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Extreme drought impacts have been underestimated in grasslands and shrublands globally

Melinda D. Smith[a,b,1,2], Kate D. Wilkins[c,1], Martin C. Holdrege[d], Peter Wilfahrt[e], Scott L. Collins[f], Alan K. Knapp[a,b], Osvaldo E. Sala[g], Jeffrey S. Dukes[h], Richard P. Phillips[i], Laura Yahdjian[j], Laureano A. Gherardi[k], Timothy Ohlert[a], Claus Beier[l], Lauchlan H. Fraser[m], Anke Jentsch[n], Michael E. Loik[o], Fernando T. Maestre[p,q], Sally A. Power[r], Qiang Yu[s], Andrew J. Felton[t], Seth M. Munson[u], Yiqi Luo[v], Hamed Abdoli[w], Mehdi Abedi[w], Concepción L. Alados[x], Juan Alberti[y], Moshe Alon[z], Hui An[aa], Brian Anacker[bb], Maggie Anderson[e], Harald Auge[cc,dd], Seton Bachle[ee,ff], Khadijeh Bahalkeh[w], Michael Bahn[gg], Amgaa Batbaatar[hh,ii], Taryn Bauerle[v], Karen H. Beard[d], Kai Behn[jj], Ilka Beil[kk], Lucio Biancari[j], Irmgard Blindow[ll], Viviana Florencia Bondaruk[j], Elizabeth T. Borer[e], Edward W. Bork[li], Carlos Martin Bruschetti[y], Kerry M. Byrne[mm], James F. Cahill Jr.[hh], Dianela A. Calvo[nn], Michele Carbognani[oo], Augusto Cardoni[y], Cameron N. Carlyle[ii], Miguel Castillo-Garcia[x], Scott X. Chang[pp], Jeff Chieppa[r], Marcus V. Cianciaruso[qq], Ofer Cohen[z], Amanda L. Cordeiro[rr], Daniela F. Cusack[rr], Sven Dahlke[ll], Pedro Daleo[y], Carla M. D'Antonio[ss], Lee H. Dietterich[rr,tt], Tim S. Doherty[uu], Maren Dubbert[vv], Anne Ebeling[ww], Nico Eisenhauer[dd,xx], Felícia M. Fischer[xx,zz], T'ai G. W. Forte[oo], Tobias Gebauer[aaa,3], Beatriz Gozalo[q], Aaron C. Greenville[uu], Karlo G. Guidoni-Martins[qq], Heather J. Hannusch[bbb], Siri Vatsø Haugum[ccc], Yann Hautier[ddd], Mariet Hefting[ddd], Hugh A. L. Henry[eee], Daniela Hoss[dd,xx,yy], Johannes Ingrisch[gg], Oscar Iribarne[y], Forest Isbell[e], Yari Johnson[fff], Samuel Jordan[g], Eugene F. Kelly[ggg], Kaitlin Kimmel[hhh], Juergen Kreyling[kk], György Kröel-Dulay[iii], Alicia Kröpfl[jjj], Angelika Kübert[kkk], Andrew Kulmatiski[d], Eric G. Lamb[lll], Klaus Steenberg Larsen[l], Julie Larson[mmm], Jason Lawson[nnn], Cintia V. Leder[nn], Anja Linstädter[ooo], Jielin Liu[ppp], Shirong Liu[qqq], Alexandra G. Lodge[bbb], Grisel Longo[rrr], Alejandro Loydi[sss], Junwei Luan[ttt], Frederick Curtis Lubbe[uuu], Craig Macfarlane[vvv], Kathleen Mackie-Haas[www], Andrey V. Malyshev[kk], Adrián Maturano-Ruiz[q], Thomas Merchant[xxx], Daniel B. Metcalfe[yyy], Akira S. Mori[zzz,aaaa], Edwin Mudongo[bbbb], Gregory S. Newman[cccc], Uffe N. Nielsen[r], Dale Nimmo[dddd], Yujie Niu[n], Paola Nobre[qq], Rory C. O'Connor[mmm], Romà Ogaya[eeee,ffff], Gastón R. Oñatibia[j], Ildikó Orbán[iii,ooo], Brooke Osborne[gggg], Rafael Otfinowski[hhhh], Meelis Pärtel[iiii], Josep Penuelas[eeee,ffff], Pablo L. Peri[jjjj], Guadalupe Peter[nn], Alessandro Petraglia[oo], Catherine Picon-Cochard[kkkk], Valério D. Pillar[yy], Juan Manuel Piñeiro-Guerra[j,llll], Laura W. Ploughe[mmmm,4], Robert M. Plowes[nnn], Cristy Portales-Reyes[nnnn], Suzanne M. Prober[vvv], Yolanda Pueyo[x], Sasha C. Reed[oooo], Euan G. Ritchie[pppp], Dana Aylén Rodríguez[sss], William E. Rogers[bbb], Christiane Roscher[dd,qqqq], Ana M. Sánchez[rrrr], Bráulio A. Santos[ssss], María Cecilia Scarfó[sss], Eric W. Seabloom[e], Baoku Shi[tttt], Lara Souza[cccc,uuuu], Andreas Stampfli[www,vvvv,wwww], Rachel J. Standish[vvvv,xxxx], Marcelo Sternberg[z], Wei Sun[tttt], Marie Sünnemann[dd,xx], Michelle Tedder[yyyy], Pål Thorvaldsen[zzzz], Dashuan Tian[aaaaa], Katja Tielbörger[bbbbb], Alejandro Valdecantos[p,q], Liesbeth van den Brink[bbbbb], Vigdis Vandvik[ccc], Mathew R. Vankoughnett[ccccc], Liv Guri Velle[ddddd], Changhui Wang[eeeee], Yi Wang[ttt], Glenda M. Wardle[uu], Christiane Werner[kkk], Cunzheng Wei[fffff], Georg Wiehl[vvv], Jennifer L. Williams[ggggg], Amelia A. Wolf[hhhhh], Michaela Zeiter[www,vvvv,wwww], Fawei Zhang[iiiii], Juntao Zhu[aaaaa], Ning Zong[aaaaa], and Xiaoan Zuo[iiiii]

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Climate change is increasing the frequency and severity of short-term (~1 y) drought events—the most common duration of drought—globally. Yet the impact of this intensification of drought on ecosystem functioning remains poorly resolved. This is due in part to the widely disparate approaches ecologists have employed to study drought, variation in the severity and duration of drought studied, and differences among ecosystems in vegetation, edaphic and climatic attributes that can mediate drought impacts. To overcome these problems and better identify the factors that modulate drought responses, we used a coordinated distributed experiment to quantify the impact of short-term drought on grassland and shrubland ecosystems. With a standardized approach, we imposed ~a single year of drought at 100 sites on six continents. Here we show that loss of a foundational ecosystem function—aboveground net primary production (ANPP)—was 60% greater at sites that experienced statistically extreme drought (1-in-100-y event) vs. those sites where drought was nominal (historically more common) in magnitude (35% vs. 21%, respectively). This reduction in a key carbon cycle process with a single year of extreme drought greatly exceeds previously reported losses for grasslands and shrublands. Our global experiment also revealed high variability in drought response but that relative reductions in ANPP were greater in drier ecosystems and those with fewer plant species. Overall, our results demonstrate with unprecedented rigor that the global impacts of projected increases in drought severity have been significantly underestimated and that drier and less diverse sites are likely to be most vulnerable to extreme drought.

climate extreme | Drought-Net | International Drought Experiment | productivity

Most terrestrial ecosystems are impacted to some degree by drought, defined meteorologically as an anomalous period of low precipitation relative to normal (1). While droughts vary widely with respect to severity, duration, and spatial extent, multi-year drought events that incur catastrophic ecological, economic, and societal impacts tend to capture the lion's share of the attention by scientists and the public (e.g., the 1930's US Dust Bowl, ref. 2; the 2000 to 2003 US Southwest drought, ref. 3; the 2012 to 2016 California Drought,

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[1]M.D.S. and K.D.W. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: melinda.smith@colostate.edu.

[3]Present address: Geo-konzept Society of Environmental Planning mbH, Adelschlag D-85111, Germany.

[4]Present address: National Park Service, Flagstaff, AZ 86001.

