Article

Contrasting drought sensitivity of Eurasian and North American grasslands

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Extreme droughts generally decrease productivity in grassland ecosystems[1–3] with negative consequences for nature's contribution to people[4–7]. The extent to which this negative effect varies among grassland types and over time in response to multi-year extreme drought remains unclear. Here, using a coordinated distributed experiment that simulated four years of growing-season drought (around 66% rainfall reduction), we compared drought sensitivity within and among six representative grasslands spanning broad precipitation gradients in each of Eurasia and North America—two of the Northern Hemisphere's largest grass-dominated regions. Aboveground plant production declined substantially with drought in the Eurasian grasslands and the effects accumulated over time, while the declines were less severe and more muted over time in the North American grasslands. Drought effects on species richness shifted from positive to negative in Eurasia, but from negative to positive in North America over time. The differing responses of plant production in these grasslands were accompanied by less common (subordinate) plant species declining in Eurasian grasslands but increasing in North American grasslands. Our findings demonstrate the high production sensitivity of Eurasian compared with North American grasslands to extreme drought (43.6% versus 25.2% reduction), and the key role of subordinate species in determining impacts of extreme drought on grassland productivity.

The severity and frequency of extreme climate events have increased substantially due to global environmental change, often with devastating consequences[8]. For example, extreme droughts can cause widespread damage to regional economies, environments and human health[9,10]. Previous studies have shown that extreme droughts can have profound impacts on ecosystem functioning[11], such as substantially reducing plant productivity[1,3,6,7]—a fundamental component of the global carbon cycle[5,12]. As climate models predict future increases in the probability of multi-year extreme drought events in many regions of the world[9,13,14], there is a pressing need to understand their impacts on ecosystem function. Such understanding is crucial for accurate assessments of ecosystem resistance to climate change, as well as for the provisioning of ecosystem services.

Theoretical studies have put forward two different hypotheses regarding the response of ecosystem productivity to multi-year extreme drought: the stress-accumulation hypothesis suggests that the negative effects of drought increase with duration; and the drought-acclimatization hypothesis postulates that the negative effects of drought stabilize or even diminish with duration[15,16]. Although multi-year extreme drought experiments are relatively rare, their results provide support for both theories. For example, in a semi-arid grassland in China, drought impact was accumulative[3],

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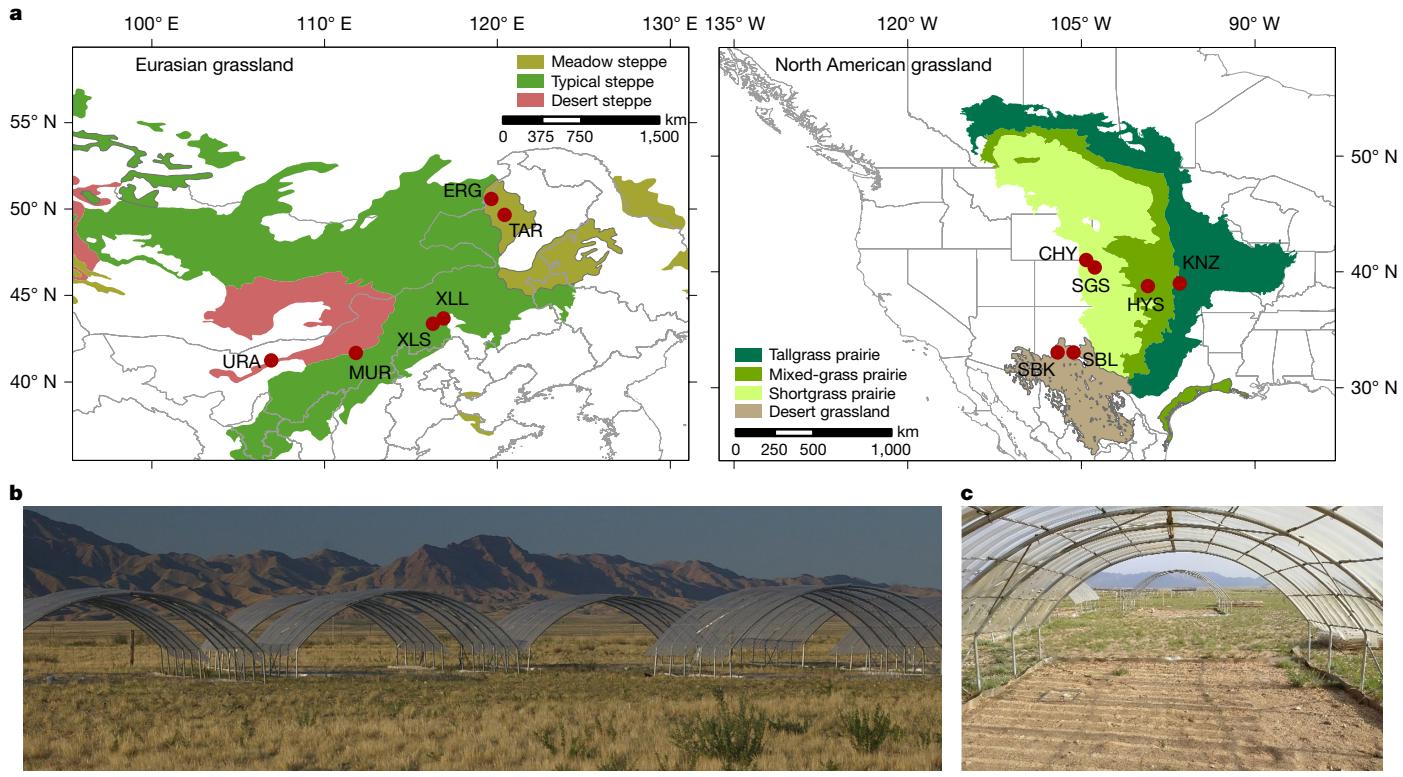

Fig. 1 | The EDGE. a, The geographical distribution of experimental sites in Eurasia and North America (additional information is provided in Supplementary Table 1). The data of distribution of grassland types were sourced from a previous study[52]. CHY, Cheyenne; ERG, Erguna; HYS, Hays Agricultural Research Center; KNZ, Konza Prairie; MUR, Sheila MuRen; SGS, Shortgrass Steppe; TAR, Sher Tara; URA, Urat; XLL, Xilingol-*Leymus chinensis*; XLS, Xilingol-*Stipa grandis*. **b**, Photograph of experimental treatments at the Xilingol-*Stipa grandis* site in Eurasian grasslands. **c**, Example of the effect of the extreme drought treatment at the Sheila MuRen site.

whereas Mediterranean grasslands exhibited acclimatization[17]. These two hypotheses are mechanistically based on a variety of biotic and abiotic factors. For example, stress-accumulative ecosystems have been associated with low biodiversity[4], the loss of subordinate species[18] or a history of water limitation (low mean annual precipitation and soil moisture)[7]. By contrast, ecosystems may be better able to acclimatize to drought owing to higher biodiversity[19], higher drought resistance of dominant species[20] or historical adaptation to chronic water limitation[21]. Although these insights are valuable, past studies often used disparate methods at different locations, rendering comparisons among ecosystems challenging. An alternative approach to evaluate these competing hypotheses and reveal the underlying mechanisms is to conduct large-scale coordinated experiments that simulate comparable multi-year extreme drought at multiple sites[22].

Grassland ecosystems, which cover around 40% of the Earth's surface[23], are particularly responsive to changes in precipitation[5,24] and their production responses to interannual variation in precipitation across climatic gradients can be highly similar[25]. However, two of the largest grass-dominated biomes in the Northern Hemisphere, the Eurasian and North America grasslands, differ in biodiversity, species identity, evolutionary histories, C_3:C_4 ratio, environmental and edaphic characteristics[26], all of which may influence their vulnerability to drought. Thus, understanding how these two major grassland biomes respond to extreme drought is essential to improve forecasts of how grassland ecosystems will respond in the future to prolonged drought under climate change[16,27].

Here we investigated how a foundational process for ecosystem functioning and the carbon cycle—aboveground net primary productivity (ANPP)—responded to a four-year period of experimentally simulated extreme drought (Extended Data Fig. 1), as well as the mechanisms underlying their responses, across six Eurasian and six North American grasslands (Methods). These 12 grassland sites were selected specifically because they are representative of the major grassland types of the Eurasian Steppe and North American Great Plains regions, both of which also encompass broad precipitation gradients (Fig. 1 and Supplementary Table 1). As such, these representative sites differed strongly in plant species and community composition, including the identity of dominant and less-common species, both within each region and between the two continents. For example, the North American sites are dominated primarily by C_4 grasses, whereas the Eurasian grasslands are dominated by C_3 grasses, with little overlap of species between the biomes (Supplementary Table 1). Drought experiments were established at each grassland site, collectively comprising what we refer to as the internationally coordinated Extreme Drought in Grasslands Experiment (EDGE). Coordinated, distributed experiments are powerful tools to generate more accurate predictions about the effects of global change on grassland ecosystem processes[1,22,28–30]. The EDGE contrasted ambient precipitation (ambient treatment) with an experimentally imposed 66% reduction in each precipitation event throughout the growing season (drought treatment; Methods). The drought treatments were classified as four-year extreme droughts for all sites (lower than the fifth percentile of historical growing season precipitation amounts; Extended Data Fig. 1), based on an estimated probability density function of precipitation calculated from 37 years (1982–2018) of mean annual precipitation (MAP; Methods).

