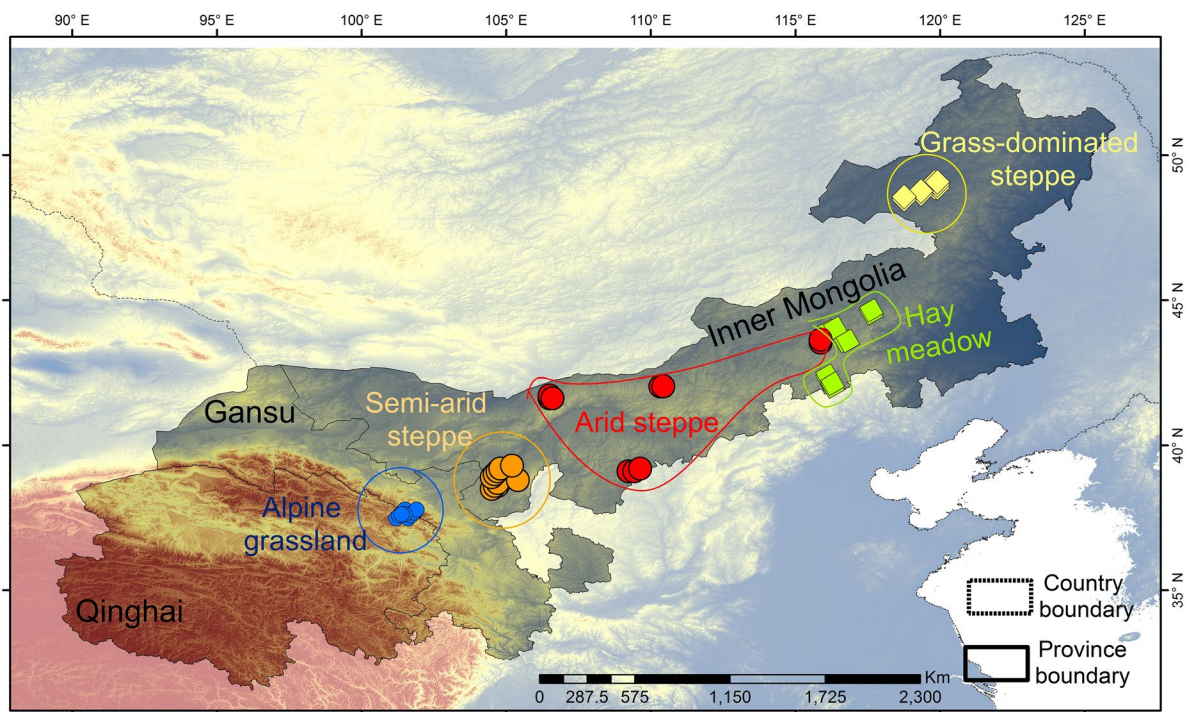


Fig. 1 Locations of the study sites in five continental grassland types (alpine grassland, grass-dominated steppe, hay meadow, arid steppe, and semi-arid steppe) in Qinghai, Gansu,

and Inner Mongolia (China). Detailed information for site locations, including references, is documented in supplementary information Table S1

(June–August) NDVI data with an 8-km spatial resolution are available in the third-generation Global Inventory Modeling and Mapping Services (GIMMS 3 g) dataset generated from the NOAA Advanced Very High Resolution Radiometer (AVHRR) (Guay et al., 2015). SPEI values indicate the water balance of a particular area based on month-by-month variations in climate since January 1901. SPEI is a site-specific drought index that is employed to depict dry or wet conditions on a global scale. The SPEI dataset was obtained from the SPEIbase v2.5 dataset, which was created based on the CRU 3.24.01 precipitation and potential evapotranspiration to detect and classify climatic conditions (Vicente-Serrano et al., 2010).

Data processing

The growing season NDVI of each grassland type over 31 years (1982–2012) was extracted based on longitude and latitude using statistical software R version 4.0.3 (R Core Team, 2020). We selected point locations in grassland types from the given coordinates of the known grassland types (Wang et al., 2019b; Yang et al., 2021). For example, the coordinates of alpine grassland ranged between 37.48° and 37.76° N and 101.20° and 101.57° E (Yang et al., 2021), and we selected a fixed interval of 0.1° latitude and longitude (e.g., 37.48° N and 101.20° E and 37.58° N and 101.30° E) for extracting the growing season NDVI of 10 sites in this grassland. In addition, for grassland types where the coordinate range is not given, we extracted the growing season NDVI of the given sites. For example, we extracted the growing season NDVI of the given coordinates in the hay meadow for two sites (Yang et al., 2021). For each grassland type, 10 sites were selected (Table S1, Wang et al., 2019b; Yang et al., 2021) and thus the growing season NDVI of 50 sites in 5 grassland types were extracted for this study (Fig. 1). Based on the different types of grasslands, the retrieved growing season NDVI data were grouped.

The normality of growing season NDVI values was tested using both the visual method and a formal statistical test. First, we checked the normality of the dataset by using quantile-quantile (Q-Q) plots for the respective grassland types. We found that data points did not follow the straight diagonal line in the Q-Q

plot. Second, as significance test provides more accuracy than visual method, we also tested the normality of the data using the Shapiro-Wilk test and found a p value < 0.05 (Gargano et al., 2022). According to this test, if $p > 0.05$, then the data is assumed to be normally distributed. We applied the log-transformation (natural logarithms) to normalize the data in the statistical software R (R Core Team, 2020). After the log-transformation, we confirmed the normality of the data using both the Q-Q plot (Fig. S1) and the Shapiro-Wilk test (Table S2; $p > 0.05$ for all grasslands). The log-transformed growing season NDVI is denoted by $NDVI_{gs}$, and we used this log-transformed data in the analysis.