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ref. 4; the 2001 to 2009 Millennium Drought in Australia, ref. 5; the 2015 to 2017 drought in Cape Town, South Africa, ref. 6). Yet, globally most droughts are *short-term*, lasting ~1 y in duration (7). Because short-term droughts are so numerous, they can cause substantial loss of ecosystem functioning at local, regional, and global scales (8, 9). As Earth's climate continues to change, short-term droughts that are statistically extreme in intensity (e.g., rare with respect to the long-term climate record, ref. 10) will become more common (11, 12), with 1-in-100-y droughts potentially happening every 2 to 5 y (7). Indeed, evidence of such drought intensification already exists for some regions (13). Unfortunately, because of the historic rarity of extreme drought, we have limited, and primarily anecdotal, estimates of the magnitude of their ecological consequences.

Knowledge of how short-term extreme drought may alter ecosystem functioning is particularly important for grasslands and shrublands. These ecosystems cover more than 40% of the ice-free terrestrial land surface (14, 15) and are found in every region of the globe (15). Grasslands and shrublands are characterized by high variability and frequent deficits in precipitation (16), and thus, are expected to be the most vulnerable to climate change (17). Moreover, grasslands and shrublands store more than 30% of the global stock of carbon (15) and contribute significantly to variability in global terrestrial carbon sinks (18) and atmospheric CO_2 concentrations (19). Thus, grassland and shrubland ecosystems can be expected to cause greater variation in global carbon cycling with intensifying droughts in the future.

Fortunately, many drought experiments have been conducted in grasslands and shrublands, relative to other ecosystems (e.g., forests, ref. 1), and a consensus has emerged based on recent meta-analyses of these studies. These meta-analyses show the expected—that drought has negative impacts on multiple aspects of ecosystem functioning, particularly those functions related to C cycling (e.g., productivity)—but also that considerable variation in terrestrial ecosystem responses is observed among studies (20, 21). Much of this variation could be caused by differences in the magnitude and duration of the droughts (or alteration in precipitation) imposed among the experiments included in these meta-analyses (20, 21). Although most droughts imposed are not statistically extreme, Wang et al. (21) showed that magnitude and duration were important factors for determining variation in ecosystem responses to experimental alterations in precipitation. They found a linear decrease in ecosystem functioning with greater reductions in precipitation; but, over time, productivity became less responsive to altered precipitation (21). One might conclude from this analysis that the effects of droughts, when imposed at statistically (i.e., historically) extreme levels, would result in even further declines in function with the greatest effects manifested in the short term. However, such extreme reductions in precipitation are uncommon in experiments (10); instead, precipitation reductions are for the most part within the range of nominal variability of a particular ecosystem. Consequently, we lack the critical understanding of how grassland and shrubland ecosystems will respond to a future where historically extreme droughts will become the norm rather than the exception.

Here we report results from the first-of-its-kind coordinated distributed experiment—the International Drought Experiment or IDE—designed to impose a statistically extreme, short-term (~1 y, *Materials and Methods*) drought across grassland and shrubland sites globally, using a common methodology (22). At the time of analysis, IDE consisted of 44 sites that experimentally imposed a historically extreme, 1-in-100-y drought treatment for at least a full growing season. The IDE network also provided an additional 56 sites imposing a less severe drought treatment, one that was not extreme by our definition but rather within the range of historic variability (hereafter referred to as nominal drought; Fig. 1 and *Materials and Methods*). These 100 sites were arrayed across six continents and spanned broad climatic (Fig. 1 and *SI Appendix*, Table S2) and edaphic gradients (23). At all sites, we measured annual aboveground net primary production (ANPP, *Materials and Methods*), a foundational component of the global carbon cycle, as a metric of drought-induced loss of ecosystem functioning in these grasslands and shrublands.

The results from this globally distributed experiment allowed us to 1) quantify the effects of short-term extreme drought on ANPP and determine if this effect differed between grassland and shrubland ecosystems globally, 2) compare the effects of extreme drought to less severe, nominal (or non-extreme) drought on ANPP, and 3) broadly assess factors potentially contributing to variation in ecosystems' responses to both extreme and nominal drought. We expected to observe a significant loss in ANPP with extreme drought, and that this loss in ANPP would be greater in grasslands vs. shrublands, consistent with past studies (24–26). Furthermore, we expected that extreme drought would suppress ANPP substantially more than nominal drought. We also expected that the extreme drought effects would differ from those derived in previous meta-analyses of

Significance

Drought has well-documented societal and economic consequences. Climate change is expected to intensify drought to even more extreme levels, but because such droughts have been historically rare, their impact on ecosystem functioning is not well known. We experimentally imposed the most frequent type of intensified drought—one that is ~1 y in duration—at 100 grassland and shrubland sites distributed across six continents. We found that loss of aboveground plant growth, a key measure of ecosystem function, was 60% greater when short-term drought was extreme (≤1-in-100-y historical occurrence). This drought-induced loss in function greatly exceeds previously reported losses for grasslands and shrublands, suggesting that the global impacts of projected increases in drought severity have been substantially underestimated.