Here we report experimental evidence that these two grassland biomes exhibit contrasting responses to extreme drought—the six Eurasian grasslands were more responsive to drought over time (43.6% reduction in ANPP on average), while sites in North American grasslands were more stable in their response (25.2% reduction). For the Eurasian grasslands, extreme drought decreased ANPP across the six sites (Extended Data Fig. 2a), and the magnitude of the ANPP

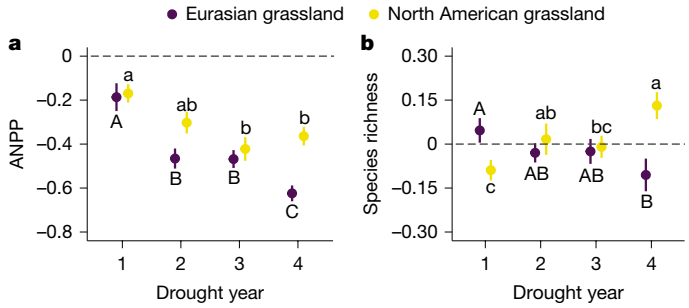

Fig. 2 | Effects of four years of extreme drought on plant productivity and richness. a,**b**, The response ratios (Methods) of ANPP (**a**) and plant species richness (**b**) over the four-year drought period. Data are mean ± s.e.m. of the response ratios of ANPP and species richness (Methods) in six Eurasian grasslands (n = 36) and six North American grasslands (n = 60). Different uppercase letters and lowercase letters indicate significant differences in response ratios among treatment years in Eurasian and North American grasslands, respectively, assessed using two-sided Tukey's honest significant difference (HSD) tests.

response to drought (expressed as a response ratio; Methods) increased over time (Fig. 2a), supporting the stress-accumulation hypothesis[3]. Extreme drought also reduced ANPP of the North American grasslands (Extended Data Fig. 2a); however, the magnitude of the reductions in ANPP stabilized by the second year (Fig. 2a), supporting the drought-acclimatization hypothesis[17]. The patterns of ANPP response observed in each individual site matched the overall trends within each biome (Extended Data Fig. 3). The contrasting patterns of ANPP responses between the two continents align well with previous expectations that, in general, C_4 plants should exhibit physiological advantages in drought resistance compared with C_3 plants, attributed to their more efficient photosynthetic pathway, and higher water-use and nutrient-use efficiencies[31]. Although no experimental studies have explored multi-year drought effects on ANPP across such extensive geographical and climate gradients, the results from past site-based studies conducted on either continent correspond well with our results. For example, ANPP declined strongly over time in two Eurasian grasslands[3,32] but not in North American grasslands[33–36], suggesting that accumulation and acclimatization responses to drought are representative of Eurasian and North American grasslands, respectively. However, ANPP stabilized after five years of drought in a Eurasian grassland in a six-year extreme drought experiment[32], suggesting that acclimatization may eventually occur with even more prolonged drought. Furthermore, even when C_4 grasses were replaced by C_3 species during extended drought in North America, there was little impact on the stability of ANPP[36]. Overall, our coordinated network of experiments with identical treatments across 12 sites revealed a robust pattern of Eurasian grasslands experiencing increasing losses in ecosystem functioning, accumulating effects, whereas North American grasslands are more resistant to losses in function as extreme drought extends over time, indicative of acclimatization.

Although there are many factors that may contribute to site-level ANPP responses[1,7], we focused on seven key abiotic variables that may reflect historical drivers of adaptation to drought[1], including historic drought frequency, soil moisture, MAP, coefficient of interannual precipitation variation (CV of MAP), aridity index, mean annul temperature (MAT) and the amount of annual precipitation removed by the drought treatment. The results showed no significant differences between Eurasian and North American grasslands for historic drought frequency (Extended Data Fig. 4a), and no clear differences were found among sites and over time for soil moisture, although on average soil moisture decreased significantly with extreme drought across all sites (Extended Data Fig. 4c–e). Previous observational and experimental studies found that historic drought frequency[2], soil moisture[37] and MAT[38] regulated the response of ANPP to drought. However, we found no such effects in this study (Extended Data Fig. 5a,b,f), consistent with other drought experiments[1,39–41]. We then examined the role of four indictors related to precipitation in regulating ANPP responses. There was no relationship between the response of ANPP and the amount of annual precipitation removed by the drought treatment (Extended Data Fig. 5g). Moreover, there were no significant differences between the pre-drought precipitation and MAP for both continents, as well as precipitation during drought (Extended Data Fig. 4b). These results suggest that the amount of precipitation removed, and precipitation before and during drought, did not drive the contrasting responses between the two continents. The MAP, CV of AP and aridity index were significantly correlated with ANPP responses for the North American grasslands only (Extended Data Fig. 5c–e and Supplementary Table 2). Although no significant relationships were found in Eurasian grasslands, the wettest site (Sher Tara) showed a similar ANPP response to North American grasslands (Extended Data Fig. 3a) while the driest grasslands (Sevilleta Blue Grama (SBL) and Sevilleta Black Grama (SBK)) in North America showed the largest drought responses similar to Eurasian grasslands (Extended Data Fig. 3b). Thus, corresponding well to other studies[1,7,24,42], our results suggest that MAP is an important determinant of the response of ANPP to extreme drought in grasslands.

Ecological theory predicts that plant diversity promotes the resistance of ecosystem productivity to environmental changes[43]. Here we examined whether species richness was correlated with the responses of productivity to prolonged extreme drought. On average, species richness was higher in North American than Eurasian grasslands (Extended Data Fig. 2b). Species richness was positively correlated with the response ratios of ANPP for the North American grasslands (Extended Data Fig. 2c and Supplementary Table 3), indicating that less diverse sites experienced greater losses in ANPP with drought than those with more plant species. Although some past studies have reported that productivity in ecosystems with lower plant diversity exhibited higher drought resistance[44], our results are consistent with a substantial body of previous research that directly[4] or indirectly[45] manipulated grassland plant diversity. Collectively, these results demonstrate that plant diversity is positively related to resistance of productivity to drought, especially when species richness is high. By contrast, the response ratios of ANPP were not correlated with species richness in the Eurasian grasslands (Extended Data Fig. 2c and Supplementary Table 3). A previous review also found no significant interaction between species richness and climate extremes due to differences in the extent of climate extremes and ecosystem resistance, as well as interactions with plant community composition[46]. It is important to note that, for the two driest North American grasslands, SBL and SBK, richness was lowest (Extended Data Fig. 6b), but the magnitude of ANPP responses was similar to Eurasian grasslands (Extended Data Fig. 3a,b). These results suggest that the role of plant diversity in regulating ANPP responses to extreme drought is dependent on species richness, that is, regulation of productivity is stronger under higher compared with under lower species richness.

With respect to how plant diversity may influence drought response, it is important to consider that species richness may respond to extreme drought over time. In the Eurasian grasslands, the response of plant species richness shifted from positive to negative over time but from negative to positive in the North American grasslands (Fig. 2b and Extended Data Fig. 6). Furthermore, the ANPP response to drought was positively correlated with richness responses to drought across these two biomes irrespective of site identity (Fig. 3a and Supplementary Tables 4 and 5). These results indicate that the largest losses in ANPP resulting from multi-year extreme drought are consistently associated with the largest losses in species richness while, conversely, smaller losses in ANPP are associated with increased richness. Biodiversity–ecosystem-function relationships are usually associated with two

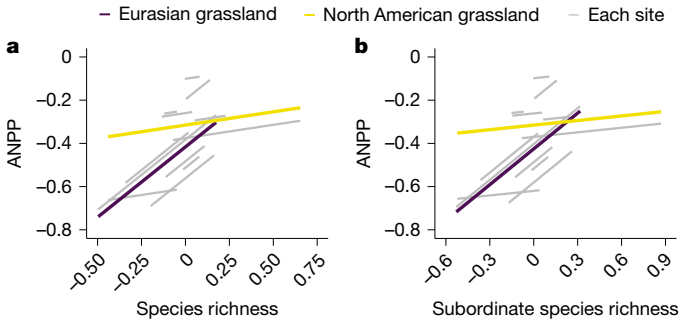

Fig. 3 | The relationships between plant species richness response to extreme drought and ANPP response to extreme drought. a, The relationship between the response ratio of total species richness and the response ratio of ANPP. **b**, The relationship between the response ratio of subordinate species richness and the response ratio of ANPP. Fitted lines are from linear mixed-effects models. The purple, yellow and grey lines indicate the trends averaged across all Eurasian grassland sites ($n = 24$), averaged across all North American grassland sites ($n = 24$) and the trends for each site ($n = 4$), respectively (the detailed model specification and summary statistics are provided in Supplementary Table 4).

common mechanisms—species stability and temporal asynchrony[47]. The increase in species richness in North American grasslands may maintain the resistance of ANPP to drought through higher species stability and stable species asynchrony (Extended Data Fig. 7). Thus, the temporal decline in species richness corresponds to a cumulative negative impact of multi-year extreme drought on ANPP in Eurasian grasslands, and the persistent increase in species richness in North American grasslands may contribute to what appears to be acclimatization of ANPP response to multi-year extreme drought.

