Mean annual precipitation predicts primary production resistance and resilience to extreme drought

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HIGHLIGHTS

- Whether forests and grasslands respond similarly to extreme drought is unknown.
- Meta-analysis compared forest and grassland production resistance and resilience.
- Resistance followed a common continuum of mean annual precipitation (MAP).
- Grassland resilience increased, forest resilience decreased, with increasing MAP.
- Dry grasslands are most vulnerable; dry forest response requires more research.

GRAPHICAL ABSTRACT
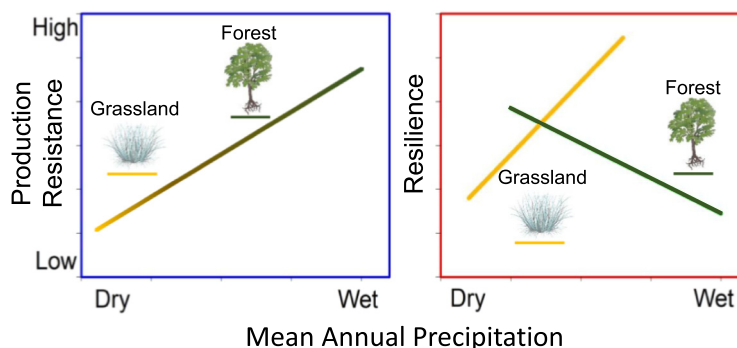
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ABSTRACT

Extreme drought is increasing in frequency and intensity in many regions globally, with uncertain consequences for the resistance and resilience of ecosystem functions, including primary production. Primary production resistance, the capacity to withstand change during extreme drought, and resilience, the degree to which production recovers, vary among and within ecosystem types, obscuring generalized patterns of ecological stability. Theory and many observations suggest forest production is more resistant but less resilient than grassland production to extreme drought; however, studies of production sensitivity to precipitation variability indicate that the processes controlling resistance and resilience may be influenced more by mean annual precipitation (MAP) than ecosystem type. Here, we conducted a global meta-analysis to investigate primary production resistance and

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resilience to extreme drought in 64 forests and grasslands across a broad MAP gradient. We found resistance to extreme drought was predicted by MAP; however, grasslands (positive) and forests (negative) exhibited opposing resilience relationships with MAP. Our findings indicate that common plant physiological mechanisms may determine grassland and forest resistance to extreme drought, whereas differences among plant residents in turnover time, plant architecture, and drought adaptive strategies likely underlie divergent resilience patterns. The low resistance and resilience of dry grasslands suggests that these ecosystems are the most vulnerable to extreme drought – a vulnerability that is expected to compound as extreme drought frequency increases in the future.

1. Introduction

The frequency and intensity of extreme droughts are predicted to increase throughout the century in many regions across the globe (IPCC, 2013), with widespread effects on ecosystem functioning anticipated but poorly quantified or understood (Bahn et al., 2014; Easterling et al., 2000; Ingrisch and Bahn, 2018). Ecosystem sensitivity to climate extremes is commonly characterized as *resistance* and *resilience*: *resistance* quantifies the immediate change in ecosystem functioning (e.g., primary production) following a perturbation; and *resilience* is the extent to which ecosystem functioning returns to pre-event levels (Lloret et al., 2011; MacGillivray et al., 1995). Global understanding of how these measures of drought sensitivity relate to one another is limited, with most studies examining resistance or resilience to drought, but not both (Donohue et al., 2016). Moreover, whether grasslands and forests within the same geographic regions follow similar, or unique, patterns of primary production resistance and resilience within the same climate space is unknown, but essential in order to generalize the stability of ecosystem functioning across the global climatic continuum.