Many drought indices, such as the SPEI, Standardized Precipitation Index (SPI), Standardized Terrestrial Water Storage Index (STI), and Palmer Drought Severity Index (PDSI) have been applied to characterize climatic conditions (Cui et al., 2021; Isbell et al., 2015; Wang et al., 2020; Zhang et al., 2012, 2019). Due to its capability to detect water shortages and surpluses over a range of time periods (e.g., 1, 2, 3, ..., 48 months), SPEI has been found to be more suitable than other indices (Vicente-Serrano et al., 2012). We extracted a 3-month SPEI value of each August, which represents the wet/dry conditions of the growing season (June–August), as the growing season climate has been proven to be the most important determinant in explaining the functioning of grassland ecosystems (Grant et al., 2017). These 3-month SPEI values represent the different climatic conditions (wet, normal, and dry) during the growing season. Following Isbell et al. (2015), SPEI values were then categorized into five classes (SPEI values for extreme dry: ≤ -1.28 , moderate dry: > -1.28 to < -0.67 , normal: -0.67 to < 0.67 , moderate wet: 0.67 to < 1.28 , and extreme wet: ≥ 1.28). Each class represents a particular intensity of the climatic conditions. This classification is broadly used to detect and quantify the intensity and direction of climatic conditions (Hossain et al., 2021, 2022; Isbell et al., 2015). A value of $SPEI-3 \leq -1.28$ (≥ 1.28) for August 2000 at a specific place corresponds to a degree of seasonal extreme dry (extreme wet) climate that has historically occurred at that site once per decade from June to August. Similarly, $SPEI-3$ values < -0.67 (≥ 0.67) for August 2000 at a particular location correspond to a degree of seasonal moderate dry

(moderate wet) climate that has happened once every 4 years at that location from June to August (Isbell et al., 2015).

Defining and calculating resistance and resilience Two crucial components determine the health and stability of an ecosystem (i.e., resistance and resilience, Pimm, 1984). Resistance denotes an ecosystem's power to tolerate a disturbance (such as droughts), while resilience represents an ecosystem's capacity and speed of returning to its pre-disturbance state (i.e., normal climatic conditions) after a disturbance. Based on the following equations, NDVI_{gs} resistance and resilience were computed (Hossain et al., 2022; Isbell et al., 2015):

$$\text{Resistance } (\Omega) = \frac{\overline{Y}_n}{|Y_e - \overline{Y}_n|} \quad (1)$$

$$\text{Resilience } (\Delta) = \left| \frac{Y_e - \overline{Y}_n}{Y_{e+1} - \overline{Y}_n} \right| \quad (2)$$

where \overline{Y}_n is the NDVI_{gs} values during normal years (i.e., SPEI values are between > -0.67 and < 0.67) for the period 1982–2012; Y_e is the NDVI_{gs} values during an extreme climate event (i.e., SPEI values are between ≥ 0.67 and ≤ -0.67); and Y_{e+1} is the NDVI_{gs} values during a normal year after an extreme climate event.

Because resistance and resilience have no dimensions and are symmetric (i.e., directly comparable between wet and dry climatic conditions), they can be directly compared across grasslands that have varying levels of productivity (i.e., lower or higher NDVI_{gs} values; Hossain & Li, 2021c) as well as across different climatic conditions (Hossain et al., 2022; Isbell et al., 2015). For example, if the NDVI_{gs} during an extreme dry condition decline by 25% and 50% from its normal climatic condition, then $\Omega=4$ and $\Omega=2$, respectively. A higher Ω value indicates greater resistance of the vegetation in respective grasslands. Quantifying Δ necessitates additional information (Y_{e+1}) than quantifying Ω . In the event of 2 (3) successive extreme climatic conditions (e.g., moderate dry climate in 2010 and extreme dry climate in 2011), we determined the level of Δ using Y_{e+2} (Y_{e+3}) instead of Y_{e+1} in Eq. (ii). If during Y_{e+1} NDVI_{gs} value recovers from 0.30 in Y_e to 0.50, then $\Delta=1.4$.

The higher (lower) Δ values than 1 indicates higher (lower) vegetation resilience.

Data analysis

Assessing the differences and temporal patterns of NDVI_{gs} The extracted log-transformed NDVI_{gs} values of five grassland types were plotted using boxplots. The differences in the mean NDVI_{gs} among the 5 grassland types were first tested using a one-way ANOVA (Kaufmann & Schering, 2014). Second, as the difference in the mean NDVI_{gs} of the studied grasslands was found statistically significant ($p < 0.05$), a post-hoc Tukey's honest significance difference (HSD) test was used to assess the pairwise comparisons of NDVI_{gs} between grassland types (e.g., between alpine grassland and hay meadow and between arid steppe and semi-arid steppe) (Tukey, 1949). Finally, using the "ggplot" package in the statistical software R, temporal patterns in NDVI_{gs} for each type of grassland were displayed (R Core Team, 2020). We applied the Mann-Kendall test (Mann, 1945) to detect statistically significant trends in NDVI_{gs} in respective grassland types over 31 years (Ran et al., 2019). Here, the year was the independent variable and NDVI_{gs} was the dependent variable.

Assessing the correlation between NDVI_{gs} and SPEI We assessed the autocorrelation of the residuals by the ACF function (Fig. S2) and Durbin-Watson test (Table S3) to confirm that the residuals of the model satisfy the assumption of no autocorrelation (Durbin & Watson, 1992). The Pearson's correlation (r) was used to analyze the correlation between NDVI_{gs} and SPEI at < 0.05 significance (p) level (Freedman et al., 2007). Here, the dependent variable was NDVI_{gs} and the independent variable was SPEI.

Response of NDVI_{gs} to climatic conditions As we categorized SPEI values into 5 climatic conditions in order to examine the response of NDVI_{gs} to a particular climate condition, using "ggplot," we plotted the number of climatic conditions for 31 years in each grassland type. The differences in the mean NDVI_{gs} among five climatic conditions were determined using a one-way ANOVA. When differences in the mean NDVI_{gs} among the five climatic conditions were significant (ANOVA $p < 0.05$), we compared

NDVI_{gs} between climatic conditions using pairwise comparisons. To analyze the pairwise comparisons of NDVI_{gs} between the climatic conditions and between the NDVI_{gs} of a particular climatic condition and their base-mean, a post hoc Tukey’s HSD test was used. Here, base-mean NDVI_{gs} is the mean NDVI_{gs} of all climatic conditions. The pairwise comparisons between the NDVI_{gs} of a climatic condition and the base-mean NDVI_{gs} explain whether the NDVI_{gs} in a given climatic condition is significantly higher, lower, or not significant, compared to the base-mean NDVI_{gs}.