Finally, we examined the relationships between the response of dominant and subordinate species richness and the drought responses of ANPP. The results for the response of subordinate species richness were similar to those of total species richness in influencing ANPP (Fig. 3b, Extended Data Figs. 2d and 8 and Supplementary Tables 4 and 5), indicating that the response of subordinate species, which make up the bulk of diversity in all sites, was the primary driver of ANPP sensitivity to drought in both Eurasian and North American grasslands. By definition, dominant species within ecosystems can have a pivotal role in ecosystem functioning and, as a consequence, alteration in dominant species abundance or their complete loss probably exerts the greatest influence on ecosystem dynamics[48]. However, our results suggest that increased subordinate species richness with prolonged extreme drought, which was correlated with decreased cover of dominant species but not with their loss (Extended Data Figs. 8, 9a and 10 and Supplementary Table 6), enhances the drought resistance of ANPP in North American grasslands. Compared with previous studies[46], the different role of the subordinate species observed in our study is probably due to the timescale of the current research, which allowed for more life history and population-specific responses to emerge[49]. Corresponding well with our findings, non-random species-removal experiments and anthropogenic environmental change experiments also have found that the loss of subordinate species disproportionately affected ecosystem stability compared with dominant species[18,50]. The buffering effects of subordinate species could result from the increase in drought tolerance traits (higher water-use efficiency, deeper rooting system, more interactions with mycorrhizal fungi)[18] or drought avoidance and escape traits (lower specific leaf area, less negative turgor loss point)[49]. Moreover, the lower ratio of forbs (Extended Data Fig. 9b), which usually are more sensitive to drought[3], might also contribute to the higher resistance of North American grasslands. We posit that the contrasting responses of species richness between the biomes resulting from divergent changes of subordinate species richness may have led to the accumulative or acclimatizing responses of total ANPP in Eurasian grasslands versus North American grasslands. It may be that, if drought was even further prolonged, loss of dominant species may occur[37], potentially resulting in convergence in drought responses between the two biomes.

In conclusion, we have shown, through a coordinated, four-year extreme drought experiment, contrasting responses of ANPP to a multi-year extreme drought between two of the Northern Hemisphere's major grassland regions. Sites characteristic of the three major grassland types in the Eurasian Steppe experienced greater losses in productivity over time with extreme drought, while those representing the five major grassland types of the North American Great Plains were more resistant to losses in function over time. Moreover, evidence suggests that differing responses of plant species richness, especially subordinate species richness, may underlie the contrasting patterns between these two biomes. While our experiment included the major grasslands of the Eurasian Steppe and Great Plains, our study is limited to a single, carefully selected site in each grassland type. However, despite this limitation, we believe that our results are robust for capturing the major ways in which the two grassland regions respond to extreme drought. Using sites that are representative of major ecosystems is the hallmark of many macroscale ecological studies, and inclusion of multiple sites that span broad climatic gradients across continents is key for increasing generality[51]. Our results have two important implications for climate change predictions for the future. First, the productivity of Eurasian grasslands and those with lower species richness appears to be quite vulnerable to prolonged extreme droughts. Second, management strategies that increase and maintain plant diversity, particularly focusing on subordinate species, may enhance grassland resistance to extreme drought events under climate change.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-024-08478-7.

1. Smith, M. D. et al. Extreme drought impacts have been underestimated in grasslands and shrublands globally. *Proc. Natl Acad. Sci. USA* **121**, e2309881120 (2024).
2. Du, Q. et al. Legacy effects of extreme drought and wetness events on mountain grassland ecosystems and their elevation dependence. *J. Hydrol.* **630**, 130757 (2024).
3. Xu, C. et al. Resistance and resilience of a semi-arid grassland to multi-year extreme drought. *Ecol. Indic.* **131**, 108139 (2021).
4. Isbell, F. et al. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577 (2015).
5. Knapp, A. K., Ciais, P. & Smith, M. D. Reconciling inconsistencies in precipitation-productivity relationships: implications for climate change. *N. Phytol.* **214**, 41–47 (2017).
6. Xu, C. et al. Increasing impacts of extreme droughts on vegetation productivity under climate change. *Nat. Clim. Change* **9**, 948–953 (2019).
7. Knapp, A. K. et al. Field experiments have enhanced our understanding of drought impacts on terrestrial ecosystems—but where do we go from here? *Funct. Ecol.* **38**, 76–97 (2024).
8. IPCC. *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Masson-Delmotte, V., P. et al.) 1767–1926 (Cambridge Univ. Press, 2021).
9. Chiang, F., Mazdiyasni, O. & AghaKouchak, A. Evidence of anthropogenic impacts on global drought frequency, duration, and intensity. *Nat. Commun.* **12**, 2754 (2021).
10. Lesk, C., Rowhani, P. & Ramankutty, N. Influence of extreme weather disasters on global crop production. *Nature* **529**, 84–87 (2016).
11. Rammig, A. & Mahecha, M. D. Ecosystem responses to climate extremes. *Nature* **527**, 315–316 (2015).
12. Grace, J. B. et al. Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390–393 (2016).
13. Spinoni, J. et al. Future global meteorological drought hot spots: a study based on CORDEX data. *J. Clim.* **33**, 3635–3661 (2020).
14. Easterling, D. R. et al. Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074 (2000).
15. Ploughe, L. W. et al. Community Response to Extreme Drought (CRED): a framework for drought-induced shifts in plant-plant interactions. *N. Phytol.* **222**, 52–69 (2019).
16. Smith, M. D. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* **99**, 656–663 (2011).
17. Tielborger, K. et al. Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment. *Nat. Commun.* **5**, 5102 (2014).

18. Mariotte, P., Vandenberghe, C., Kardol, P., Hagedorn, F. & Buttler, A. Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *J. Ecol.* **101**, 763–773 (2013).
19. Dietrich, P. et al. Plant diversity and community age stabilize ecosystem multifunctionality. *Glob. Change Biol.* **30**, e17225 (2024).
20. Ma, F. et al. Opposing effects of warming on the stability of above- and belowground productivity in facing an extreme drought event. *Ecology* **105**, e4193 (2024).
21. Sasaki, T. et al. Dryland sensitivity to climate change and variability using nonlinear dynamics. *Proc. Natl Acad. Sci. USA* **120**, e2305050120 (2023).
22. Fraser, L. H. et al. Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Front. Ecol. Environ.* **11**, 147–155 (2013).
23. Bardgett, R. D. et al. Combatting global grassland degradation. *Nat. Rev. Earth Environ.* **2**, 720–735 (2021).
24. Huxman, T. E. et al. Convergence across biomes to a common rain-use efficiency. *Nature* **429**, 651–654 (2004).
25. Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E. & Peters, D. Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philos. Trans. R. Soc. B* **367**, 3135–3144 (2012).
26. Stroemberg, C. A. E. in *Annual Review of Earth and Planetary Sciences* (eds Jeanloz, R. & Freeman, K. H.) 517–544 (Annual Reviews, 2011).
27. Smith, M. D. et al. Shared drivers but divergent ecological responses: insights from long-term experiments in mesic savanna grasslands. *Bioscience* **66**, 666–682 (2016).
28. Borer, E. T., Grace, J. B., Harpole, W. S., MacDougall, A. S. & Seabloom, E. W. A decade of insights into grassland ecosystem responses to global environmental change. *Nat. Ecol. Evol.* **1**, 0118 (2017).
29. Borer, E. T. et al. Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* **5**, 65–73 (2014).
30. Borer, E. T. et al. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**, 517–520 (2014).
31. Taylor, S. H. et al. Ecophysiological traits in C_3 and C_4 grasses: a phylogenetically controlled screening experiment. *N. Phytol.* **185**, 780–791 (2010).
32. Zhang, B. et al. Plants alter their vertical root distribution rather than biomass allocation in response to changing precipitation. *Ecology* **100**, e02828 (2019).
33. Batbaatar, A., Carlyle, C. N., Bork, E. W., Chang, S. X. & Cahill, J. F. Multi-year drought alters plant species composition more than productivity across northern temperate grasslands. *J. Ecol.* **110**, 197–209 (2022).
34. Munson, S. M., Bradford, J. B., Butterfield, B. J. & Gremer, J. R. Primary production responses to extreme changes in North American Monsoon precipitation vary by elevation and plant functional composition through time. *J. Ecol.* **110**, 2232–2245 (2022).
35. Song, L. et al. Grassland sensitivity to drought is related to functional composition across East Asia and North America. *Ecology* **105**, e4220 (2024).
36. Knapp, A. K. et al. Resolving the Dust Bowl paradox of grassland responses to extreme drought. *Proc. Natl Acad. Sci. USA* **117**, 22249–22255 (2020).
37. Muldavin, E. H., Moore, D. I., Collins, S. L., Wetherill, K. R. & Lightfoot, D. C. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* **155**, 123–132 (2008).
38. Stotz, G. C., Salgado-Luarte, C., Escobedo, V. M., Valladares, F. & Gianoli, E. Global trends in phenotypic plasticity of plants. *Ecol. Lett.* **24**, 2267–2281 (2021).
39. Robertson, T. R., Bell, C. W., Zak, J. C. & Tissue, D. T. Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. *N. Phytol.* **181**, 230–242 (2009).
40. Liu, D. J. et al. Increasing climatic sensitivity of global grassland vegetation biomass and species diversity correlates with water availability. *N. Phytol.* **230**, 1761–1771 (2021).
41. Hoover, D. L., Knapp, A. K. & Smith, M. D. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**, 2646–2656 (2014).
42. Maurer, G. E., Hallmark, A. J., Brown, R. F., Sala, O. E. & Collins, S. L. Sensitivity of primary production to precipitation across the United States. *Ecol. Lett.* **23**, 527–536 (2020).
43. Bazzichetto, M. et al. Biodiversity promotes resistance but dominant species shape recovery of grasslands under extreme drought. *J. Ecol.* **112**, 1087–1100 (2024).
44. Pfisterer, A. B. & Schmid, B. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* **416**, 84–86 (2002).
45. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
46. De Boeck, H. J. et al. Patterns and drivers of biodiversity-stability relationships under climate extremes. *J. Ecol.* **106**, 890–902 (2018).
47. Wang, S., Lamy, T., Hallett, L. M. & Loreau, M. Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data. *Ecography* **42**, 1200–1211 (2019).
48. Smith, M. D. et al. Mass ratio effects underlie ecosystem responses to environmental change. *J. Ecol.* **108**, 855–864 (2020).
49. Kooyers, N. J. The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Sci.* **234**, 155–162 (2015).
50. Mortensen, B. et al. Herbivores safeguard plant diversity by reducing variability in dominance. *J. Ecol.* **106**, 101–112 (2018).
51. Yahdjian, L. et al. Why coordinated distributed experiments should go global. *Bioscience* **71**, 918–927 (2021).
52. Dixon, A. P., Faber-Langendoen, D., Josse, C., Morrison, J. & Loucks, C. J. Distribution mapping of world grassland types. *J. Biogeogr.* **41**, 2003–2019 (2014).