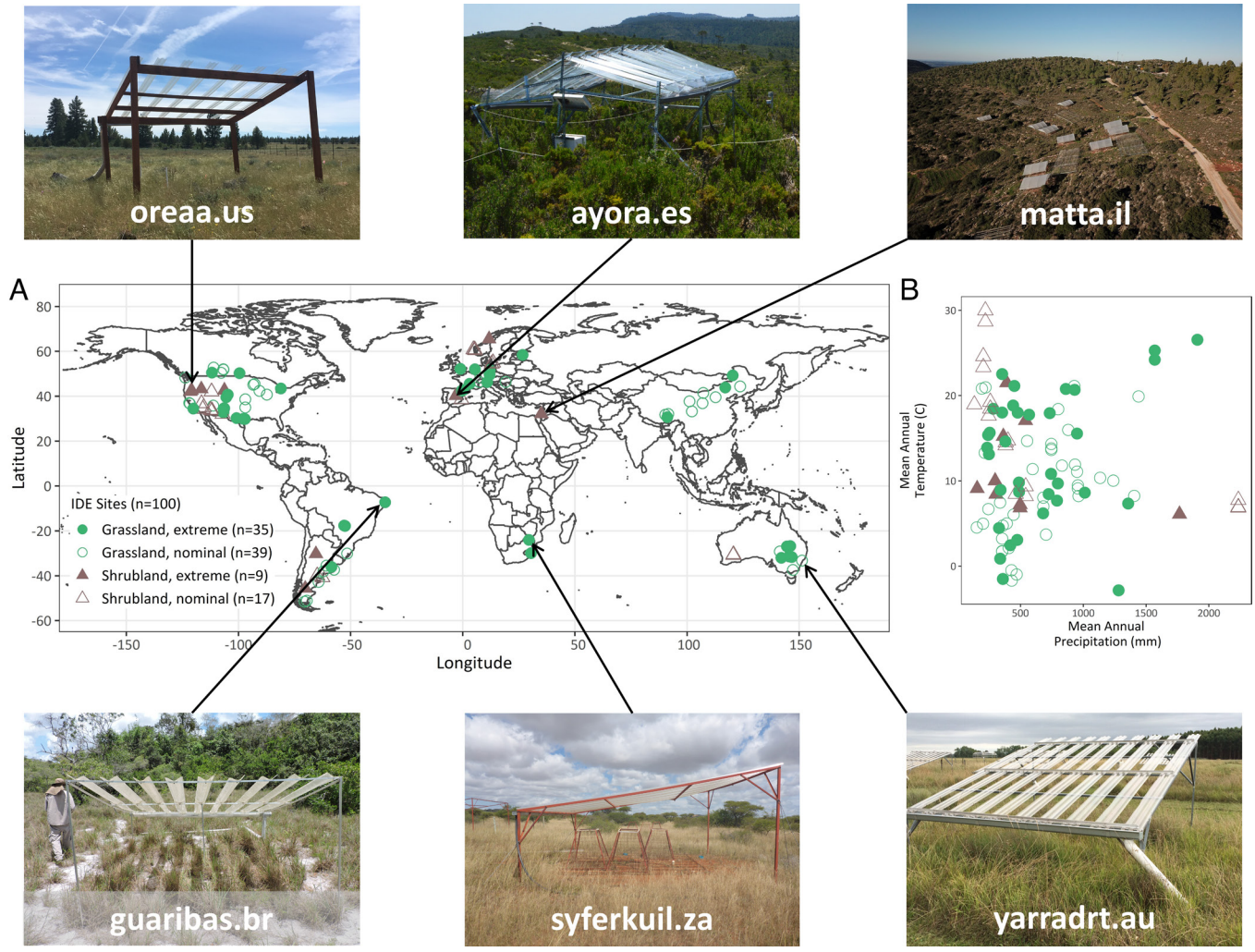

Fig. 1. Geographic extent and climate space encompassed by the IDE. The 100 grasslands (green circles) and shrublands (brown triangles) included in the analysis spanned six continents (*A*) and broad gradients of mean annual temperature and MAP (*B*). Closed symbols denote sites (n = 44) that experienced statistically extreme 1-in-100-y drought (i.e., below average annual precipitation during the experiment year). Open symbols denote IDE sites (n = 56) that experienced nominal (not statistically extreme) drought (i.e., average or above-average annual precipitation during the experiment year). Photos: Shown are drought shelters at representative sites on each continent. Drought shelters were designed to exclude a fixed proportion of each rainfall event from the plots below. The proportion excluded was selected to impose a 1-in-100-y drought for each site during years with average annual precipitation (based on long-term precipitation records, see *Materials and Methods* for details; see *SI Appendix*, Table S2 for site codes).

experimental drought results (20, 21, 27), given that past meta-analyses are subject to publication bias (28) and that their effect sizes were based on studies that varied widely in the type, duration, and magnitude of the drought imposed (29–31).

Results and Discussion

Consistent with most previous research, drought experimentally imposed over ~1 y (<2 y), whether nominal or extreme in magnitude, reduced ANPP relative to ambient conditions (Fig. 1 and *SI Appendix*, Table S3). For those sites that experienced extreme drought, ANPP was reduced on average by ~35% overall; by ~38% and 21% for grasslands and shrublands, respectively (Fig. 2*A*). Thus, across the 44 sites that experienced extreme drought, grasslands incurred greater losses in ANPP than shrublands, consistent with previous studies (24–26), though this difference was not statistically significant (*SI Appendix*, Table S4). For those sites that experienced nominal drought, ANPP was suppressed by ~21%, much less (>half) than in sites experiencing extreme drought, and there was a smaller difference between grasslands and shrublands in these nominal drought responses (Fig. 2*A*). This suggests that ANPP of grasslands and shrublands responds similarly to drought unless droughts are extreme, in which case these ecosystems are more likely to diverge in their average response to even a single year of drought.

The 95% CIs for mean reductions in ANPP due to nominal (non-extreme) droughts, and for grasslands and shrublands separately, overlapped with the range of mean effects reported in recent meta-analyses of drought experiments (Fig. 2*A*). This equivalence between the mean effects of nominal droughts in the IDE network and past meta-analyses occurred despite the wide variety of experimental protocols for imposing drought treatments included in the meta-analyses. In contrast, the effect of extreme drought on ANPP was well outside the range of these past reported effects, with the reduction in ANPP more than 1.5-fold greater. Thus, our results suggest that past studies have underestimated the ecosystem effects of statistically extreme droughts—the droughts of the future.

While it is reassuring that there is similarity among the full suite of sites in our study (n = 100), the subset of sites subjected to nominal drought (n = 56), and the mean effect sizes of meta-analyses, there are several reasons to view the IDE estimates as being more robust. First, by including results from all sites (including those

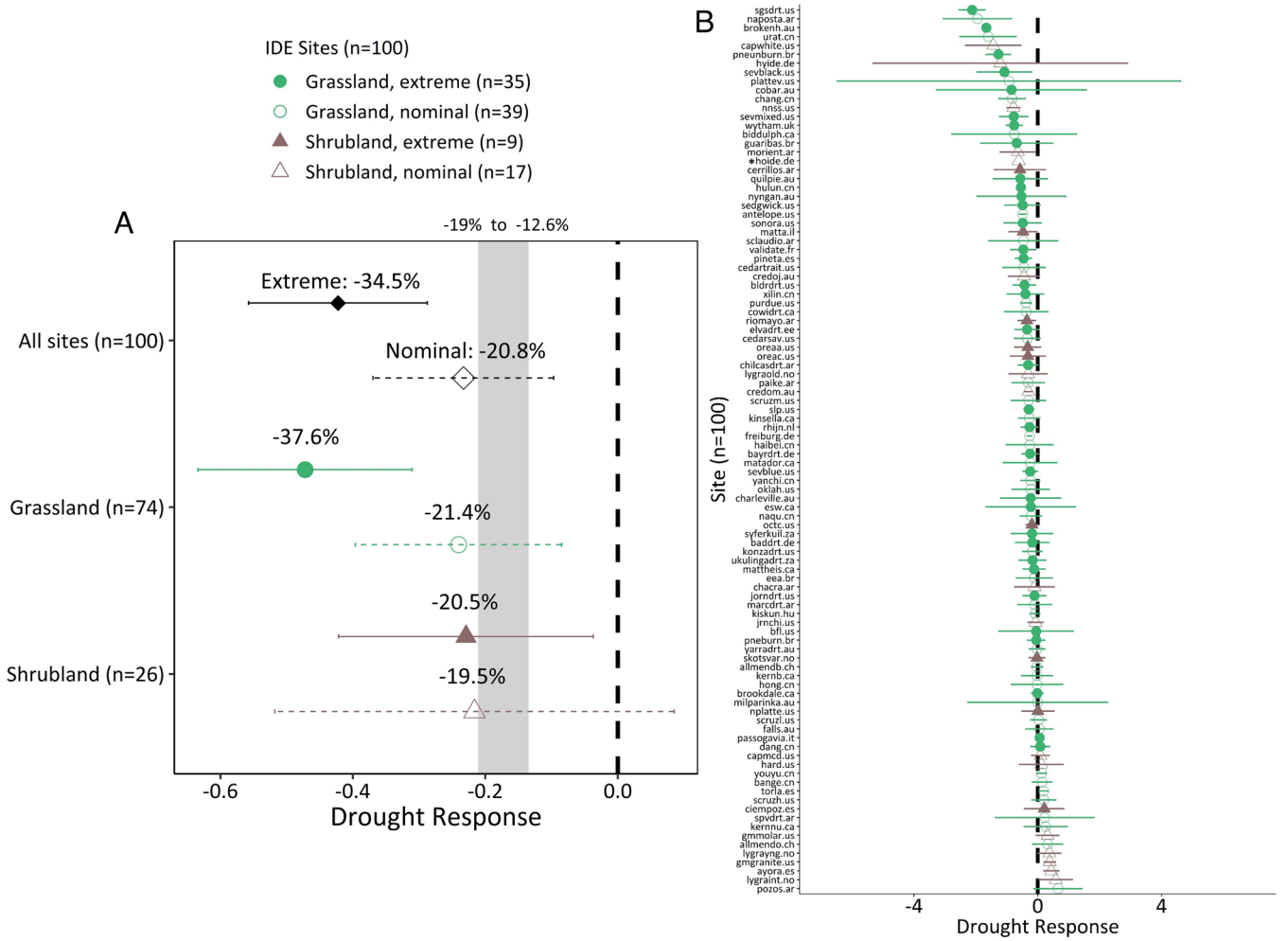

Fig. 2. Response of ANPP to a standardized 1-y drought for 100 IDE sites. (*A*) Mean drought response for sites that experienced extreme drought or nominal conditions for: all sites, grasslands, and shrublands (*SI Appendix*, Tables S3 and S4). The gray bar indicates the range of ANPP loss from −19 to −12.6% found in Song et al. and Wang et al. (20, 21), respectively. Drought response is calculated as: ln(average $ANPP_{DROUGHT}$/average $ANPP_{CONTROL}$); 0 (black dashed line) represents no effect of drought, and negative numbers indicate less ANPP in drought vs. control plots. (*B*) Mean drought response for each site ordered from negative (*Top*) to positive (*Bottom*). Site codes and corresponding site information are listed in *SI Appendix*, Table S2. Shown are 95% CIs for mean site-level drought responses. *Indicates site with CI that was omitted for clarity because it exceeds the *x* axis scale.

with no evidence of a drought effect, Fig. 2*B*), we eliminated the long-standing issue of publication bias affecting meta-analysis effect sizes (i.e., bias towards significant results, (28, 32)). In addition, although the statistical power was relatively low for detecting drought effects at individual sites—a concern of many global change experiments (32)—the large number of IDE sites, almost twice as many as included in Song et al. (20) and Wang et al. (21), provided broader and in some cases denser geographic coverage.