Resistance and resilience of NDVI_{gs} to extreme climate Like the analysis of NDVI_{gs} and climatic conditions, using a one-way ANOVA and post hoc tests, we also examined the resistance and resilience of all grasslands for four extreme climate events (i.e., extreme dry, moderate dry, moderate wet, and extreme wet). As the resistance and resilience of NDVI_{gs} in hay meadow did not significantly differ (ANOVA $p > 0.05$) among the four climatic conditions, a post hoc test was not applied for assessing the pairwise comparisons of resistance and resilience between climatic conditions in this grassland type.

Results

Differences and temporal patterns of NDVI_{gs}

The NDVI_{gs} showed obvious differences in five grassland types, and the mean NDVI_{gs} differed significantly among each other (Fig. 2, $p < 0.001$). The mean NDVI_{gs} was the lowest in semi-arid steppe (0.18) and the highest in alpine grassland (0.42), followed by grass-dominated steppe (0.39), hay meadow (0.25), and arid steppe (0.19) (Fig. 2).

The temporal patterns of NDVI_{gs} showed a large variability (Fig. 3). This variability resulted from the differences in site, as we considered 10 sites in each grassland. When all sites in respective grassland assessed together, we found that the mean NDVI_{gs} in alpine grassland, grass-dominated steppe, and hay meadow showed a significant increasing trend (albeit low R value), while the temporal trends of mean NDVI_{gs} in arid and semi-arid steppes were not significant (Fig. 3). The annual increasing rate of mean NDVI_{gs} in alpine grassland was 0.0001 (from 0.420 in 1982 to 0.423 in 2012, $p < 0.001$), in grass-dominated steppe was 0.0042 (from 0.334 in 1982 to 0.473 in 2012, $p < 0.05$), and in hay meadow was 0.0039 (from 0.226 in 1982 to 0.339 in 2012, $p < 0.001$, Fig. 3).

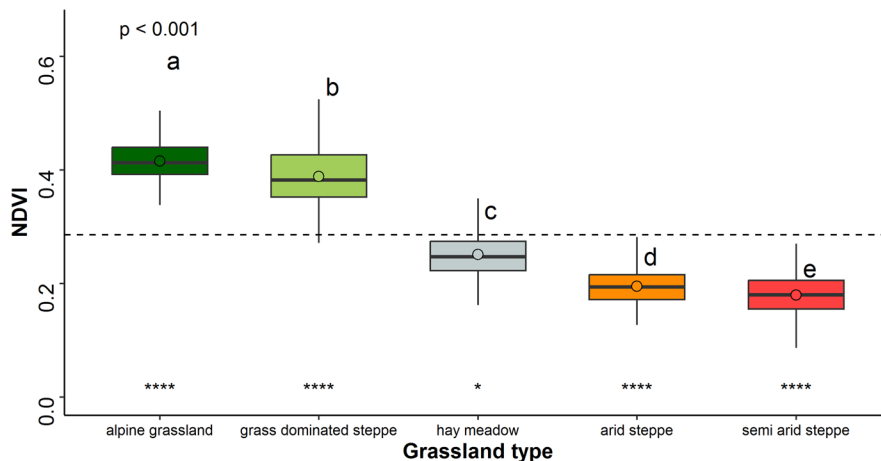


Fig. 2 Differences in NDVI_{gs} in five grassland types during the period 1982–2012. One-way ANOVA is used to analyze the differences in mean NDVI_{gs} among the various grassland types. In the post hoc Tukey’s HSD test, different letters (a–e) at the top of boxes indicate statistically significant differences in NDVI_{gs} between grassland types at $p < 0.05$. The significance of the difference between the NDVI_{gs} of each grassland

and the base-mean (mean NDVI_{gs} of five grasslands) is indicated by the asterisk (*) beneath the boxes. The 25th percentile and the 75th percentile are used as the lower and upper quartiles, respectively, to show the interquartile range in boxes. The median (50th percentile) and mean are indicated by the horizontal line and circle close to the center of the box, respectively

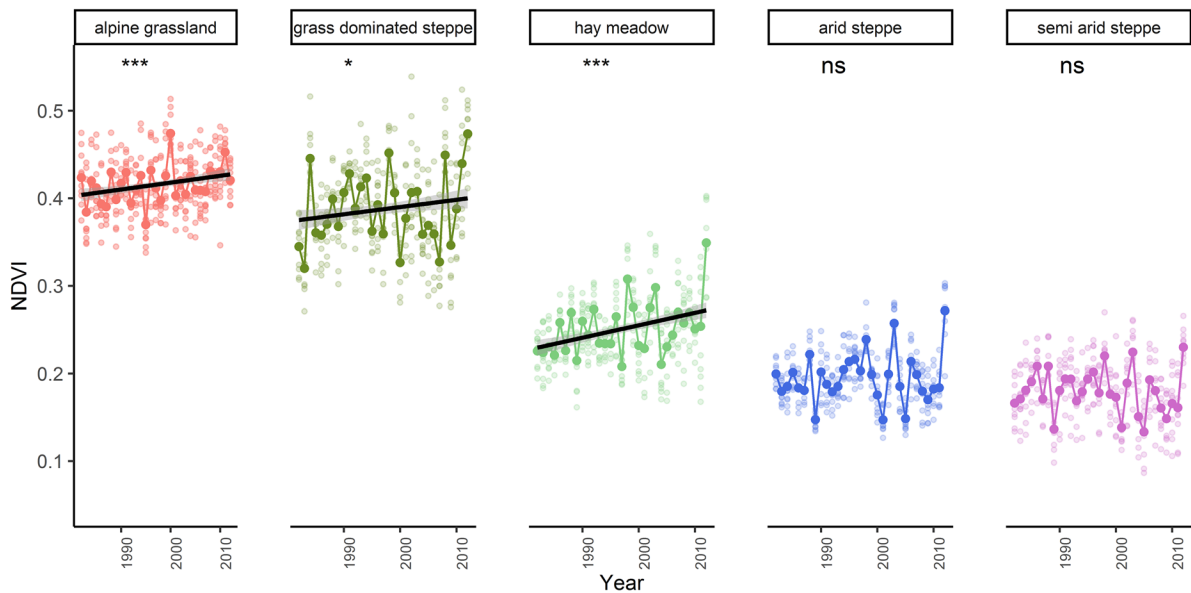


Fig. 3 Inter-annual variability in $NDVI_{gs}$ in five grassland types. Solid black lines represent the trends of $NDVI_{gs}$ over the period 1982–2012, detected by the Mann–Kendall test. Confidence intervals of 95% of changes in $NDVI_{gs}$ are represented by bands near the solid lines. The solid points indicate the mean $NDVI_{gs}$ values of all sites in the respective year,

and the transparent points represent the site-level $NDVI_{gs}$ values. Asterisks (*, **, and ***) indicate the significance of the changes in $NDVI_{gs}$ at $p < 0.05$, < 0.01 , and < 0.001 . “NS” indicates that the trends of inter-annual changes in $NDVI_{gs}$ in arid steppe and semi-arid steppe are not significant