Methods

Site information

The EDGE is a coordinated, distributed experiment established in the Inner Mongolian region of southeastern Eurasia and the southwest and Central Plains (that is, Great Plains) regions of North America (Fig. 1). We chose to focus on this intercontinental comparison, because the 12 sites selected encompass representative sites within 2 of the largest grassland regions in the Northern Hemisphere and span broad precipitation gradients on both continents. Such intercontinental comparisons that encompass broad climatic gradients are needed to increase generality regarding the ecosystem impacts of drought[51]. Site selection included meadow steppe, typical steppe and desert steppe in southeast Eurasia, along with tallgrass prairie, mixed-grass prairie, shortgrass prairie and desert grassland in North America (Fig. 1 and Supplementary Table 1). These sites include the vegetation typical of each grassland type (both in number and composition of plant species) and capture key climate differences (primarily precipitation) of the grasslands in each region. Thus, the 12 sites are ideal for the broad intercontinental comparisons of drought response assessed with the EDGE experiment.

Experimental design

The EDGE is a randomized block design. All 12 sites included ambient plots (ambient precipitation) and plots with extreme drought—imposed as a 66% reduction of each precipitation event throughout the growing season (May–August for all Eurasian grassland sites; April–September for KNZ, HYS, CHY, and SGS; April–October for SBL and SBK). There were two 6 × 6 m plots per block and six replicate blocks in Eurasian grasslands, two 6 × 6 m plots per block and ten replicate blocks in North American grasslands. Rainout shelters equipped with strips of corrugated polycarbonate were used to reduce precipitation to the target amount[53]. All 12 sites underwent a 4-year-long growing season drought treatment: from 2015 to 2018 in Eurasian grasslands; from 2014 to 2017 in 4 prairie sites (KNZ, HYS, CHY, SGS); and from 2013 to 2016 in 2 desert grassland sites (SBL and SBK), respectively.

ANPP

ANPP was estimated each year during peak biomass by clipping all aboveground biomass of individual plants at ground level rooted within two 0.5 × 0.5 m strips for six Eurasian grassland sites and three 0.2 × 0.5 m strips for four North American sites (KNZ, HYS, CHY and SGS). Live biomass was dried at 60 °C to constant mass before weighing to the nearest 0.01 g, then converted to g m^{-2}. ANPP was estimated using a non-destructive volumetric method for SBL and SBK[54]. Volume measurements (percentage cover × height) of all individual plants were recorded in four permanently located 1 m^2 quadrats in each replicate plot at peak biomass (September) during each growing season. Volume was then converted to biomass through allometric equations derived from coupled volume measurements and destructive harvests of biomass outside of the experimental plots.

Plant species richness

A randomly designated 2 × 2 m area divided into four 1 × 1 m subplots within each rainout shelter and ambient plot was permanently marked for the measurement of plant species richness and composition. The number of species in each subplot was recorded annually at peak biomass and these subplots were averaged to determine species richness in each plot.

Plant cover

Cover of individual plant species rooted in each permanently marked subplot was estimated visually to the nearest 1% annually at the same time as the estimation of species richness. To test the potential differences resulting from different aboveground biomass sampling methods, we analysed the relationship between cover and ANPP, which showed strong positive associations both in Eurasian grasslands (R^2 = 0.74) and North American grasslands (R^2 = 0.73) (Extended Data Fig. 10a,b and Supplementary Table 7). Moreover, the results based on cover showed the consistent pattern with those obtained using ANPP (Extended Data Fig. 10c).

Dominant and subordinate plant species

We defined dominant species as those with a relative frequency greater than 0.8 (80%) and a relative cover greater than 12%, and the rest as subordinate species[55] (Extended Data Fig. 9c,d). The identity of each dominant and subordinate species is provided in Supplementary Tables 8–10.

Climate data

Climate data for each grassland site were retrieved from China Meteorology Administration (http://data.cma.cn/) and NOAA's National Climate Data Center (http://www.ncdc.noaa.gov/). Long-term precipitation data from 1982 to 2018 were used to calculate MAP and to estimate the probability density function (PDF) for each site (Extended Data Fig. 1). The PDF for each site was then used to determine the number of years with extreme drought (defined as below the 5% of PDF), normal precipitation (5 to 95% of PDF) and extreme precipitation years (above the 95% of PDF; Extended Data Fig. 4a). The annual average aridity index was calculated as MAP/mean annual potential evapotranspiration[56] for each site, using estimates from World Clim v2[57].

Soil moisture

Soil moisture was recorded at the depth of 0–20 cm using soil moisture Time-Domain Reflectometer probes (CS616, Campbell Scientific) at 30 min intervals, inserted diagonally (45°) in the centre of each plot.

Statistical analysis

To explore the annual effects of extreme drought on ANPP, plant community cover and species richness, we calculated the response ratio ((extreme drought − ambient)/ambient) of ANPP, plant community cover and species richness for each year in each block for each site. Mixed-effects models were used to test the duration effects in each grassland biome (that is, Eurasian versus North American grasslands). Fixed effects were specified as treatment year, random effects as site and block within site, and the error structure as correlation = corAR1(form ~ year|site/block). The error structure accounted for repeated measurements within experimental plots across years. Tukey's HSD tests were used to assess the significant differences among treatment years.

General linear models were used to analyse the relationships between the response ratio of ANPP and seven abiotic factors in each grassland biome, that is, historic drought frequency, the response ratio of soil moisture, MAP, historical variability in annual precipitation (CV of AP), aridity index, mean annual temperature (MAT) and the amount of annual precipitation removed by the drought treatment at site level.

To examine the relationship between the response of ANPP and species richness, we calculated the mean response ratios of ANPP (mean_ANPP_RR) and species richness (mean_ric_RR) at each site for each year. The relationships between the mean response ratios of ANPP and the mean response ratios of species richness were examined by fitting a mixed-effects linear model: mean_ANPP_RR ~ mean_ric_RR × biome + (1|site), which included the potential interactions between species richness and different grassland biomes as fixed effects and site as a random effect. Furthermore, a mixed-effects linear model was used to analyse the relationship between the mean species richness in ambient plots (mean_rich) and the mean response ratio of ANPP to extreme drought in each grassland biome: mean_ANPP_RR ~ mean_rich + (1|site), including site as a random effect.

We used species cover data to measure species stability and species asynchrony for each plot. Species stability (S) was calculated as $S = \frac{\sum_{i=1}^{N} \frac{\mu_i}{\sigma_i}}{N}$, where μ_i and σ_i are the interannual mean and s.d. of cover of species i in a plot with N species over the four years. Species asynchrony ($1 - \varphi_b$) was calculated as $1 - \varphi_b = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{N} \sigma_i\right)^2}$, where φ_b is species synchrony and σ^2 is the temporal variance of community cover. Mixed-effects models with site and block within site as random effects and treatment as fixed effects were used to test the extreme drought effects in each grassland biome. Tukey's HSD tests were used to assess the significant differences among treatments.

To identify how dominant and subordinate species contributed to the responses of ANPP and species richness, we used the same calculation method as for the response ratio of ANPP and species richness to calculate the response ratios of cover and species richness for dominant and subordinate species separately. We first compared the differences of the response ratios of the cover and species richness of dominant and subordinate species among treatment years using the mixed-effects models followed by Tukey's HSD tests in each grassland biome. Fixed effects were specified as treatment year, random effects as site and block within site and the error structure as correlation = corAR1(form ~ year|site/block). We then used a mixed linear model to determine the relationship between the response ratios of subordinate species richness (Subric_RR) and the response ratios of dominant species cover (Domcover_RR): Subric_RR ~ Domcover_RR + (1|site/block), including site and block within site as random effects. We further analysed the relationship between the response of ANPP and the response of subordinate species richness following the same method as for the relationships between the mean response ratios of ANPP and the mean response ratios of total species richness. Moreover, the method used for the relationships between the mean species richness in ambient plots and the mean response ratio of ANPP was used to analyse the relationship between mean subordinate species richness in ambient plots and mean response ratio of ANPP in each grassland biome.

For the comparisons of absolute values of ANPP, total species richness, soil moisture, dominant and subordinate species cover and richness between ambient plots and plots with extreme drought in each grassland biome, mixed linear models were used with treatment as a fixed effect, and site and block within site as random effects, followed by Tukey's HSD tests. At the site level, mixed linear models with treatment as a fixed effect and block as a random effect were used for the comparisons of these absolute values between ambient plots and plots with extreme drought, followed by Tukey's HSD tests. For the comparisons of frequency of historical extreme drought, normal precipitation and extreme precipitation years between Eurasian and North American grassland sites, t-tests were used. Moreover, we used t-tests to determine significant difference in relative cover (functional group cover/plant community cover) of each functional group in subordinate species in ambient plots between Eurasian and North American grassland sites.