Furthermore, the standardized experimental design and sampling protocols we used ensured drought treatments were imposed, and responses assessed comparably, across all sites. Thus, variation in our dataset should be attributable to ecological differences among sites and not methodological differences inherent in meta-analyses. By reducing methodological differences, we anticipated that site-to-site variability would be reduced in this coordinated, distributed experiment (22, 23), at least relative to previous studies. Contrary to that expectation, a surprising amount of variation was still observed in ANPP responses to both extreme and nominal drought across sites (Fig. 2*B*). While 79 sites experienced the expected losses in ANPP, 21 sites were insensitive to the 1-y extreme drought, i.e., control and treatment ANPP means differed by <1% or were slightly higher in treatment plots, suggestive of high resistance to short-term drought (Fig. 2*B*). Variation in ecosystem responses was also observed with nominal drought, with 39 of 56 sites experiencing a loss in ANPP, but 17 sites displaying high drought resistance. Thus, individual IDE sites still differed in their responsiveness to both extreme and nominal drought despite the use of common protocols. This begs the question: What factors are contributing to the large variation in drought response among sites?

Determinants of Variation in Ecosystem Response to Drought. Although there are myriad factors that may contribute to site-level variation in the ANPP responses observed, we focused on seven key abiotic and biotic variables that were reliably available for >75% of the IDE sites. These included mean annual precipitation (MAP), previous year's precipitation (relativized by MAP), historic variability in precipitation (expressed as the interannual coefficient of variation of MAP), aridity index (AI), soil texture, plant species richness, and the dominant plant growth-form (expressed as proportion of graminoids) of the ecosystem (*Materials and Methods* and *SI Appendix*, Table S5).

Past empirical studies have indicated that the factors above may underpin variations in ANPP responses among sites to drought. For example, evidence suggests that drier and more arid sites (low MAP and AI) tend to be more sensitive to drought than wetter or less arid sites (33–36). But, in addition to MAP (or AI), historic

variability in precipitation also may contribute to variation in drought responses (37, 38). In this case, sites that experience higher year-to-year variation in MAP are expected to be less sensitive to extreme drought, a product of these ecosystems being adapted to large interannual variations in precipitation. Research also suggests that legacy effects of the previous year's precipitation may play an important role in determining plant productivity, such that responses lag behind the increases or decreases in precipitation from the previous year (39–41). Finally, the inverse soil texture hypothesis (42) proposes that plants growing in coarse-textured (sandy) soils should experience less water stress than plants growing in fine-textured soils in relatively arid ecosystems, with the opposite pattern for ecosystems with higher precipitation. This interaction between soil texture and MAP is expected to be amplified with drought, but this prediction has rarely been tested (43). With IDE spanning a broad range of edaphic conditions (23), we provide one of the first tests of the inverse soil texture hypothesis on drought responses.

In addition to the abiotic factors listed above, plant species richness has been shown to influence the magnitude of ecosystem response to drought, with more species-rich communities being more resistant to drought than less species-rich communities (44). There is also abundant evidence that growth forms differ in their sensitivity to drought, with grasses and grass-like plants (i.e., graminoids) typically more sensitive to water deficits than woody plants (45, 46) or forbs (47). Given that the IDE sites represent a range of plant species richness and graminoid abundance (*SI Appendix*, Table S5), we evaluated the relationship between average plot-level species richness and abundance of graminoids and the magnitude of the drought response observed.

Three of these potential sources of variation in drought response had statistical support in the IDE dataset. We found weak evidence ($P = 0.08$) for MAP and moderate evidence ($P = 0.02$) for aridity (low values indicate lower plant water availability or more arid sites) being related to magnitude of drought responses (*SI Appendix*, Table S6). Drier sites (lower MAP or greater aridity) experienced greater losses in productivity than wetter grassland and shrublands. This finding matches studies demonstrating that production losses at more arid sites are greater in response to drought (32, 35–37) and supports the Huxman-Smith model (35) of greater sensitivity of ANPP to interannual variation in precipitation (and dry years) in more arid sites. Finally, as demonstrated previously (44), there was moderate evidence for more species-rich sites being more resistant to a loss in productivity than less rich sites ($P = 0.04$).

In contrast, we found no evidence that previous year's precipitation (as relativized by MAP), CV in MAP, percent sand (a key component of soil texture), or the proportion graminoids explained the variation in drought responses observed across all sites (Fig. 3 and *SI Appendix*, Table S6). We also found no evidence for an interactive effect between MAP and percent sand on drought response (*SI Appendix*, Table S7), and thus no support for the inverse soil texture hypothesis affecting differential drought sensitivity.

The Importance of Drought Severity. As indicated above, drought magnitude or severity (i.e., % reduction in precipitation relative to the control) was an important predictor of ecosystem response to drought in the recent meta-analysis by Wang and et al. (21). Because the passive approach to imposing drought employed with IDE (Fig. 1; *Materials and Methods*) relies on ambient precipitation levels, the actual amount of precipitation that was reduced with the drought treatment at each site (with respect to the long-term record, i.e., MAP) varied with the amount of annual precipitation received during the year of the experiment. We used this variation in drought severity to determine if differences in drought responses could be explained simply by the magnitude of drought imposed (calculated