Correlation between $NDVI_{gs}$ and SPEI

Correlation analysis of SPEI and $NDVI_{gs}$ exhibited that $NDVI_{gs}$ in all grassland types decreased with increasing intensity of dry climates (alpine grassland: $r = -0.21$, $p < 0.001$, grass-dominated steppe: $r = -0.43$, $p < 0.001$, hay meadow: $r = -0.28$, $p < 0.001$, arid steppe: $r = -0.49$, $p < 0.001$, and semi-arid steppe: $r = -0.45$, $p < 0.001$) (Fig. 4).

$NDVI_{gs}$ responses to extreme climate events

In order to assess the impact of different climatic conditions on $NDVI_{gs}$, we categorized the SPEI values into five classes (i.e., extreme dry, moderate dry, normal, moderate wet, and extreme wet). Overall, across all grassland types, every 5 years there was one extreme dry event, of which semi-arid steppe grasslands encountered frequent extreme dry events (every 4 years) and grass-dominated steppe grasslands experienced a lower number of extreme dry events (every 7.4 years) (Fig. 5). Alpine grassland and hay meadow exhibited higher extreme wet events (every 6.2 years),

compared with all grassland types (every 7.3 years). For moderate dry climates across all grasslands, a higher number of events were observed in grass-dominated steppe (every 3.1 years) and lower in alpine grassland (every 20 years). Considering moderate wet events across all grassland types, arid and semi-arid steppes experienced a lower number of moderate wet events (every 10 years), while alpine grassland encountered more cases of moderate wet events (every 3.4 years) (Fig. 5).

Irrespective of grassland types, wet conditions (moderate and extreme) enhanced $NDVI_{gs}$, while dry conditions reduced $NDVI_{gs}$, compared with regular (normal) climatic conditions (Fig. 6). $NDVI_{gs}$ significantly varied among the climatic conditions in respective grassland types (Fig. 6, all $p < 0.01$). In alpine grassland, compared with the base-mean (i.e., mean $NDVI_{gs}$ for all climatic conditions), extreme dry condition significantly reduced the $NDVI_{gs}$. Pairwise comparisons revealed that $NDVI_{gs}$ during extreme and moderate wet conditions was significantly higher than that in normal climatic conditions in alpine grassland (Fig. 6a, all $p < 0.05$). $NDVI_{gs}$ in

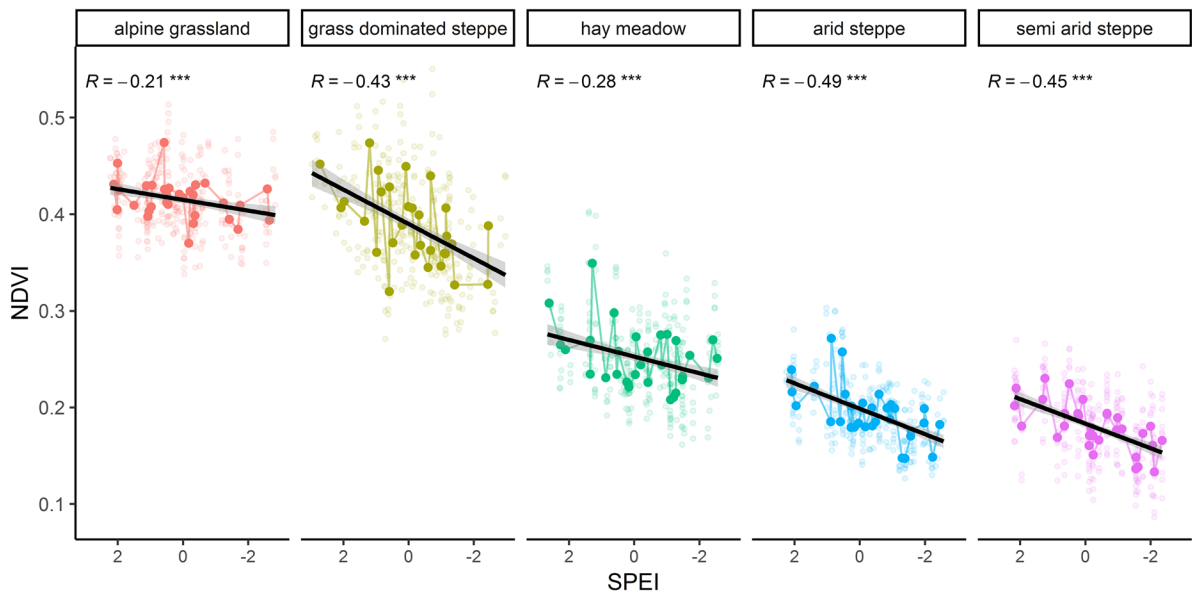
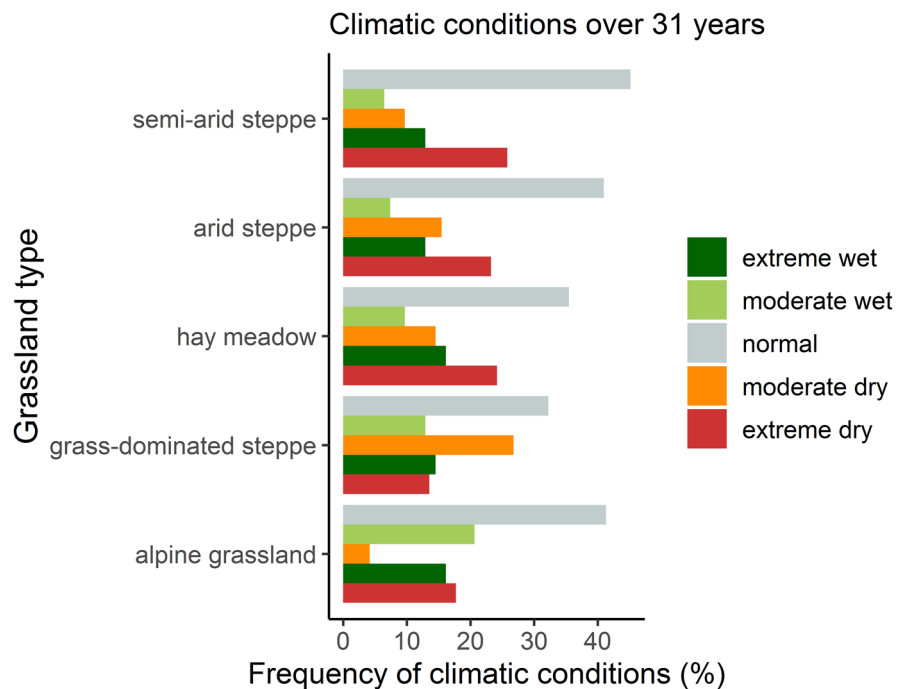