We used 'lme' function from 'nlme' package to build all of the mixed-effects models. All statistical analyses and figures in this study were implemented in R v.4.3.1 (R Foundation for Statistical Computing). The maps of the geographic distribution of experimental sites in Eurasia and North America were created by ArcGIS v.10.8.2 (Environmental Systems Research Institute) with the data of distribution of grassland types sourced from a previous study[52].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Experimental data of this study are available at Zenodo[58] (https://doi.org/10.5281/zenodo.14004857). Maps were created using ArcGIS v.10.8.2 (Environmental Systems Research Institute), and the GIS data of distribution of grassland types are available online (https://www.worldwildlife.org/publications/world-grassland-types).

Code availability

R code for statistical analyses and visualization is available at Zenodo[58] (https://doi.org/10.5281/zenodo.14004857).

53. Yahdjian, L. & Sala, O. E. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* **133**, 95–101 (2002).
54. Rudgers, J. A. et al. Sensitivity of dryland plant allometry to climate. *Funct. Ecol.* **33**, 2290–2303 (2019).
55. Mariotte, P. Do subordinate species punch above their weight? Evidence from above- and below-ground. *N. Phytol.* **203**, 16–21 (2014).
56. Zomer, R. J., Xu, J. & Trabucco, A. Version 3 of the global aridity index and potential evapotranspiration database. *Sci. Data* **9**, 409 (2022).
57. Fick, S. E. & Hijmans, R. J. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
58. Yu, Q. et al. Data and code for 'Contrasting drought sensitivity of Eurasian and North American grasslands'. *Zenodo* https://doi.org/10.5281/zenodo.14004857 (2024).

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Author contributions Q.Y., M.D.S, A.K.K. and X.H. conceived, designed and supervised the project. C.X., Q.Y., M.D.S., A.K.K., S.L.C., J.A.R., W.L., H. Wang, W.M. and X.Z. gathered data. C.X. and Y.K. developed the statistical analyses. Q.Y. and C.X. wrote the paper. H. Wu, Y.K., Q.G., C.W., M.D.S., A.K.K., S.L.C., Y.H., Y.L., X.X., H.R., J.A.R., Z.W., Y.J., G.H., Y.G., N.H., J.Z., S.D., G.Y., L.L. and X.H. revised the manuscript. All of the authors read and revised the final version of the manuscript.

Competing interests The authors declare no competing interests.

Additional information

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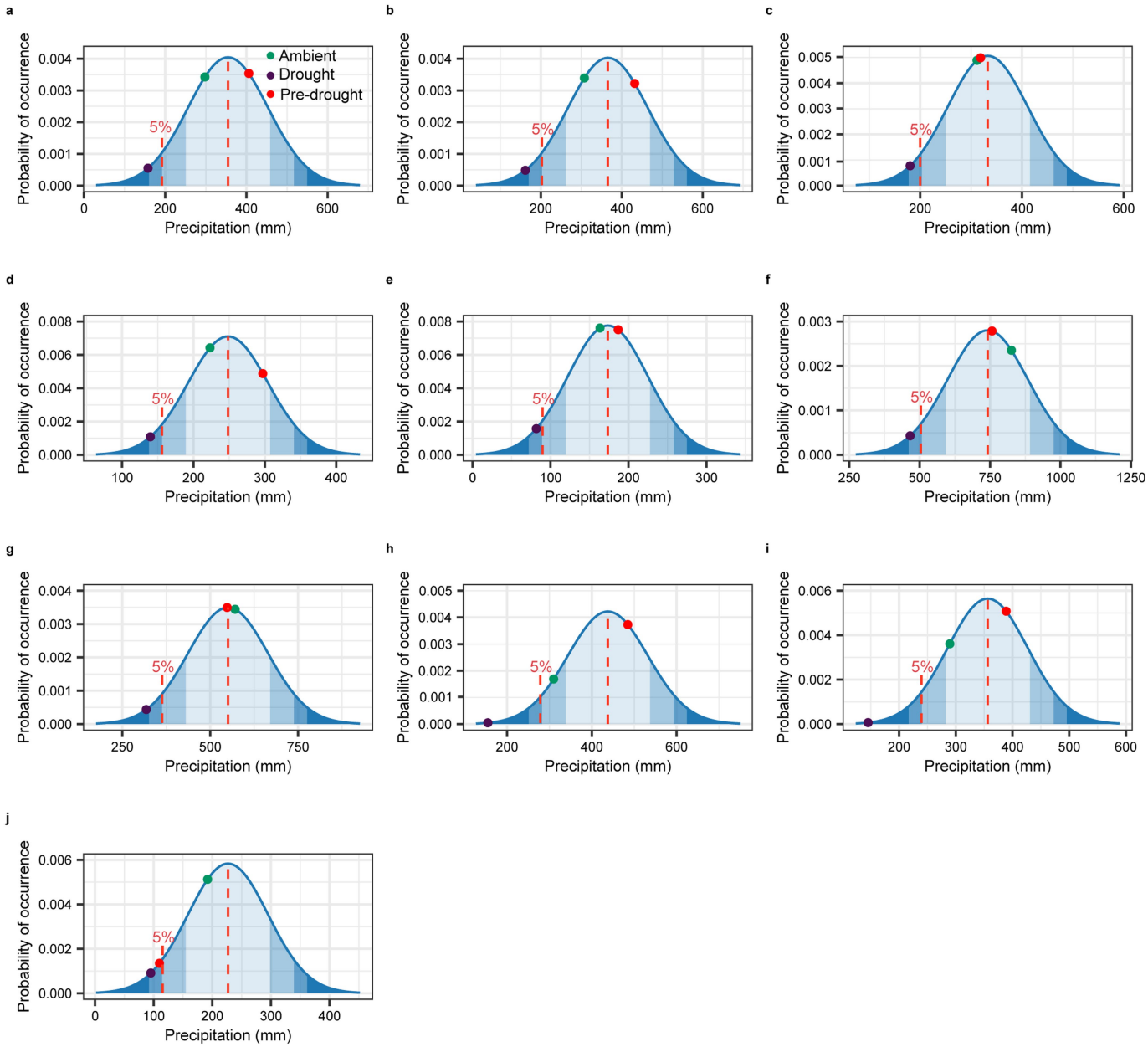
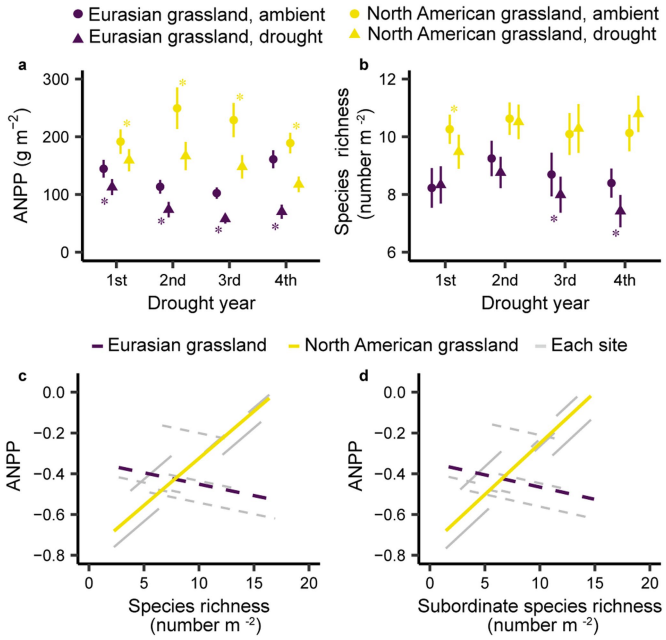
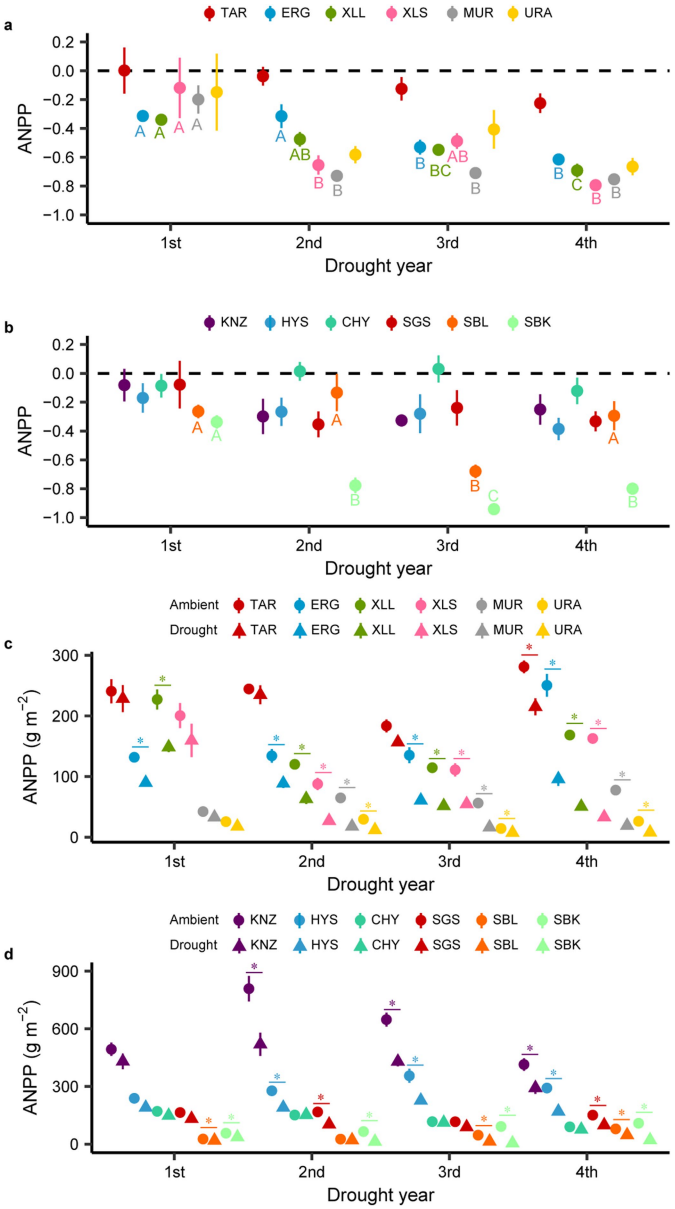