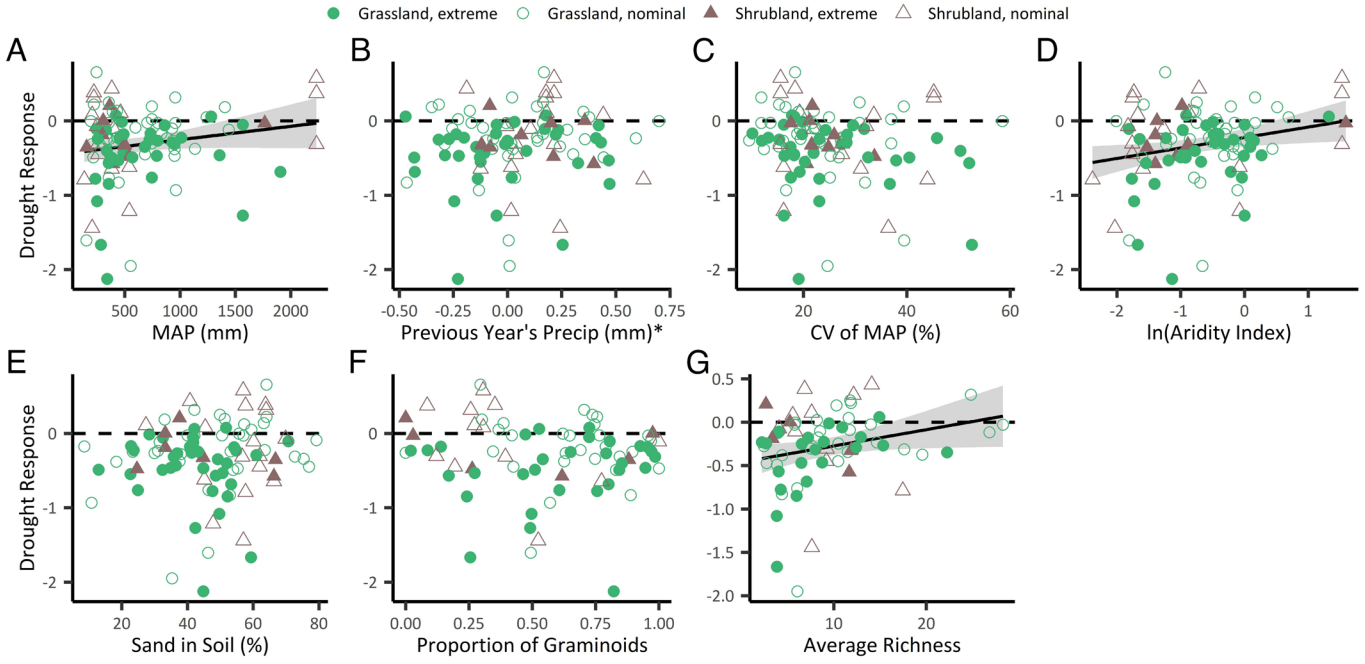

Fig. 3. Effect of abiotic and biotic factor on drought response. Relationships between 1-y drought responses across IDE sites and (*A*) MAP, (*B*) previous year's precipitation (relativized by MAP), (*C*) interannual percent coefficient of variation (CV) of MAP, (*D*) natural log of the AI, (*E*) percent sand, (*F*) average proportion of graminoids, and (*G*) average richness of plant species. Information on abiotic and biotic characteristics for each site can be found in *SI Appendix*, Table S5. Model results are summarized in *SI Appendix*, Table S6. Drought response is calculated as: ln(average $ANPP_{DROUGHT}$/average $ANPP_{CONTROL}$); 0 (black dashed line) represents no effect of drought, and negative numbers indicate less ANPP in drought vs. control plots. Lines are shown only for significant relationships. Shaded area represents the 95% CI. *Previous year's precipitation included the precipitation in the 365 to 730 d preceding the biomass collection date and was relativized by MAP.

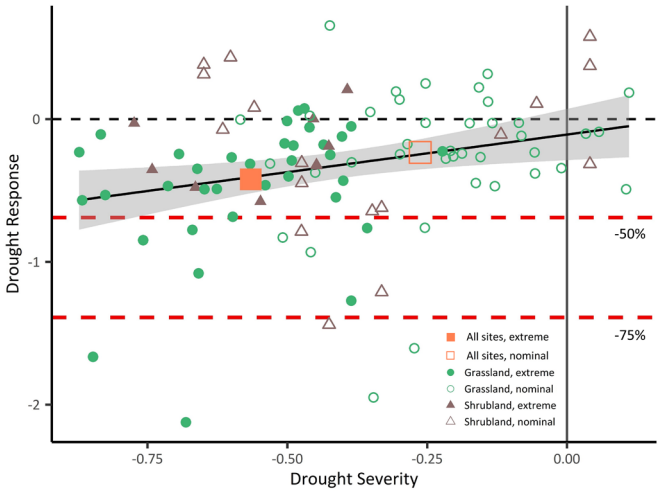

Fig. 4. Relationship between drought severity and drought response. A linear mixed effects model found strong evidence for a negative effect of increasing drought severity (becoming more negative) on drought response for 1 y of drought across all sites (intercept = −0.11; slope = 0.53; $P = 0.009$; adjusted $R^2 = 0.06$). Model results for the effects of drought severity on drought response for extreme and nominal sites are summarized in the Main Text. Shaded area represents the 95% CI. Drought response is calculated as: ln(average $ANPP_{DROUGHT}$/average $ANPP_{CONTROL}$). For drought responses, 0 represents no effect of drought, negative numbers indicate less ANPP in drought vs. control plots. Drought severity is calculated as: ($Precip_{DROUGHT}$-MAP)/MAP; MAP = mean annual precipitation. Because ambient precipitation during the experiment year determines the severity of the imposed drought, positive drought severity can occur during anomalously wet years when plots beneath drought shelters also experience above average precipitation. The open symbols denote those IDE sites (n = 56) where ambient precipitation was above average, and thus the imposed drought was not statistically extreme (1-in-100 y). Closed symbols denote those sites (n = 44) with average or below average annual precipitation during the experiment year. All of these IDE sites experienced statistically extreme drought. The filled orange square denotes the mean drought response for sites experiencing extreme drought whereas the open orange square is the mean for sites that experienced less severe drought. Note that there was no relationship between drought severity and drought response when only those sites that experienced extreme drought are considered. The red dashed lines provide visual guides for 50% and 75% reductions in ANPP.

as drought severity = ($Precipitation_{DROUGHT}$-MAP)/MAP). As expected, we found strong evidence ($P = 0.009$) that increasing (more negative) drought severity led to larger reductions in ANPP when examined across all 100 sites (Fig. 4). Further, the amount of variability explained doubled when drought severity, MAP, previous year's precipitation, CV in MAP, percent sand, and proportion of graminoids were included together in the model (*SI Appendix*, Table S8); though, drought severity remained the only significant factor in the model, underscoring the primary importance of this metric in determining the magnitude of the drought response.

One concern with passively reducing ambient precipitation is that in particularly dry years, differences in ecosystem responses between drought and control treatments tend to be minimized (48). In other words, if ambient precipitation is well below average, ANPP would be expected to be low even in control treatments and further reductions in precipitation with the drought treatment may not cause any additional appreciable reductions in ANPP. Thus, the difference between the drought and control treatments would be small, resulting in an effect size close to zero. This would give the appearance of the site being highly resistant to drought. We examined whether this was a possibility for sites with a large drought severity index (45% reduction in precipitation) and yet a drought response close to zero. We found that this phenomenon may indeed be responsible for the high resistance observed for these few sites (n = 4), but for most sites that exhibited resistance to drought (n = 17), this potential experimental phenomenon could be dismissed, suggesting that other factors are contributing to high resistance of these sites to a single year of extreme drought.

With the above analyses, we were able to evaluate how climate, soil texture, vegetation structure, and drought severity broadly influence drought response. However, given that drought severity was the primary determinant of variation in drought response, other factors that we were unable to include in our analyses are likely contributing to observed high variability in ecosystem response to extreme drought. Moving forward, a key challenge is to determine what these other factors are and identify those ecosystem attributes (e.g., soil fertility, root:shoot ratios, plant community composition, plant-microbe interactions, etc.) that may strongly influence resistance to a single year of extreme drought. Measurement of these factors at the site level and inclusion of these factors in future analyses will be crucial for predicting and mitigating the impacts of extreme drought as climate changes.

Despite the uncertainty of what may be determining variation in drought response in grasslands and shrublands globally, our analysis suggests that overall, ANPP declines as a linear function of increasing drought severity (Fig. 4). In other words, there was no evidence for catastrophic or nonlinear losses in ANPP when single-year droughts become statistically extreme. However, the results from this globally distributed drought experiment do indicate that losses in ANPP are greater than previously expected when drought is historically extreme. With climate change, droughts are not only expected to become more extreme, but also more frequent and longer in duration. It remains unknown what effects these aspects of intensified drought may have when overlaid with greater losses in ANPP with increased drought severity.

In conclusion, given that many ecosystems, particularly grasslands and shrublands, experience substantial interannual variability in precipitation (16, 49), it is not surprising that short-term precipitation reductions that are not statistically extreme would result in only "moderate" (~20%) losses in productivity. Even such moderate responses are likely to have important implications for the global carbon cycle and the wildlife, livestock, and human populations that rely on plant production. Of greater concern, however, is that grassland sites and grassland and shrubland sites combined experienced a magnified loss of function (more than 1.8- and 1.5-fold greater reduction, respectively) when drought was statistically extreme for ~1 y. Clearly, with climate change increasing drought intensity and frequency (50), and given that effects can linger long after drought ends, even more substantial impacts on the global carbon cycle can be expected. Indeed, reductions in ANPP exceeding 35% are not often observed in moderate droughts of longer duration (24, 51), and a recent study suggests that experimental droughts may underestimate the magnitude of ANPP loss by more than half when compared to naturally-occurring droughts (52). Thus, results from our distributed experimental approach reveal that extreme droughts are likely to substantially slow C sequestration in grasslands and shrublands, surpassing predictions from past meta-analyses (20, 53) and experiments (9, 52). Finally, the underlying cause of the striking range in ecosystem responses to short-term extreme drought, from highly resistant to highly vulnerable, remains unresolved. Results from our globally distributed and standardized drought experiments demonstrated little to no evidence for key factors typically thought to drive ecosystem variability in response to drought: CV of MAP, previous year's precipitation, soil texture, and proportion of graminoids. Yet, we found strong support for MAP/aridity and plant species richness being at least partially predictive of ANPP response to extreme drought. If traditionally invoked variables do not explain most of the cross-site variation in responses to intensified droughts, we must rethink our measurements and experiments to allow us to identify

other underexplored factors. Understanding the determinants of differences in both short- and longer-term drought vulnerability will provide critical insight into both the mitigation potential and adaptative capacity of ecosystems in a future where today's extremes become the norm rather than the exception.