Fig. 4 Correlation between SPEI and NDVI_{gs} in five grassland types. The 95% confidence intervals of the correlations between the SPEI and NDVI_{gs} are represented by bands close

to the solid lines. The Pearson’s correlation coefficient between SPEI and NDVI_{gs} is displayed with an *R* and significance level (***) for $p < 0.001$

Fig. 5 Observations of climatic conditions (i.e., extreme wet, moderate wet, normal, moderate dry, and extreme dry) in five grassland types over the period 1982–2012



grass-dominated steppe showed higher sensitivity to a drier climate, as we found NDVI_{gs} during extreme and moderate dry conditions were significantly lower

than the base-mean and normal climatic conditions (Fig. 6b, all $p < 0.05$). In contrast, extreme wet condition had significant positive effects on NDVI_{gs}

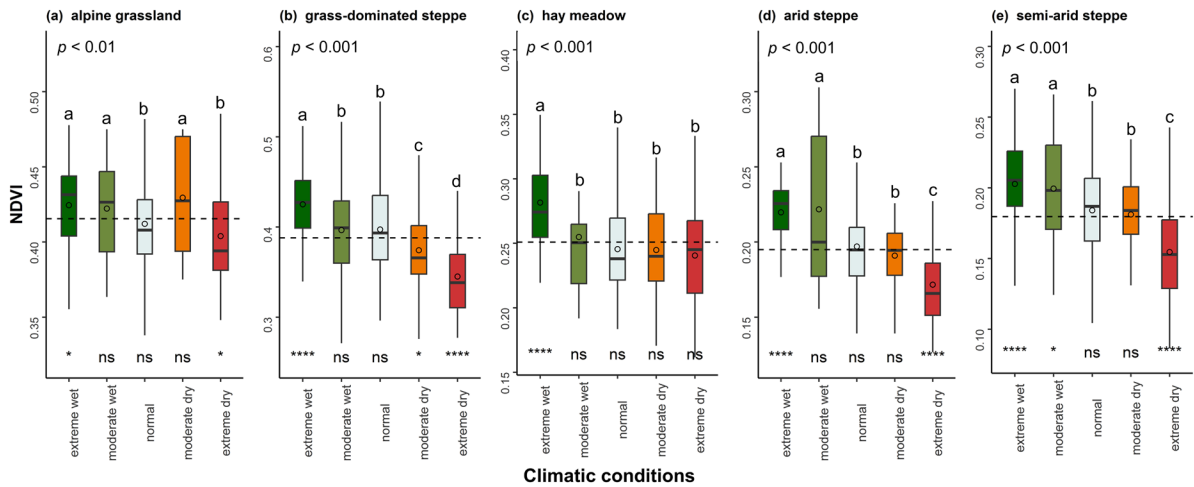


Fig. 6 The response of NDVI_{gs} to climatic conditions (extreme dry, moderate dry, normal, moderate wet, and extreme wet) in five grassland types: **a** alpine grassland, **b** grass-dominated steppe, **c** hay meadow, **d** arid steppe, and **e** semi-arid steppe. The p values indicate the significant differences in NDVI_{gs} between the five intensities of climatic conditions in the specific grassland types. The significance of the difference between the NDVI_{gs} of each climatic condition and the base-mean is indicated by the asterisk (*) beneath the boxes. In the post hoc Tukey's test, different letters (a–d) at the

top of each box denote statistically significant differences in NDVI_{gs} between climatic conditions at $p < 0.05$. The 25th percentile and the 75th percentile are used as the lower and upper quartiles, respectively, to show the interquartile range in boxes. The median (50th percentile) and mean are indicated by the horizontal line and circle close to the center of the box, respectively. "NS" beneath the boxes indicate the differences between the NDVI_{gs} in a climatic condition and the NDVI_{gs} in all climatic conditions are not significant

in comparison with the normal climatic condition and the base-mean (Fig. 6b, all $p < 0.001$). In hay meadow, NDVI_{gs} in extreme wet condition was significantly higher than NDVI_{gs} in extreme dry, moderate dry, normal climatic conditions and their base-mean (Fig. 6c, all $p < 0.001$). Neither moderate dry nor extreme dry conditions had significant effects on NDVI_{gs} in hay meadow (Fig. 6c, all $p > 0.05$). Like grass-dominated steppe, compared with the normal climatic condition and base-mean, significant gains and losses of NDVI_{gs} were observed in extreme wet and extreme dry conditions, respectively, in arid steppe (Fig. 6d, all $p < 0.001$) and semi-arid steppe (Fig. 6e, all $p < 0.001$). Notably, none of these two grasslands showed significant changes in NDVI_{gs} between normal and moderate dry climatic conditions (Fig. 6d and e, all $p > 0.05$).

Resistance and resilience of grasslands to extreme climate events

Resistance and resilience of five grassland types were assessed for four extreme climate intensities

(i.e., extreme dry, moderate dry, moderate wet, and extreme wet) (Figs. 7 and 8). Resistance and resilience of NDVI_{gs} showed large variations across extreme climate intensities, of which alpine grassland and all steppes (grass-dominated, arid, and semi-arid steppes) showed significant differences among four intensities (Figs. 7 and 8, all $p < 0.05$), while no significant differences among the extreme climate intensities were observed for hay meadow (Figs. 7c and 8c, all $p > 0.05$).