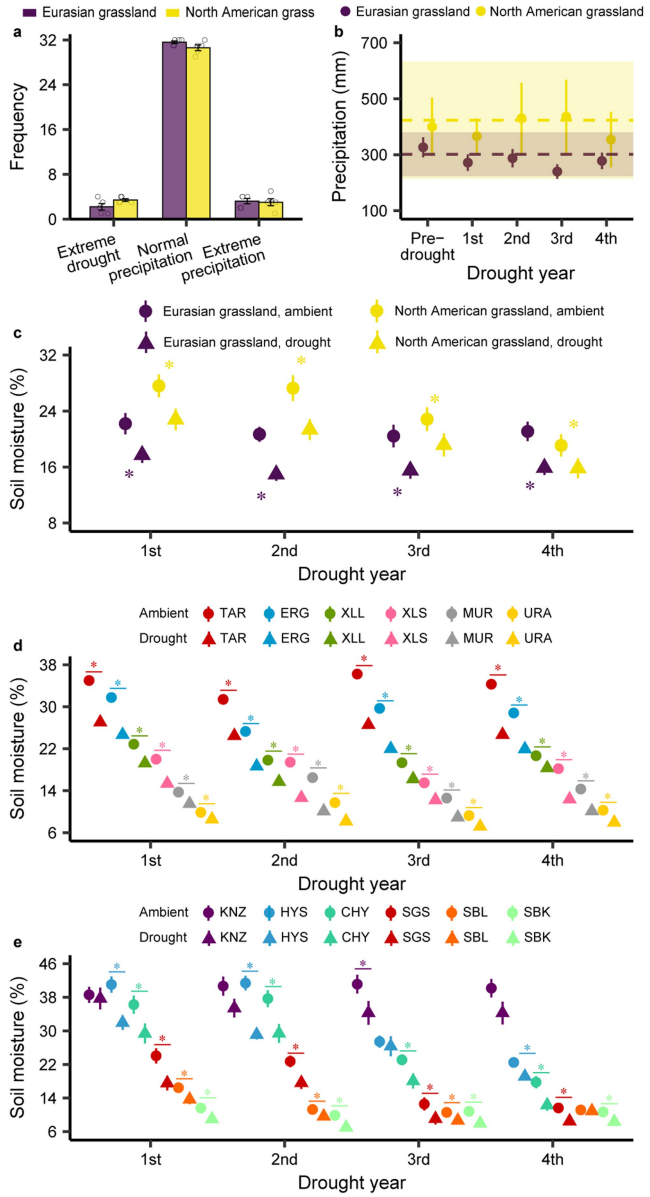
Extended Data Fig. 1 | The probability density function of long-term growing season precipitation for the 12 grassland sites. a, TAR. **b**, ERG. **c**, XLL/XLS. **d**, MUR. **e**, URA. **f**, KNZ. **g**, HYS. **h**, CHY. **i**, SGS. **j**, SBL/SBK. The probability density function is based on 37-year historical climate data from 1982 to 2018 for each site (see Methods). Mean precipitation of ambient plots and extreme drought plots during the four-year experiment as well as pre-treatment precipitation are overlaid on the estimated probability density function.



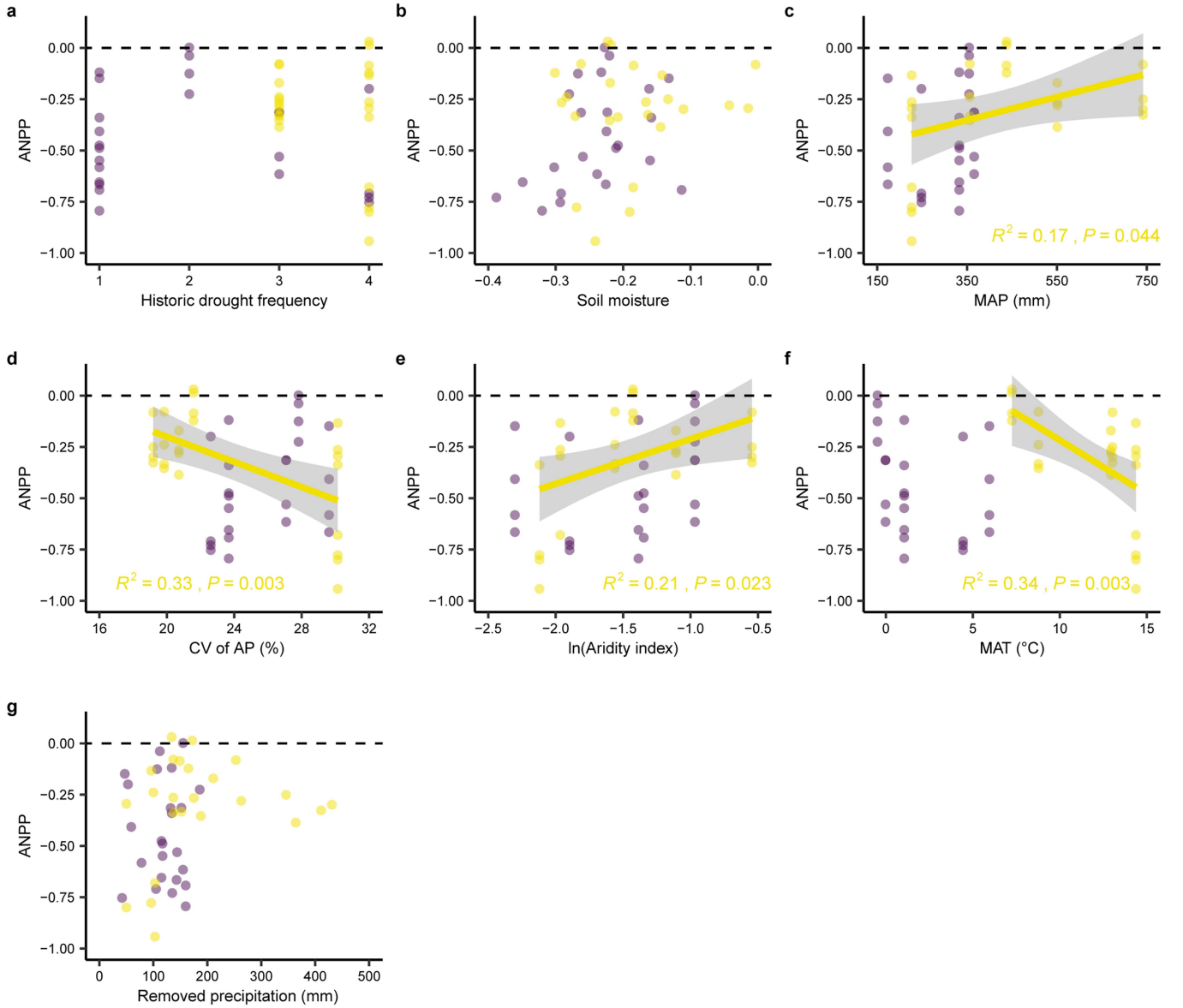
Extended Data Fig. 2 | Effects of four years of extreme drought on absolute value of ecosystem productivity and species richness, and the relationship between species richness and the response of productivity to extreme drought. a, the response of aboveground net primary productivity (ANPP). **b**, the response of plant species richness. **c**, the relationship between total species richness and the response ratio of ANPP. **d**, the relationship between subordinate species richness and the response ratio of ANPP. Total and subordinate species richness were the absolute values observed in ambient plots. Values are mean ± s.e.m. of the absolute values of ANPP and species richness in six Eurasian grasslands (n = 36) and six North American grasslands (n = 60). Statistical significance of the values between treatments is depicted as *, $p < 0.05$, which was assessed by Tukey's HSD tests (two-sided). Lines are mixed-effects model fits for each trend. The purple, yellow and grey lines indicate the trends averaged across all Eurasian grassland sites (n = 24), averaged across all North American grassland sites (n = 24) and the trends for each site (n = 4), respectively. Solid lines indicate significant associations, while dashed lines indicate non-significant associations (see Supplementary Table 3 for detailed model specification and summary statistics).