Materials and Methods

The IDE. IDE was initiated in 2013 as part of the Drought-Net Research Coordination Network, funded by the US NSF. Drought-Net is a global network of researchers committed to understanding how terrestrial ecosystems respond to extreme drought. For all network investigators, we provided and continue to provide standard experimental protocols on the DroughtNet website (droughtnet.weebly.com). Sites must follow these protocols for their data to be included in our analyses. At the time of analysis, 141 sites had joined our network, but data from only 100 of the sites (Fig. 1*A* and *SI Appendix*, Table S2) had been submitted and/or met our criteria for inclusion in this analysis (*SI Appendix*, Table S9). These 100 sites were well distributed across gradients of MAT and MAP (Fig. 1*B*) and represented two ecosystem types: grasslands and shrublands. Most (>90%) of the sites were dominated by perennials. Furthermore, like most grasslands and shrublands globally, all the sites had some history of management (*SI Appendix*, Table S10), but only 13 sites that we know of were actively mowed (n = 6), burned (n = 5), or grazed (n = 2).

The target for the IDE drought treatment was a statistically extreme, 1-in-100-y drought imposed year-round. To achieve the target level of extremeness, each site's treatment magnitude (reduction in precipitation) was based on the past 100 y of climate data from the site or 100 y of interpolated data from the Terrestrial Precipitation Analysis tool (54). Because precipitation history and variability are unique to each site, this approach allowed us to target the common level of statistical extremeness by allowing the proportional reduction in precipitation to vary across sites (55 and *SI Appendix*, Fig. S1). This contrasts with the alternative approach of imposing a fixed reduction in precipitation (e.g., 50%), which can result in very different levels of extremeness across sites (55).

The target level of extreme drought was imposed at each site using infrastructure that is commonly used in short-statured ecosystems (56). The infrastructure consisted of two or more open-sided shelters, each a minimum of 2 m × 2 m, with roofs that were partially covered with transparent strips of plastic (either V-shaped or corrugated). The percentage roof coverage was dictated by the target level of precipitation reduction (Fig. 1). This shelter design has been shown to have minimal effects on microclimate (57–59), while matching key characteristics (e.g., number of consecutive dry days, size of events, number of events) of naturally occurring extreme dry years across a range of ecosystems (55). For those sites (n = 9) with both control plots (no infrastructure) and plots with an infrastructure control (i.e., structures that mimic the shading of shelters but allow rain to pass through), there was no evidence that ANPP was affected by the shelter infrastructure (mean difference = 5.25%; 95% CI = −6.39%, 18.33%; t-value = 0.89; df = 33; $P = 0.38$). This suggests an absence of significant non-target effects of the drought shelters, which has also been demonstrated in other experiments (57–59).

We also chose the shelter infrastructure to impose drought because it is highly cost-effective and can be consistently deployed across a range of short-statured ecosystems, making it amenable for use in a coordinated distributed experiment (22). However, because we manipulate precipitation passively, the target level of drought extremeness may or may not be achieved in any given year, depending on ambient precipitation amount (48). For example, an above-average year of precipitation will result in drought treatments that are less severe, while a below-average precipitation year will result in an even more extreme drought than the target level. In total, 44 of the 100 IDE sites received average or below-average precipitation in the first year of the treatment, and thus imposed the target statistically extreme, 1-in-100-y drought (*SI Appendix*, Fig. S2). The remaining 56 sites received above-average precipitation, and thus imposed a non-extreme ("nominal") drought, which was within the range of historic variability.

To be included in this analysis, sites needed to collect peak live aboveground biomass as an estimate of annual ANPP (60). While we recognize that there are numerous other ecosystem processes that can be impacted by drought, ANPP was selected because it can be comparably estimated and readily standardized across sites. Moreover, ANPP is a low-cost measurement that requires much less investment of time than other measures of ecosystem functioning–a crucial feature of response variables in CDEs and other successful experimental networks, such as the Nutrient Network (22, 61). ANPP was estimated either destructively and/or non-destructively using methods appropriate for the particular ecosystem as cited in Fahey and Knapp (62), with herbaceous-dominated sites encouraged to follow the Nutrient Network's protocols (https://nutnet.org/). We relied on investigators to use their expertise in determining the most appropriate methods–either destructive or non-destructive–to estimate ANPP for their study system. Sites then separated ANPP estimates into live and dead before further classifying live biomass by growth form (graminoid, grass, forb, woody, etc.) and submitting all estimates in grams of dry biomass per m^2. Standing dead biomass could be separated into current and previous year's growth where appropriate.

Drought Response Metric. For each site, we calculated relative drought response as the ratio of average ANPP in the drought plots compared to average ANPP in the control plots, as a metric of ecosystem response to imposed drought. Specifically, we adapted equations from Smith et al. (63) and Kreyling et al. (64) to define relative drought response as: $\ln(ANPP_{DROUGHT}/ANPP_{CONTROL})$.

Drought Severity Metric. We calculated the actual severity of the drought that was imposed during the year of precipitation manipulation using meteorological data that was either collected 1) on-site (site-submitted) or 2) from a nearby weather station (mean distance = 10.2 km). The nearby weather station data was obtained either from the Global Historical Climatology Network (GHCN, 65) or the Climate Hazards Group InfraRed Precipitation with Stations (CHIRPS, 66). When data from GHCN, CHIRPS, or local weather stations were not available, we used site-submitted annual precipitation estimates. We first calculated the amount of precipitation each site received in the 365 d preceding collection of ANPP. We then used this precipitation calculation, the site-reported percent reduction in precipitation imposed with the drought treatment, and days the drought shelters were in place prior to the collection of ANPP to estimate the total amount of precipitation reduced at each site. To qualify as 1 y of drought, a site's shelters needed to be in place for at least one full growing season (within 1 wk of 120 treatment days prior to harvest), but less than 2 y (within 1 wk of 650 d). For the drought severity metric, we compared the estimated precipitation received in drought plots to MAP (mm) as reported by each site, and calculated the deviation from this number: $(Precip_{drought} - MAP)/MAP$.

Abiotic and Biotic Factors. We included in our analysis seven abiotic and biotic factors that have been hypothesized to be important in influencing variability in drought response among sites (*SI Appendix*, Table S5). These factors included: MAP (mm), previous year's precipitation (mm), historical variability in MAP (interannual CV), AI, soil texture, proportion of graminoids, and site richness. As indicated above, we used MAP as reported by each site. We used either site-submitted, GHCN, or CHIRPS data to calculate how much precipitation each site received in the 365 to 730 d preceding the ANPP harvest and then relativized this value by site MAP. We refer to this as previous year's precipitation in our analyses. Historical variability of precipitation was estimated using the average coefficient of variation for the 30 y of precipitation from each site using GHCN station data. The AI (an estimate of plant moisture availability), was calculated as the MAP divided by potential evapotranspiration (67); Trabucco et al. (67) uses estimates from World Clim v2 (68) to calculate these values. Lower AI values indicate lower plant water availability. For the interannual coefficient of variation in MAP, we pulled data from the Multi-Source Weighted-Ensemble Precipitation tool (69).

As a proxy for soil texture, we used a weighted mean for percent sand in the top 100 cm of soil for each site (n = 96) available in the ISRIC World Soil Information (70), which yielded information for 96 sites. We used this global dataset because site-level data was only available for 27 of the sites. However, for those 27 sites we conducted a Pearson correlation test between site-derived values and the global dataset to confirm whether the global dataset measures were accurate, which we found to be the case ($r = 0.67$, $P < 0.001$). To calculate the proportion of graminoids, we used 77 sites that submitted ANPP data for each functional group. For each plot at a site, we divided the ANPP of graminoids by the total ANPP (all functional groups added together). We then averaged these proportions across plots for each site. For richness, we used plant species composition data submitted by 68 of the 100 sites at the time of analysis. We only used data from control plots and averaged richness at the plot level for each site.