Alpine grassland and grass-dominated steppe showed higher (lower) resistance against extreme wet (dry) climate (Fig. 7a and b), while lower (higher) resilience towards extreme wet (dry) climate (Fig. 8a and b). In arid and semi-arid steppes, vegetation showed higher resistance against moderate dry climate, but resistance decreased with increasing drought intensity (i.e., from moderate to extreme dry conditions) in these grasslands (Fig. 7d and e). Conversely, vegetation in these two grassland types showed higher resilience towards increasing drought intensity from moderate to extreme dry climate (Fig. 8d and e). Vegetation resistance and

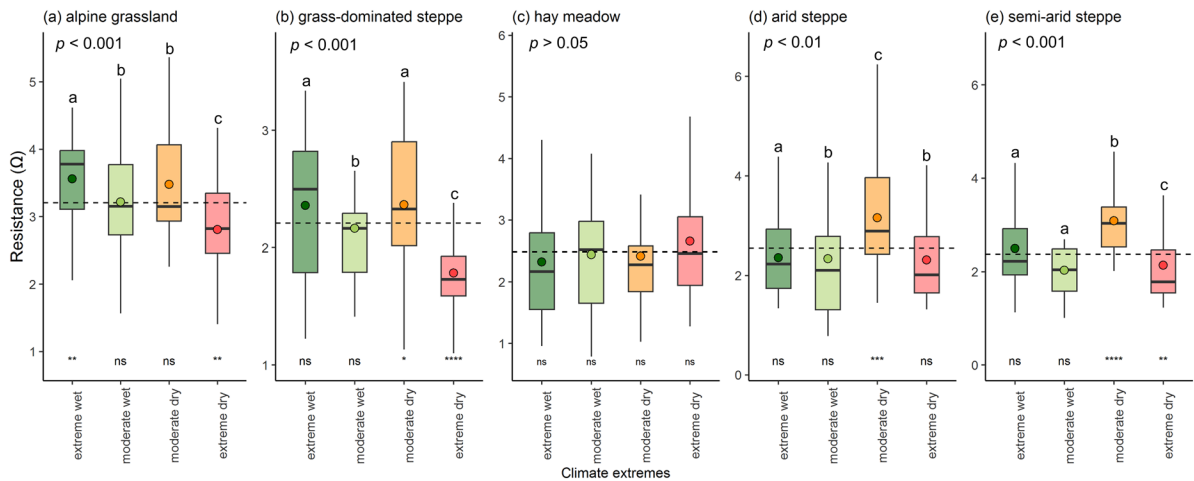


Fig. 7 Vegetation resistance against extreme climate in five grassland types: **a** alpine grassland, **b** grass-dominated steppe, **c** hay meadow, **d** arid steppe, and **e** semi-arid steppe. A one-way ANOVA was used to analyze the significance of the differences in the mean grassland NDVI_g resistance among the four extreme climate event intensities. In the post hoc Tukey’s HSD test, different letters on the top of boxes indicate significant dif-

ferences in vegetation resistance between the extreme climate event intensities at $p < 0.05$. The 25th percentile and the 75th percentile are used as the lower and upper quartiles, respectively, to show the interquartile range in boxes. The median (50th percentile) and mean are indicated by the horizontal line and circle close to the center of the box, respectively

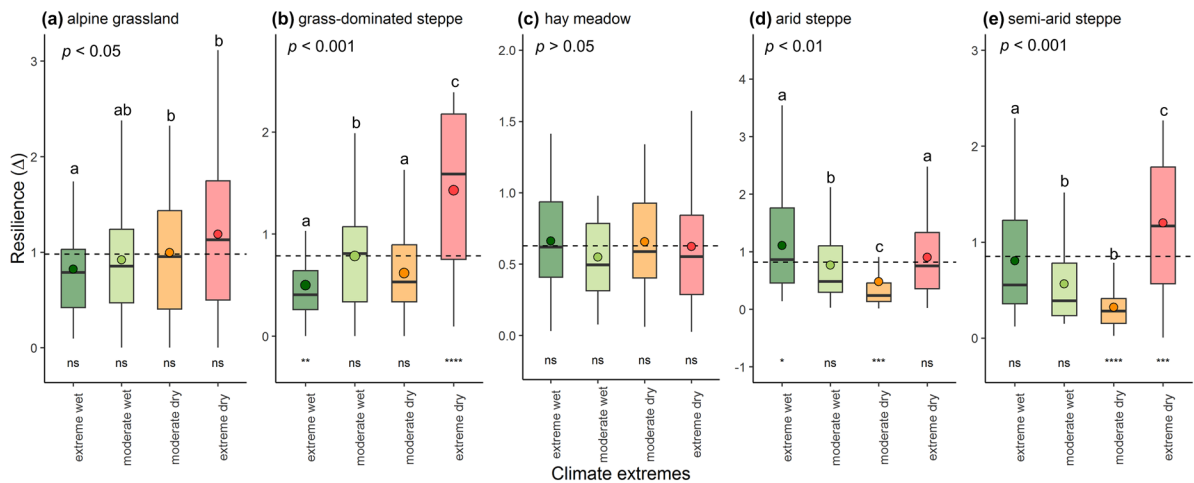


Fig. 8 Vegetation resilience towards extreme climate events in five grassland types: **a** alpine grassland, **b** grass-dominated steppe, **c** hay meadow, **d** arid steppe, and **e** semi-arid steppe. The statistical details of the figure are the same as those in Fig. 7

resilience of arid and semi-arid steppes increased with increasing intensity of wet climate (i.e., from moderate to extreme wet) (Fig. 8d and e). No detectable patterns were observed for the resistance and resilience of hay meadow across extreme climate event intensities (Figs. 7c and 8c).

Discussion

Satellite-derived NDVI, a proxy of vegetation vitality, is utilized to assess the functioning and stability of ecosystems under climate stress. In this study, using the SPEI and NDVI_{gs}, grassland response,

resistance, and resilience were examined for alpine grassland, grass-dominated steppe, hay meadow, and arid and semi-arid steppes in northern China for the period 1982–2012. The study findings are important to assess the future development of grassland ecosystems and the implementation of nature-based adaptation measures (Beierkuhnlein, 2021).