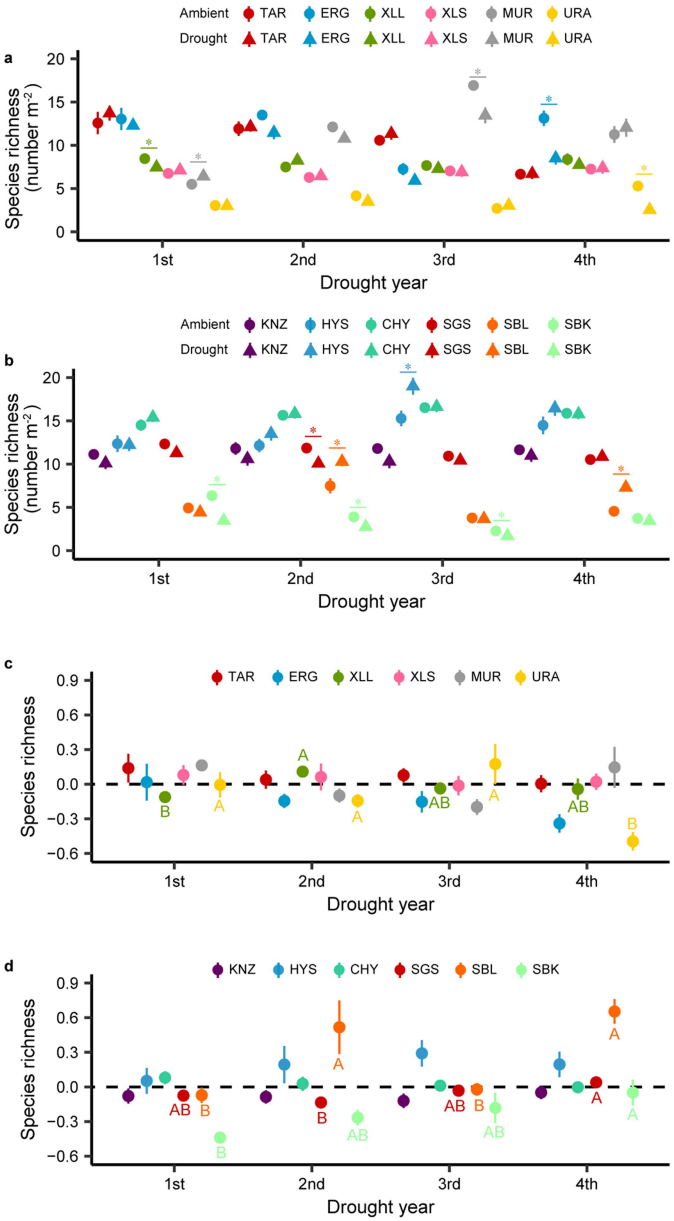
Extended Data Fig. 3 | Effects of four years of extreme drought on the productivity for each site. a, the response ratios of aboveground net primary productivity (ANPP) for Eurasian grasslands (n = 6). **b**, the response ratios of ANPP for North American grasslands (n = 10). **c**, the absolute value of ANPP for Eurasian grasslands (n = 6). **d**, the absolute value of ANPP for North American grasslands (n = 10). Values are mean ± s.e.m. Different uppercase letters with the same colour indicate significant differences in response ratio to extreme drought among treatment years, and statistical significance of the values between treatments is depicted as * ($p < 0.05$). The significances were assessed by Tukey's HSD tests (two-sided).



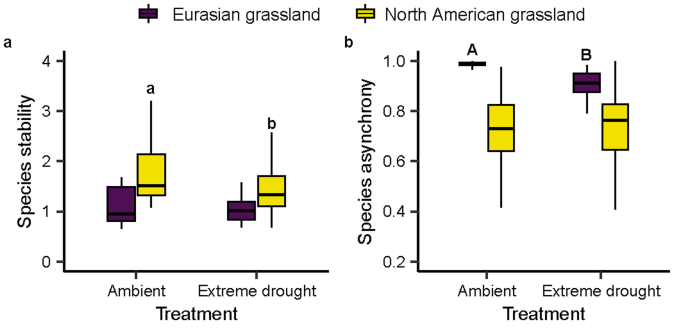
Extended Data Fig. 4 | The patterns of abiotic factors in Eurasian and North American grasslands. a, Frequency of historical extreme drought, normal precipitation, and extreme precipitation years (n = 6). **b**, Ambient precipitation (n = 6). **c**, Effects of extreme drought on soil moisture in Eurasian (n = 36) and North American grasslands (n = 60). **d**, Effects of extreme drought on soil moisture for each site in Eurasian grasslands (n = 6). **e**, Effects of extreme drought on soil moisture for each site in North American grasslands (n = 10). Values are mean ± s.e.m. Significance was assessed by t-tests (two-sided) in a, and no significant difference was found (all $p > 0.05$). The frequencies and precipitation are based on 37-year historical weather data from 1982 to 2018 for each site (see Methods). Purple and yellow dashed lines represent averaged precipitation across all Eurasian grassland sites and North American grassland sites, with their 95% CI, respectively. Statistical significance of the values between treatments is depicted as *($p < 0.05$), which was assessed by Tukey's HSD tests (two-sided).



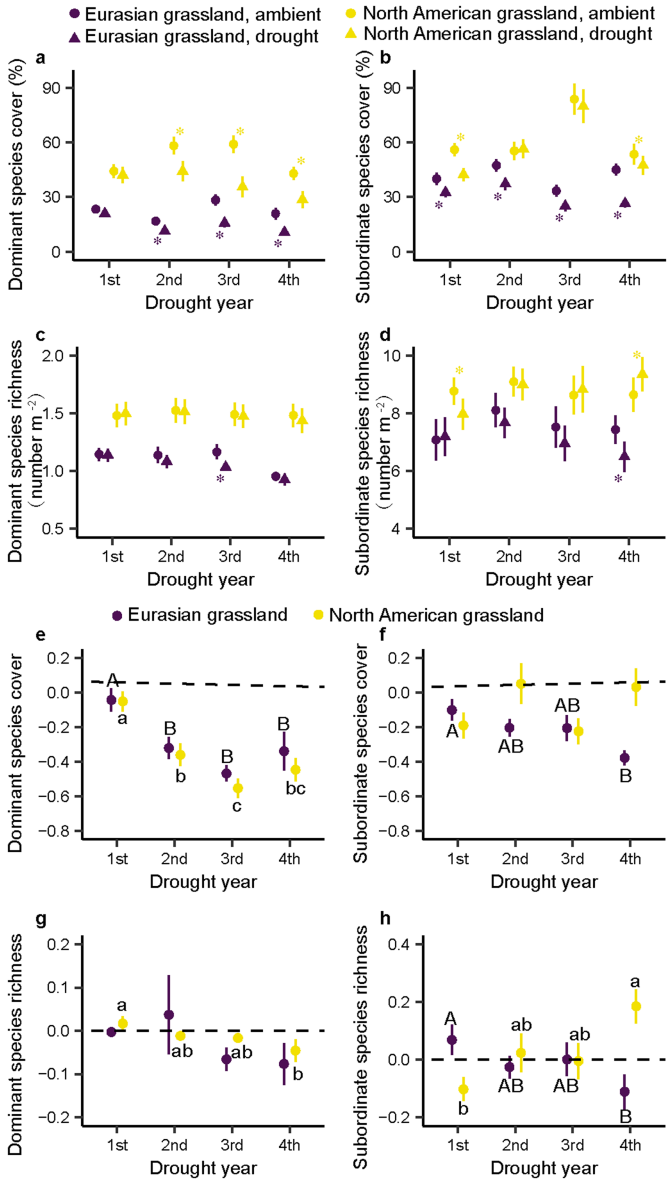
Extended Data Fig. 5 | Effect of abiotic factors on drought response. Relationships between the response ratio of aboveground net primary productivity and **a**, historic drought frequency, **b**, soil moisture, **c**, mean annual precipitation (MAP), **d**, coefficient of variation of annual precipitation (CV of AP), **e**, natural log of the aridity index (AI), **f**, mean annual temperature (MAT), and **g**, the amount of annual precipitation removed by the drought treatment. Historic drought frequency, MAP, CV of AP and MAT were calculated based on 37-year historical climate data from 1982 to 2018 for each site, and soil moisture values were observed under the four-year extreme drought plots (see Methods). AI was calculated as MAP/mean annual potential evapotranspiration. Purple and yellow points represent values of Eurasian and North American grasslands, respectively. Fitted lines are from general linear models. The yellow lines indicate the trends across all North American grassland sites and the grey bands indicate 95% confidence interval (see Supplementary Table 2 for detailed model specification and summary statistics).



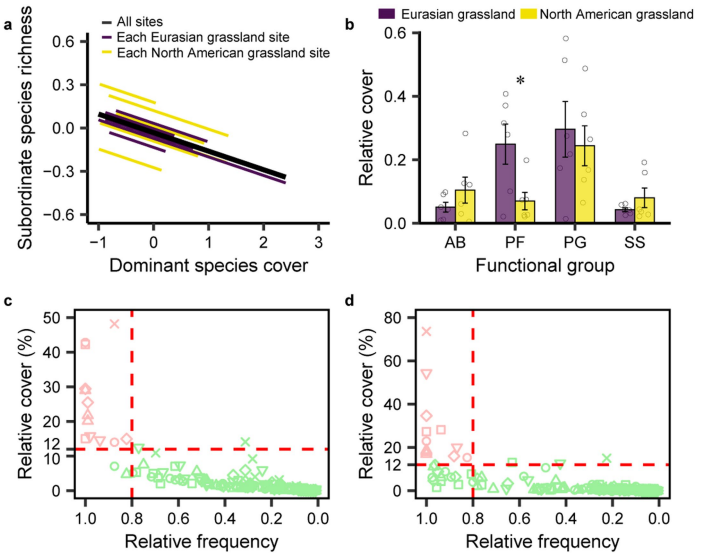
Extended Data Fig. 6 | Effects of four years of extreme drought on species richness for each site. a, the absolute value of species richness in Eurasian grasslands (n = 6). **b**, the absolute value of species richness in North American grasslands (n = 10). **c**, the response ratio of species richness in Eurasian grasslands (n = 6). **d**, the response ratio of species richness in North American grasslands (n = 10). Values are mean ± s.e.m. Statistical significance of the values between treatments is depicted as * ($p < 0.05$), and different uppercase letters with the same colour indicate significant differences in response ratio to extreme drought among treatment years. The significances were assessed by Tukey's HSD tests (two-sided).