Statistical Analyses. For all statistical analyses, we used the language of evidence (71) to describe our results as an alternative to typical statistical significance testing (i.e., using a significance cut-off of P-value ≤ 0.05). With this approach, we ascribe P-values as following Muff et al. (71): >0.1 = little or no evidence, between 0.05 and 0.10 = weak evidence, between 0.01 and 0.05 = moderate evidence, and ≤0.01 = strong evidence.

To test whether ANPP in drought plots differed from that in control plots, we used six one-sided t tests in R (version 4.0.2, 72), identifying whether responses were significantly less than 0. We chose to use one-sided t tests given that out a priori hypothesis was for drought to result in a reduction in ANPP (rather than either a decrease or increase, which would be relevant for an expectation of increased ANPP with drought). However, to examine whether results differed based on one-sided vs. two-sided t tests, we conducted two-sided t tests for the six comparisons and found that this did not affect the results, except in the case of the shrubland nominal drought test (one-sided P-value = 0.07, two-sided P-value = 0.15). We tested sites with nominal and extreme droughts separately, and tested ecosystem types together and separately (*SI Appendix*, Table S3). To test for differences in grassland and shrubland responses to drought across all sites, we used linear regression (*SI Appendix*, Table S4).

To examine whether the seven abiotic and biotic factors described above explained any variation in the drought response observed, we used linear mixed effects models for all 100 sites, or separately for sites that experienced extreme or nominal drought. We built separate models that tested the following explanatory variables: ecosystem type (grassland or shrubland), MAP (mm), previous-year's precipitation (mm, relativized by MAP), average coefficient of variation (%) for MAP, AI (scaled using the natural log), average percent sand, average proportion of graminoids, and average plot-level richness. We also explored the inverse soil texture hypothesis using a linear mixed effects model (site set as a random effect) to test how the interaction of average percent sand and MAP affected drought response.

We used a Pearson correlation to test collinearity among drought severity (proportion), length of drought (days), and a categorical variable for whether sites had ambient precipitation equal to or above (group 1) or below (group 2) MAP. We set drought severity as our fixed effect as it integrates the length of drought ($r = -0.59$, $P < 0.001$), deviation in ambient precipitation from MAP ($r = 0.60$, $P < 0.001$), and a site's drought shelter design into a single variable. To test the nature of the relationship between drought response and various factors (drought severity, MAP, previous year's precipitation, aridity, coefficient of variation, and plant community richness) we compared both linear and non-linear models (asymptotic regression and general additive model with a spline function set to 3) using AIC. We did not find evidence for a non-linear response (*SI Appendix*, Table S11) and proceeded with building linear models using the lmer function (package stats) in R. We also built a multiple linear regression to see whether drought severity combined with MAP, previous year's precipitation, proportion graminoids, CV, and average percent sand could further explain variation in drought response.

Data, Materials, and Software Availability. Derived data are provided in *SI Appendix*, Table S5. All code and derived data have been deposited in Dryad (73). All other data are included in the manuscript and/or *SI Appendix*.