Ecological theory (Grime, 2001) and observations (Petrakis et al., 2016; Schwalm et al., 2012; Zhao et al., 2015) suggest a tradeoff between the resistance and resilience of primary production, with the different life and evolutionary histories of resident grassland and forest plant species portending different functional responses to extreme drought. Forests, containing assemblages of long-lived woody species completing life cycles over decades to centuries, are expected to be more resistant and less resilient because of the increased energetic cost and time associated with rebuilding biomass prior to reproduction (MacGillivray et al., 1995). Conversely, grassland plant species with annual turnover of production may be less resistant but more resilient, exhibiting greater immediate vulnerability to extreme drought but capable of rapid re-establishment, growth, and reproduction by resident plants (Hoover et al., 2014). Forest drought resistance has been attributed to mechanisms that limit water loss, increase water supply (hydraulic lift), or increase water-use efficiency (WUE) (Baldocchi et al., 2004; Wolf et al., 2013). Additionally, trees generally maintain root systems that access deep soil water (Jackson et al., 1996) while grasslands have shallower root systems and maintain high evapotranspiration rates during drought, depleting soil moisture at a faster rate (Teuling et al., 2010; Wolf et al., 2013).

Precipitation amount and variability, and how plant traits are arrayed across precipitation gradients (Engelbrecht et al., 2007; López et al., 2016), may shape an ecological and evolutionary tradeoff between primary production resistance and resilience. Though adaptations of forest and grassland plants to water availability differ, ecosystems globally exhibit lower primary production sensitivity to annual variation in precipitation when located in wet environments, suggesting more mesic grasslands and forests could exhibit greater resistance to extreme drought (Huxman et al., 2004; Knapp and Smith, 2001). Conversely, the greater sensitivity of production to year-to-year precipitation in dry ecosystems suggests more rapid and complete resilience following drought.

In order to bridge the gap between ecological theory and empirical observations of production sensitivity and functional response, we conducted a global meta-analysis of primary production resistance and resilience to extreme drought in forests and grasslands across a broad gradient of mean annual precipitation (MAP) (230 mm to 2467 mm yr^{-1}). The goals of this meta-analysis were 1) to evaluate where different ecosystems exhibit shared or divergent responses across a common precipitation continuum, 2) test the theory that forests are more resistant, but less resilient, than grasslands, and 3) observe whether traditional resistance-resilience trade-off theory applies at the ecosystem scale.

2. Methods

2.1. Study criteria

We conducted a Web Of Science search on January 6, 2017 that included the following terms: (extreme* or severe disturbance), (resistance or resilience or recovery), (biomass or productivity or production or cover), and (grass* or forest or shrubland or woodland or savannah or heath* or tundra or alpine). We used studies that crossed with these terms as well as additional studies cross-referenced from papers found in this search. Out of 435 papers, a total of 45 studies containing 72 sites (43 grasslands, 21 forests, 4 shrublands, and 4 woodlands) met our inclusion criteria. Due to the small sample size (Lemoine et al., 2016), shrublands and woodlands were eliminated from the quantitative analysis. Most of the sites selected were in North America and Europe, with one site from each of the following continents: Asia, Australia, Africa, and South America (Fig. 1).

For the resistance analysis, only studies based on terrestrial ecosystems that justified the drought as "extreme" and reported primary productivity from a true control, or a full reference year prior to the event, were included. Post-event productivity one year following the event was required for inclusion in the resilience analysis. Justification of extremity could include: 1) time-scales (Girard et al., 2012; Rondeau et al., 2013; Schwalm et al., 2012), 2) drought return time (Kreyling et al., 2008), 3) standardized precipitation-evapotranspiration index (SPEI) (Cavin et al., 2013; Falk et al., 2008), or 4) >60% decrease in annual precipitation (Hoover et al., 2015). Acceptable metrics of primary production included net primary production (NPP), gross primary production (GPP) (Litton et al., 2007), basal area increments (BAI) (for functional types in which BAI is significantly correlated with productivity) (Lempereur et al., 2015), and cover (in arid and semi-arid ecosystems only) (Zhang et al., 2016). All 64 forest and grassland sites were used in the resistance analysis, while 10 forests and 22 grasslands were included in the resilience analysis.