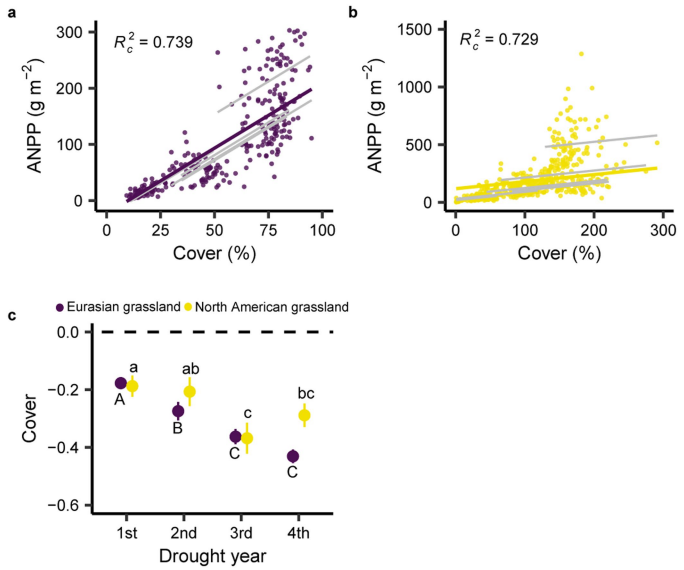
Extended Data Fig. 7 | The effect of extreme drought on species stability and species asynchrony. a, species stability, and **b**, species asynchrony. Species stability was calculated as average population stability (the interannual mean cover divided by its interannual standard deviation) across species in each plot. Species asynchrony compared the sum of the variance of individual species with the variance of the aggregated community in each plot. Center line, lower and upper limits of box, and whiskers indicated median, lower and upper quartiles, and 1.5 × interquartile range, respectively. Outliers were not shown. In Eurasian grasslands, n = 36, and in North American grasslands, n = 60, for both species stability and species asynchrony. Different uppercase and lowercase letters indicate significant differences between treatments, which were assessed by Tukey's HSD tests (two-sided).



Extended Data Fig. 8 | Effects of four years of extreme drought on dominant and subordinate species cover and richness. a, the absolute values for dominant species cover. **b**, subordinate species cover. **c**, dominant species richness. **d**, subordinate species richness. **e**, the response ratio for dominant species cover. **f**, subordinate species cover. **g**, dominant species richness. **h**, subordinate species richness. Values are mean ± s.e.m. In Eurasian grasslands, n = 36, and in North American grasslands, n = 60, for both the absolute values and response ratios of species cover and richness. Statistical significance of the absolute values between treatments is depicted as * ($p < 0.05$) and different uppercase and lowercase letters indicate significant differences in response ratio to extreme drought among treatment years for Eurasian and North American grasslands, respectively. The significances were assessed by Tukey's HSD tests (two-sided).



Extended Data Fig. 9 | The response ratio relationship between subordinate species richness and dominant species cover (a), and the characters of community composition. b, relative cover of each subordinate species functional group in ambient plots. **c**, Relative frequency-relative cover curve in Eurasian grasslands. **d**, relative frequency-relative cover curve in North American grasslands. Lines are mixed-effects model fits for each trend. The black, purple, and yellow lines indicate the trends averaged across all sites, the trends for each Eurasian grassland site, and the trends for each North American grassland site, respectively (see Supplementary Table 6 for detailed summary statistics). Values are mean ± s.e.m of the relative cover of each functional group in subordinate species in ambient plots across the six Eurasian grasslands (n = 6) and six North American grasslands (n = 6), and significance was assessed by t-tests (two-sided). Relative cover of perennial forb (PF) was significantly higher ($t = 2.60$, $P = 0.04$) in Eurasian grasslands compared with North American grasslands. No significant difference in relative cover was found for annuals and biennials (AB, $t = -1.23$, $P = 0.26$), perennial grass (PG, $t = 0.48$, $P = 0.64$), and shrubs and subshrubs (SS, $t = -1.20$, $P = 0.28$) between Eurasian and North American grassland sites. Relative frequency and relative cover are calculated based on the values over four years in ambient plots for each species at each site. Light pink and green represent dominant and subordinate species, respectively. □, ○, △, ◇, ▽, × represent TAR, ERG, XLL, XLS, MUR and URA in Eurasian grasslands, as well as KNZ, HYS, CHY, SGS, SBL and SBK in North American grasslands. Species with a relative frequency greater than 0.8 and a relative cover greater than 12% are dominant species, and the rest are subordinate species.



Extended Data Fig. 10 | The relationship between aboveground net primary productivity (ANPP) and cover, and effects of extreme drought on plant community cover. a, the relationship between ANPP and cover in Eurasian grasslands. **b**, the relationship between ANPP and cover in North American grasslands. **c**, the response ratios of plant community cover over the four-year drought period. Displayed are the absolute values of ANPP and cover for each plot during four treatment years across the 12 study sites (see Methods). Fitted lines are from linear mixed-effects models. The purple, yellow and grey lines indicate the trends averaged across all Eurasian grassland sites, averaged across all North American grassland sites and the trends for each site, respectively (see Supplementary Table 7 for detailed model specification and summary statistics). Values are mean ± s.e.m. of the response ratios of plant community cover in six Eurasian grasslands (n = 36) and six North American grasslands (n = 60). Different uppercase letters and lowercase letters indicate significant differences in response ratios among treatment years in Eurasian and North American grasslands, respectively, which were assessed by Tukey's HSD tests (two-sided).

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	N/A
Data analysis	The codes to analyze and visualize data were written in R (v4.3.1). All codes essential for the analysis are available at https://doi.org/10.5281/zenodo.14004857. R packages used include nlme (v3.1.162) and emmeans (v1.8.7).

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The Extreme Drought in Grasslands Experiment (EDGE) is a network of researchers working at herbaceous dominated ('grassland') sites across Eurasian steppes and North American grasslands, who are performing coordinated, globally distributed observations and experiments. EDGE was conducted at six Eurasian steppe and six North American grasslands sites (Fig. 1). These sites are representatives of the major grassland types (including meadow steppe, typical steppe, desert steppe, tallgrass prairie, mixed-grass prairie, shortgrass prairie and desert grassland) within their respective regions.
Research sample	The EDGE set-up at each site is a randomized block design. All 12 sites included ambient plots (ambient precipitation) and plots with extreme drought – a 66% reduction in each precipitation event throughout the growing season. There were two 6 × 6 m plots per block (ambient and drought) and six replicate blocks in Eurasian steppes, two 6 × 6 m plots per block and ten replicate blocks in North American grasslands. Passive rainout shelters were used to reduce precipitation.
Sampling strategy	Sample sizes were chosen based representative grasdsland ecosystems and on past understanding of required number of replicates to detect treatment differences in past experiments at the study sites.
Data collection	All 12 sites underwent a four year long growing season drought treatment: from 2015 to 2018 in Eurasian steppe, from 2014 to 2017 in four prairie sites (KNZ, HYS, CHY, SGS), and from 2013 to 2016 in two desert grassland sites (SBL and SBK) respectively.
Timing and spatial scale	Standing crop (ANPP) was estimated annually during peak biomass by clipping at ground level all aboveground biomass of individual plants rooted within two 0.5 × 0.5 m strips for six Eurasian steppe sites and three 0.2 × 0.5 m strips for four North American sites (KNZ, HYS, CHY and SGS). Allometric methods were used at SBL and SBK because clipping underestimates ANPP in these systems.
Data exclusions	No data were excluded from the study.
Reproducibility	The experiment was conducted one time over four years following similar protocols at all 12 sites. Other drought experiments at several of these sites contribute to reproducibility of results.
Randomization	The experimental design was a randomized block design, where plots within each block were randomly designated to the two treatments. Furthermore, 4 2 x 2 m plots within each block were randomly designated to either sampling ANPP or plant species composition. Within the 1 x 1 m plot designated for ANPP sampling, quadrats were randomly located without resampling past locations.
Blinding	Blinding was not used in data collection as this is not applied to sampling of ANPP or plant composition.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	EDGE was conducted at six Eurasian steppe and six North American grasslands sites (Fig. 1). These sites are representatives of the major grassland types (including meadow steppe, typical steppe, desert steppe, tallgrass prairie, mixed-grass prairie, shortgrass prairie and desert grassland) within their respective regions.
Location	EDGE was conducted at six Eurasian steppe and North American grasslands sites (Fig. 1). These sites are representatives of the major grassland types (including meadow steppe, typical steppe, desert steppe, tallgrass prairie, mixed-grass prairie, shortgrass prairie and desert grassland) within their respective regions.
Access & import/export	No import or export of samples occurred in this study.
Disturbance	The experimental design consisted of a drought treatment applied using rainout shelters. The construction of the rainout shelters created some soil disturbance but effort was made to minimize impacts on the study plots.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A