NDVI_{gs} trends and its relationships with SPEI

For several grassland types, the mean NDVI_{gs} values exhibited substantial differences. Alpine grassland showed a maximum NDVI_{gs} value of 0.42, whereas semi-arid steppe featured a minimum NDVI_{gs} value of 0.18 (Fig. 2). The differences of the mean NDVI_{gs} showed an increasing order of semi-arid steppe (0.18) > arid steppe (0.19) > hay meadow (0.25) > grass-dominated steppe (0.39) > alpine grassland (0.42). The spatial variation of the mean NDVI_{gs} for different grassland types was consistent with those of previous studies (Liu et al., 2017; Piao et al., 2006; Tong et al., 2017).

The results indicate that despite the large inter-annual variability in NDVI_{gs} in alpine grassland, grass-dominated steppe, and hay meadow, a slight greening tendency has been observed in these three grasslands during the investigation period (Fig. 3). This finding is consistent with Shen et al. (2015), which reported that the NDVI_{gs} in the Tibetan Plateau grassland increased over the period 1982–2010. This seems to be a general trend for East Asian grasslands as also other studies across different grassland types in northern China reported an increasing trend of NDVI (alpine grasslands: Piao et al., 2006, Inner Mongolian grasslands: Lu et al., 2019). Enhanced growing season precipitation and air temperature may account for the increasing NDVI_{gs} in productive grassland types (i.e., alpine grassland, grass-dominated steppe, and hay meadow) (Sun et al., 2021). Favorable soil moisture and temperature in the early and peak growing seasons promote plant growth (Gang et al., 2014; Sun et al., 2021). Increased temperature can boost soil nutrients by exacerbating the decomposition and mineralization of litter and roots (Melillo 2002).

However, we did not find any major changes in the greenness or brownness of the vegetation in arid and semi-arid steppes. This fact confirms the findings of Piao et al. (2011), who indicated that the

NDVI_{gs} variations for the period 1997–2006 in the Eurasian steppe grasslands were not significant. Very likely, this static behavior in the face of warming is related to the ongoing shortage of moisture in these ecosystems. Additionally, the significant decline of the NDVI_{gs} with increasing intensity of drought (i.e., decreasing SPEI values) across grassland types (Fig. 4) suggests that, as expected, drought events with deficient soil moisture and high potential evapotranspiration set limits to vegetation functioning (tissue die-back, reduced enzymatic activity, impaired photosynthesis) and plant recruitment (Zhong et al., 2010; Craine et al., 2013; Backhaus et al., 2014; Wang et al., 2019a).

Response of grasslands to climatic conditions

Compared with a normal climate, the significant reduction of the NDVI_{gs} during the extreme dry climate in grass-dominated, arid and semi-arid steppes indicates that excessive stress declines vegetation productivity as expected. The reduced NDVI_{gs} during the extreme dry climate can be explained by the weakening of plant photosynthesis caused by a decrease in soil water availability and an increase in evapotranspiration (De Boeck et al., 2011), which leads to an increase in mortality of plants and a decrease in germination of seeds (Chuai et al., 2013; Piao et al., 2014; Zhao et al., 2020).

It is expected in a water-limited environment that the increased NDVI_{gs} during extreme wet condition in all grassland types indicates that precipitation is a key determinant of vegetation growth (Chu et al., 2019). The lower (higher) NDVIs in extreme dry (extreme wet) conditions, compared to other climatic conditions in our study suggest the translocation of resources to roots in periods of drought and to shoots when other belowground resources are plentiful (Hossain & Li, 2021b).

However, the insignificant differences between the NDVIs of normal and extreme dry climatic conditions in alpine grassland and hay meadow (Fig. 6a and c) indicate possible complementarity effects among dominant and sub-ordinate species and functional groups. No effect of moderate dry climates on grassland NDVI_{gs} of all grassland types, except grass-dominated steppe suggests that vegetation in these grasslands is able to cope with a certain degree of drought (Hossain & Li, 2020; Li et al., 2019). Our

study confirmed that the intensity of the drought is clearly correlated with the impact on grassland ecosystems, which is coherent with previous findings in other grassland ecosystems (Ciais et al., 2005; Hossain et al., 2022), and Southwest China (Li et al., 2019).

Resistance and resilience of grasslands to extreme climate events

Resistance and resilience of the five studied grasslands showed clearly specific patterns in their responses to extreme climate events. For instance, alpine grassland and grass-dominated steppe featured lower resilience but higher resistance to extreme wet climates and higher resilience but lower resistance to extreme dry climates, compared to other climatic conditions. Conversely, arid and semi-arid steppes showed higher resistance (resilience) but lower resilience (resistance) to moderate (extreme) dry climates (Figs. 7 and 8). Hay meadows proved to be stable under climatic fluctuations, as no significant differences in their resistance and resilience were observed among the four climatic conditions. This illustrates that differences in grassland vegetation structure and management are translating into specific responses to climate change.

Ecosystems adapt and respond to climatic fluctuations differently, depending on their species richness (Hossain et al., 2022) and their functional traits (Jentsch et al., 2011). Species richness has been reported as the key determinant in ecosystem resistance (Hossain et al., 2022) and resilience (Vogel et al., 2012) under climatic perturbations. In this study, the apparent lower resistance of vegetation in alpine grassland and grass-dominated steppe against extreme dry climatic conditions could imply that drought-induced stress exerts resource competition among species (Pennekamp et al., 2018). This could be related to the specific sensitivity of certain plant functional types (e.g., perennial grasses that are lacking substantial storage organs below-ground or woody organs) towards short-term climatic extremes. Since alpine grassland and grass-dominated steppe have higher species richness (4–26 species/m⁻² in alpine grassland and 2–28 species/m⁻² in grass-dominated steppe; Li et al., 2020a, b), compared to the arid and semi-arid steppes (2–11 species/m⁻²; Li et al., 2020a, b), it is expected that vegetation resistance in alpine

grassland and grass-dominated steppe is not affected under moderate dry climate, but that intense drought (i.e., extreme dry) reduced resistance of these grasslands, which is consistent with our findings (Fig. 7a and b).

Examination of the resilience of these two (alpine and grass-dominated) grasslands showed opposite patterns, that is, higher resilience towards dry climatic conditions. This is in line with Isbell et al. (2015) but other studies showed reduced resilience of ecosystems towards dry climatic conditions because of higher resource competition after drought and drought memory effects (De Keersmaecker et al., 2016; Liu et al., 2018).