2.2. Extremity validation

For natural events only, modelled standardized precipitation-evapotransporation index (SPEI) for each site served as an independent check on author-reported drought extremity. Modelled SPEI values were extracted from DroughtNet using the Precipitation Trends Tool (drought-net.org). Author assessments of extreme drought and modelled SPEI agreed in >90% of the cases. The remaining 10% fell in higher latitudes where the SPEI model generates higher uncertainty (Nathan Lemoine, direct correspondence). To avoid potential experimental bias, analyses were run twice: once including all sites
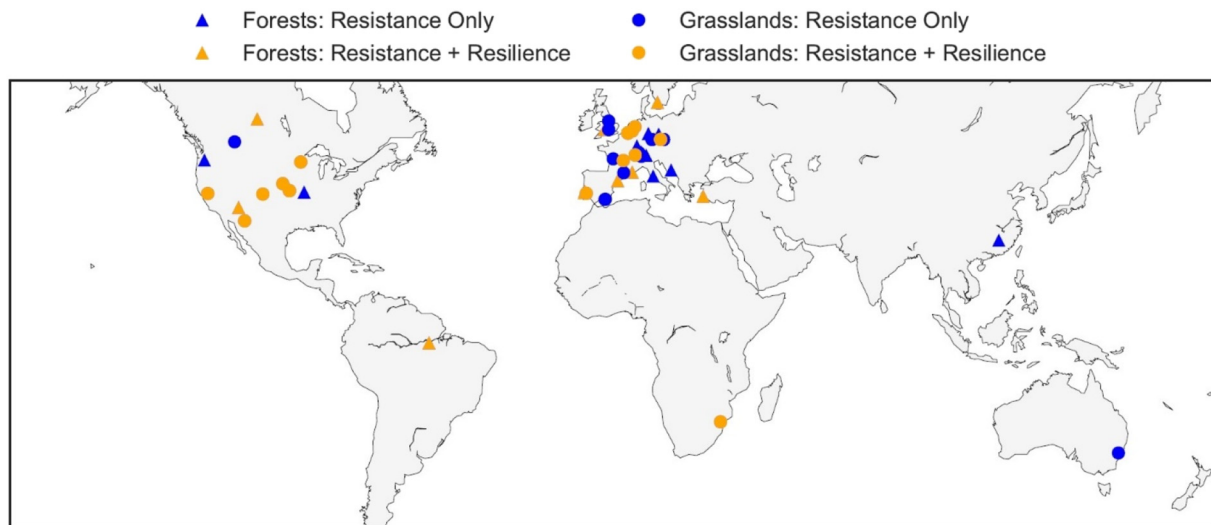
Fig. 1. Global map displaying site locations included in the analyses. Blue circles indicate use in the resistance model only while orange circles represent sites used in both the resistance and resilience models.

(experimental and natural) and then, including only natural cases that agreed with modelled SPEI.

2.3. Metrics of resistance and resilience

Using previously published metrics, resistance was quantified as the change in ecosystem functioning following drought, and resilience the extent to which ecosystem functioning returned to pre-event levels one year post-drought (Gazol et al., 2017; Hoover et al., 2014; Lloret et al., 2011; MacGillivray et al., 1995; Nimmo et al., 2015; Pretzsch et al., 2013). To standardize site comparison, we calculated the log response ratio effect sizes of primary production resistance, quantified as production during drought divided by control (or pre-drought) production, and resilience, production one-year post drought divided by control (or pre-drought) production, for each site.