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Author affiliations: [a]Department of Biology, Colorado State University, Fort Collins, CO 80523; [b]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523; [c]Denver Zoo, Denver, CO 80205; [d]Department of Wildland Resource and the Ecology Center, Utah State University, Logan, UT 84322; [e]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN 55108; [f]Department of Biology, University of New Mexico, Albuquerque, NM 87131; [g]School of Life Sciences, Global Drylands Center, Arizona State University, Tempe, AZ 85281; [h]Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305; [i]Department of Biology, Indiana University, Bloomington, IN 47405; [j]Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA), National Scientific and Technical Research Council (CONICET), Faculty of Agronomy, University of Buenos Aires, Buenos Aires C1417DSE, Argentina; [k]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; [l]Department of Geosciences and Natural Resource Management, University of Copenhagen, Frederiksberg C 1958, Denmark; [m]Department of Natural Resource Science, Thompson Rivers University, Kamloops, BC V2C 0C8, Canada; [n]Department of Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth 95447, Germany; [o]Department of Environmental Studies, University of California, Santa Cruz, CA 95064; [p]Departamento de Ecologia, Universidad de Alicante, 03690 Alicante, Spain; [q]Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef", Universidad de Alicante, 03690 Alicante, Spain; [r]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia; [s]School of Grassland Science, Beijing Forestry University, Beijing 100083, China; [t]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717; [u]U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, AZ 86001; [v]Soil and Crop Sciences Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853; [w]Department of Range Management, Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, Noor 46417-76489, Iran; [x]Departamento de Biodiversidad y Restauración, Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas (CSIC), Zaragoza 50059, Spain; [y]Laboratorio de Ecología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata (UNMdP)-Consejo Nacional de Investigación Ciencia y Técnica (CONICET), CC 1260 Correo Central, Mar del Plata B7600WAG, Argentina; [z]School of Plant Sciences and Food Security, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel; [aa]School of Ecology and Environment, Ningxia University, Yinchuan 750021, China; [bb]City of Boulder Open Space and Mountain Parks, Boulder, CO 80301; [cc]Department of Community Ecology, Helmholtz-Centre for Environmental Research–UFZ, Halle 06120, Germany; [dd]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig 04103, Germany; [ee]Division of Biology, Kansas State University, Manhattan, KS 66506; [ff]LI-COR Biosciences, 4647 Superior Street, Lincoln, NE 68505; [gg]Department of Ecology, University of Innsbruck, Innsbruck 6020, Austria; [hh]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada; [ii]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB T6G 2P5, Canada; [jj]Institute of Crop Science and Resource Conservation, Department of Plant Nutrition, University of Bonn, Bonn 53115, Germany; [kk]Institute of Botany and Landscape Ecology, Department of Experimental Plant Ecology, University of Greifswald, Greifswald D-17498, Germany; [ll]Biological Station of Hiddensee, Department of Biology, University of Greifswald, Kloster D-18565, Germany; [mm]Department of Environmental Science and Management, California State Polytechnic University, Humboldt, Arcata, CA 95521; [nn]Universidad Nacional de Río Negro, Centro de Estudios Ambientales desde la NorPatagonia (CEANPa), Sede Atlántica–CONICET, Viedma 8500, Argentina; [oo]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma I-43124, Italy; [pp]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3, Canada; [qq]Department of Ecology, Universidade Federal de Goiás, Goiânia, GO 74690-900, Brazil; [rr]Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523; [ss]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106; [tt]US Army Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS 39180; [uu]School of Life and Environmental Sciences, The University of Sydney, Camperdown, NSW 2006, Australia; [vv]Isotope Biogeochemistry and GasFluxes, Leibniz-Zentrum fürAgrarlandschaftsforschung (ZALF), Müncheberg 15374, Germany; [ww]Institute of Ecology and Evolution, Friedrich Schiller University Jena, Jena 07743, Germany; [xx]Institute of Biology, Leipzig University, Leipzig 04103, Germany; [yy]Department of Ecology, Universidade Federal do Rio Grande do Sul, Porto Alegre 91501-970, Brazil; [zz]Centro de Investigaciones sobre Desertificación, Consejo Superior de Investigaciones Científicas (CSIC)-Universitat Valencia (UV) - Generalitat Valenciana (GV), Valencia 46113, Spain; [aaa]Geobotany, Faculty of Biology, University of Freiburg, Freiburg D-79104, Germany; [bbb]Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX 77843; [ccc]Department of Biological Sciences, University of Bergen, Bergen 5007, Norway; [ddd]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, 3584 CH, Netherlands; [eee]Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada; [fff]U.S. Army Corps of Engineers, Sacramento, CA 95814; [ggg]Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO 80523; [hhh]Global Water Security Center, The University of Alabama, Tuscaloosa, AL 35487; [iii]Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót 2163, Hungary; [jjj]Departamento de Gestión Agropecuaria, Universidad Nacional del Comahue, Centro Universitario Regional Zona Atlántica, Viedma 85009, Argentina; [kkk]Ecosystem Physiology, Faculty of Environment and Natural Resources, Albert-Ludwig-University of Freiburg, Freiburg 79110, Germany; [lll]Department of Plant Sciences, University of Saskatchewan, Saskatoon, SK S7N5A8, Canada; [mmm]Range and Meadow Forage Management Research, Eastern Oregon Agricultural Research Center, US Department of Agriculture (USDA)-Agricultural Research Service, Burns, OR 97720; [nnn]Brackenridge Field Laboratory, University of Texas, Austin, TX 78747; [ooo]Department of Biodiversity Research and Systematic Botany, University of Potsdam, Potsdam 14469, Germany; [ppp]Prataculture Research Institute, Heilongjiang Academy of Agricultural Sciences, Haerbin 150086, China; [qqq]Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Ecology and Nature Conservation Institute, Chinese Academy of Forestry, Beijing 100091, China; [rrr]Programa de Posgrado en Desarrollo y Medio Ambiente–Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, João Pessoa, PB 58051-900, Brazil; [sss]Centro de Recursos Naturales Renovables de la Zona Semiárida–CONICET, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, Bahía Blanca 8000FTN, Argentina; [ttt]Institute of Resources and Environment, International Centre for Bamboo and Rattan, Key Laboratory of National Forestry and Grassland Administration and Beijing for Bamboo and Rattan Science and Technology, Beijing 100102, China; [uuu]Institute of Botany, Czech Academy of Sciences, Třeboň 379 01, Czech Republic; [vvv]Commonwealth Scientific and Industrial Research Organization (CSIRO) Environment, Wembley, WA 6913, Australia; [www]School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, Zollikofen 3052, Switzerland; [xxx]Department of Ecology and Evolutionary Biology, Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO 80309; [yyy]Department of Ecology and Environmental Science, Umeå University, Umeå S-901 87, Sweden; [zzz]Research Center for Advanced Science and Technology, University of Tokyo, Meguro, Tokyo 153-8904, Japan; [aaaa]Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama 240-8501, Japan; [bbbb]Conservancy-Communities Living Among Wildlife Sustainably (CLAWS) Botswana, Seronga 00000, Botswana; [cccc]School of Biological Sciences, University of Oklahoma, Norman, OK 73019; [dddd]Gulbali Institute, Charles Sturt University, Albury, NSW 2640, Australia; [eeee]Global Ecology Unit Center for Ecological Research and Forestry Applications (CREAF)-National Research Council (CSIC)-Universitat Autonoma de Barcelona (UAB), National Research Council (CSIC), Bellaterra, Catalonia 08194, Spain; [ffff]Center for Ecological Research and Forestry Applications (CREAF), Cerdanyola del Vallès, Barcelona, Catalonia 08193, Spain; [gggg]Department of Environment and Society, Utah State University, Moab, UT 84532; [hhhh]Department of Biology, The University of Winnipeg, Winnipeg, MB R3B 2E9, Canada; [iiii]Institute of Ecology and Earth Sciences, University of Tartu, Tartu EE50409, Estonia; [jjjj]Instituto Nacional de Tecnología Agropecuaria–Universidad Nacional d ela Patagonia Austral–CONICET, Río Gallegos, Caleta Olivia Z9011, Argentina; [kkkk]Université Clermont Auvergne, National Research Institute for Agriculture, Food and the Environment, VetAgro Sup, Research Unit for Grassland Ecosystems, Clermont-Ferrand 63000, France; [llll]Laboratório de Ecologia Aplicada e Conservação, Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, João Pessoa, PB 58051-900, Brazil; [mmmm]Department of Biological Sciences, Purdue University, West Lafayette, IN 47907; [nnnn]Department of Biology, Saint Louis University, St. Louis, MO 63103; [oooo]U.S. Geological Survey, Southwest Biological Science Center, Moab, UT 84532; [pppp]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia; [qqqq]Department of Physiological Diversity, Helmholtz-Centre for Environmental Research–UFZ, Leipzig 04318, Germany; [rrrr]Department of Biology and Geology, Rey Juan Carlos University, Madrid 28032, Spain; [ssss]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, João Pessoa, PB 58051-900, Brazil; [tttt]Institute of Grassland Science, Key Laboratory of Vegetation Ecology of the Ministry of Education, Jilin Songnen Grassland Ecosystem National Observation and Research Station, Northeast Normal University, Changchun 130024, China; [uuuu]Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019; [vvvv]Institute of Plant Sciences, University of Bern, Bern 3013, Switzerland; [wwww]Oeschger Center for Climate Change Research, University of Bern, Bern 3012, Switzerland; [xxxx]Environmental and Conservation Sciences, Murdoch University, Murdoch, WA 6150, Australia; [yyyy]School of Life Sciences, University of Kwazulu-Natal, Pietermaritzburg 3201, South Africa; [zzzz]Norwegian Institute of Bioeconomy Research, Department of Landscape and Biodiversity, Tjøtta 8860, Norway; [aaaaa]Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China; [bbbbb]Plant Ecology Group, Department of Biology, University of Tübingen, Tübingen 72076, Germany; [ccccc]Nova Scotia Community College, Annapolis Valley Campus, Applied Research, Middleton, NS B0S 1P0, Canada; [ddddd]Møreforsking, Aalesund 6021, Norway; [eeeee]College of Grassland Science, Shanxi Agricultural University, Jinzhong 030801, China; [fffff]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [ggggg]Department of Geography and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; [hhhhh]Department of Integrative Biology, University of Texas, Austin, TX 78712; [iiiii]Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, Qinghai 810008, China; and [jjjjj]Urat Desert-grassland Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Science, Lanzhou 730000, China

Author contributions: M.D.S., K.D.W., S.L.C., A.K.K., O.E.S., J.S.D., R.P.P., and L.Y. designed research; M.D.S., K.D.W., J.S.D., L.H.F., A.J., M.E.L., F.T.M., S.A.P., Q.Y., A.J.F., S.M.M., Y.L., H. Abdoli, M. Abedi, C.L.A., J.A., M. Alon, H. An, B.A., M. Anderson, H. Auge, S.B., K. Bahalkeh, M.B., A.B., T.B., K.H.B., K. Behn, I. Beil, L.B., I. Blindow, V.F.B., E.T.B., E.W.B., C.M.B., K.M.B., J.F.C., D.A.C., M.C., A.C., C.N.C., M.C.-G., S.X.C., J.C., M.V.C., O.C., A.L.C., D.F.C., S.D., P.D., C.M.D., L.H.D., T.S.D., M.D., A.E., N.E., F.M.F., T.G.W.F., T.G., B.G., A.C.G., K.G.G.-M., H.J.H., S.V.H., Y.H., M.H., H.A.L.H., D.H., J.I., O.I., F.I., Y.J., S.J., E.F.K., K.K., J.K., G.K.-D., A. Kröpfl, A. Kübert, A. Kulmatiski, E.G.L., K.S.L., J. Larson, J. Lawson, C.V.L., A. Linstädter, J. Liu, S.L., A.G.L., G.L., A. Loydi, J. Luan, F.C.L., C.M., K.M.-H., A.V.M., A.M.-R., T.M., D.B.M., A.S.M., E.M., G.S.N., U.N.N., D.N., Y.N., P.N., R.C.O., R. Ogaya, G.R.O., I.O., B.O., R. Otfinowski, M.P., J.P., P.L.P., G.P., A.P., C.P.-C., V.D.P., J.M.P.-G., L.W.P., R.M.P., C.P.-R., S.M.P., Y.P., S.C.R., E.G.R., D.A.R., W.E.R., C.R., A. Sánchez, B.A.S., M.C.S., E.W.S., B.S., L.S., A. Stampfli, R.J.S., M. Sternberg, W.S., M. Sünnemann, M.T., P.T., D.T., K.T., A.V., L.v.d.B., V.V., M.R.V., L.G.V., C. Wang, Y.W., G.M.W., C. Werner, C. Wei, G.W., J.L.W., A.A.W., M.Z., F.Z., J.Z., N.Z., and X.Z. performed research; K.D.W., M.C.H., P.W., L.A.G., and T.O. analyzed data; and M.D.S., K.D.W., M.C.H., P.W., S.L.C., A.K.K., O.E.S., J.S.D., R.P.P., L.Y., and C.B. wrote the paper.

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