The apparent discrepancy in the resilience of alpine grassland and grass-dominated steppe might be attributed to variations in plant communities (Craine et al., 2013), the gradient of species richness (Isbell et al., 2015), the existence of stress-tolerance and stress-sensitive species (Fischer et al., 2013), plant functional groups (Kreyling et al., 2017), and functional types (Hossain & Li, 2021a). It requires further field research to scrutinize in detail which processes and traits are effective. As these grassland types are species-rich (Li et al., 2020a, b), several other mechanisms (e.g., plant-plant, plant-soil, plant-environment, and plant-soil-environment interactions) can play a role in strengthening resilience towards dry climatic conditions. For instance, after dry conditions, plants in these two grasslands showed a complementarity effect between dominant and subordinate species, between shallow- and deep-rooted species, and between species belonging to different functional groups.

Grasslands in arid and semi-arid steppes have developed adaptive approaches to deal with drought-induced stresses (Volder et al., 2010). However, severe drought can weaken the capacity of the ecosystem to absorb the water-induced stress. This is evident in our study for the examination of the resistance of arid and semi-arid steppes against moderate and extreme dry climatic conditions. The observed higher resistance of vegetation in these two grasslands against moderate dry climate highlights that plants in arid and semi-arid grasslands can absorb shocks of a certain degree by stimulating fine roots, but a prolonged drought has a severe impact on their functioning due to higher evapotranspiration and lower photosynthesis (De Boeck et al., 2011). In severe

water-stress conditions, species show higher resource competition belowground, while in normal climatic conditions plants allocate more resources to shoot (Roy et al., 2016), which is evident in our arid and semi-arid steppes (i.e., lower resistance to but higher resilience towards extreme dry climatic conditions).

Given the increasing frequency and intensity of climate extremes, the sustainable management of grassland ecosystems is crucial for sustaining ecosystem health and human well-being. The resistance and resilience of hay meadows did not differ significantly among the four climatic conditions, which indicate the stability of this grassland type under perturbations. The stability of hay meadows in response to dry and wet climatic conditions suggests that these grasslands are less sensitive to short-term water shortage and logging, compared to the other four grassland types evaluated. This stability can be a reflection of the fact that plants in these meadows are adapted to loose above-ground biomass through regular mowing (Wang et al., 2022; Zhou et al., 2019). Complementary responses of both important functional groups (grasses and forbs) were observed that supported the stability of the entire ecosystems. For instance, grasses responded negatively to precipitation but positively to temperature, and forbs responded positively to climatic variability (Wang et al., 2022). In these ecosystems, grasses responded less sensitively to precipitation and were very drought-resistant (Ma et al., 2017). Moreover, forbs in hay meadows showed adaptive strategies in relation to other functional groups under resource-constrained conditions (Zhou et al., 2019).

The observed lower resistance and higher resilience of alpine grassland and grass-dominated steppe, but higher resistance and lower resilience of arid and semi-arid steppes confirm that vegetation resistance and resilience of these grasslands are inversely correlated. This supports the notion that strongly resistant ecosystems can exhibit low resilience, while less resistant ecosystems can feature high resilience. Comparable results were yielded in grassland studies on other continents (van Ruijven & Berendse, 2010; Vogel et al., 2012; Kreyling et al., 2017; Pennekamp et al., 2018). The stability of hay meadows highlights that these grasslands are less vulnerable to environmental changes in comparison with other grassland types. This can also result from the mowing regime, that is selecting species can cope with disturbances. Given the expected increases in magnitude and duration of extreme climate events in the future, our study may help to identify grasslands that are most susceptible to

losing ecosystem functions. To mitigate the impacts of climate change on these vulnerable grasslands in northern China, adapted management and conservation strategies are imperative.

Conclusion

To gain deeper insight into the long-term functioning and stability of grassland ecosystems, we conducted an evaluation of differences and temporal patterns of NDVI and their resistance to and resilience towards climate extremes across five grassland types in northern China. We draw four broad insights from our study, which are as follows:

- The productive grasslands (i.e., alpine grassland, grass-dominated steppe, and hay meadow) showed a positive trend towards increased greenness over the 31 years.
- Water surplus led to significant gains in $NDVI_{gs}$, while water shortage resulted in significant losses in $NDVI_{gs}$ across all grasslands.
- Alpine grassland and grass-dominated steppe showed lower resistance but higher resilience towards dry climatic conditions.
- Arid and semi-arid steppes exhibited higher resistance but lower resilience towards moderate dry conditions.

We conclude that plants in arid and semi-arid steppes are highly resistant to moderate dry climatic condition. However, as the intensity of dryness increases, the capacity of plants in these grasslands to absorb excessive stress decreases, resulting in reduced resistance against extreme dry climatic condition. Alpine grassland and grass-dominated steppe showed a decline in resistance and an increase in resilience from extreme wet to extreme dry climatic conditions. Thus, we conclude that because of their high productivity (reflected from higher $NDVI_{gs}$ values), alpine grassland and grass-dominated steppe are highly drought sensitive but have ability to recover faster after extreme dry climatic condition.

This study's findings imply that highly resistant ecosystems during water surplus conditions are low resilient, while low resistant ecosystems during water shortage conditions are highly resilient. Our study advances the intriguing possibility that resilience in function, rather than resistance controls the stability

of productive grasslands. Our research may assist land managers in identifying grasslands that are vulnerable to losing ecosystem functions due to projected extreme climate events. Knowledge of this study provides important information to the decision-makers that the grasslands in Gansu, Qinghai and Inner Mongolia require adapted management and conservation efforts for achieving stable delivery of ecosystem goods and services.

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Author contribution M. L. Hossain: conceptualization, methodology, software, formal analysis, writing—original draft, and writing—review and editing. J. Li: methodology, writing—review and editing, supervision, funding acquisition, and project administration. Y. Lai: methodology. C. Beierkuhnlein: conceptualization, methodology, writing—review and editing, and supervision.

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Data availability The datasets generated and/or analyzed during the current study are available in Oak Ridge National Laboratory Distributed Active Archive Center (Guay et al., 2015; (https://daac.ornl.gov/VEGETATION/guides/GIMMS3g_NDVI_Trends.html) and SPEI SPEIbase v2.5 (Vicente-Serrano et al., 2010; <http://spei.csic.es/database.html>).

Declarations

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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