2.4. Statistical analysis

Data were analyzed using two separate Bayesian analysis of covariance models, one for each response variable (resistance and resilience). Each model included ecosystem type (forest, grassland) as a categorical predictor, author-reported MAP as a continuous predictor, and the interaction between ecosystem type and MAP. We placed weakly informative priors [$N(0, 1)$] on all parameter estimates (Lemoine et al., 2016). These conservative priors state that it is unlikely that a one standard deviation change in MAP would yield a change of >1 log response ratio unit, thereby guarding against overestimated effect sizes with small datasets (Button et al., 2013; Lemoine et al., 2016). Models were allowed a warm-up of 5000 iterations for each of four Markov Chain Monte Carlo (MCMC) chains, and the next 5000 iterations from each chain were saved as posterior parameter estimates (20,000 total estimates). Convergence was checked using posterior density and trace plots.

Additional models were run using the United Nations Environment Programme (UNEP) mean site aridity index (MAI) in place of MAP, and we used Bayesian linear regression to determine how resistance varied with resilience. MAI, or MAP divided by potential evapotranspiration (PET), was calculated using modelled PET value extracted from DroughtNet. Results for MAI and MAP models were similar, but we present MAP results since the metric requires no modeling and is thus, a more accurate measurement.

Differences between forest and grassland resistance and resilience were explored using contrasts. After the model was run, we calculated the predicted resistance and resilience for forests and grasslands and the mean precipitation of each ecosystem type, respectively. This generated 20,000 posterior estimates of forest and grassland resistance/resilience. To evaluate mean differences between forests and grasslands when resistance and resilience values were normalized for precipitation, we derived adjusted values at the grand (i.e., all sites included) mean annual precipitation of MAP = 828 mm. Contrasts were conducted by calculating the difference between forests and grasslands for every posterior chain (Kruschke, 2015).

To account for potentially confounding variables, we tested for, but found no support for, significant differences between the resistance and resilience of: author-reported natural versus experimentally imposed drought events; managed versus unmanaged ecosystems; extreme drought events only versus extreme drought events with heatwaves; use of pre-event versus control production derivation of resistance/resilience; and GPP versus NPP metrics of production (SI Table 1). Similarly, we found no significant difference between the resistance and resilience of pulse (<2-year duration) versus press (>2-year duration) drought events (sensu Hoover et al., 2015). We found no correlation between modelled SPEI and resistance or resilience (SI Fig. 1). Sample sizes were too low to compare resistance and resilience of plant functional types within ecosystem functional types (see site characteristics in SI Table 1; examples include C3 versus C4 grasslands evergreen needleleaf versus deciduous broadleaf for forests).

3. Results

3.1. Resistance

We found that the resistance of both forests and grasslands increased along a common continuum of MAP [Probability of an effect: Pr(MAP slope > 0) = 0.95] (Fig. 2A, SI Table 2). Contrary to theoretical expectations, forests and grasslands exhibited the same trend across a MAP gradient of >2000 mm [Pr(Interaction) = 0.70]. Forest and grassland sites with low MAP exhibited similarly low primary production resistance, and thus were more likely to decline following extreme drought irrespective of ecosystem type, whereas forest and grassland sites with higher MAP were more resistant. Similar trends were found when MAI was substituted for MAP (SI Fig. 2, SI Table 3). Forests were, on average, wetter than grasslands and thus had higher average resistance [Pr(Forests > Grasslands) = 0.96] (Fig. 3A, SI Table 4). However, the lack of an interaction suggests that forests and grasslands exhibited similar resistance across an overlapping range of MAP (Fig. 2A). Our
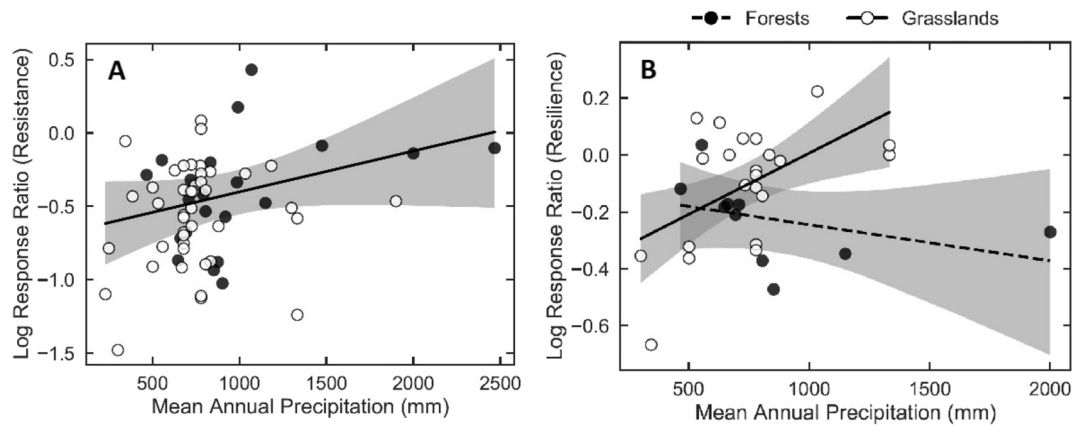
Fig. 2. Resistance (A) and resilience (B) of forest (closed circles) and grassland (open circles) primary production following extreme drought against mean annual precipitation. Resistance was calculated as the log response ratio of drought productivity divided by pre-drought productivity. Resilience was calculated as the log response ratio of post-drought productivity divided by pre-drought productivity. The shaded area depicts the 95% Bayesian credible interval of the regression.

findings demonstrate that mean differences in the resistance of forests and grasslands is attributed to their distribution in climate space rather than unique resistance sensitivities (i.e., slopes) across MAP.

3.2. Resilience

In contrast to resistance, forests and grasslands exhibited opposing primary production resilience patterns across the MAP gradient [Pr(Interaction) = 1.00]. Grassland resilience was positively correlated with both MAP [Pr(Grassland MAP slopes > 0) = 1.00] and MAI [Pr(Grassland MAI slopes > 0) = 0.96] (Fig. 2B, SI Fig. 3, SI Tables 5 & 6). Conversely, forest primary production resilience was unrelated to MAP [Pr(Forest MAP slope < 0) = 0.84], but negatively related to MAI [Pr(Forest MAI slope < 0) = 0.95]. Notably, forest resilience was negatively related to MAP when experimentally manipulated sites were removed from the analysis (N = 2) [Pr(Forest MAP slope < 0) = 0.98] (SI Fig. 4, SI Table 7). Across sites, grasslands remained more resilient than forests when resilience was normalized to mean MAP [Pr(Grasslands > Forests) = 0.97] (Fig. 3B, SI Table 8), indicating that differences in resilience were not attributed to the occupation of different climate space.

3.3. Resistance-resilience trade-off theory

We found no evidence that the theoretical assumption of a tradeoff between functional resistance and resilience applies at the ecosystem

scale [Pr(>0) = 0.55], nor did we find evidence that tradeoffs differed among ecosystem types [Pr(Interaction) = 0.80] (Fig. 4, SI Table 9).

4. Discussion

Our findings suggest that the theoretical expectations that forest and grassland ecosystems, with different life and evolutionary histories, should exhibit tradeoffs in their primary production resistance and resilience following extreme drought are not supported. Rather, grasslands and forests displayed a common resistance relationship with MAP but opposing patterns of resilience. On average, forests were more resistant than grasslands; however, differences in mean ecosystem resistance were attributed to climate space rather than inherent differences in sensitivity to precipitation. A common continuum of shifting plant physiological adaptation to increasingly dry environments, such as control of stomatal conductance, as well as functional diversity of drought "tolerating" and "avoiding" species (Anderegg and Hillerislambers, 2016; Craine et al., 2012; Dry et al., 2007), may stabilize grasslands and forests equally during periods of extreme drought with a linear decline in function (Huxman et al., 2004). Production of drier ecosystems can be more sensitive to inter-annual precipitation variability (Huxman et al., 2004), suggesting drier ecosystems may operate closer to water limitations, supporting our results. Although some observational studies found forests to have a higher water-use efficiency than grasslands during drought (Baldocchi et al., 2004; Wolf et al., 2013),
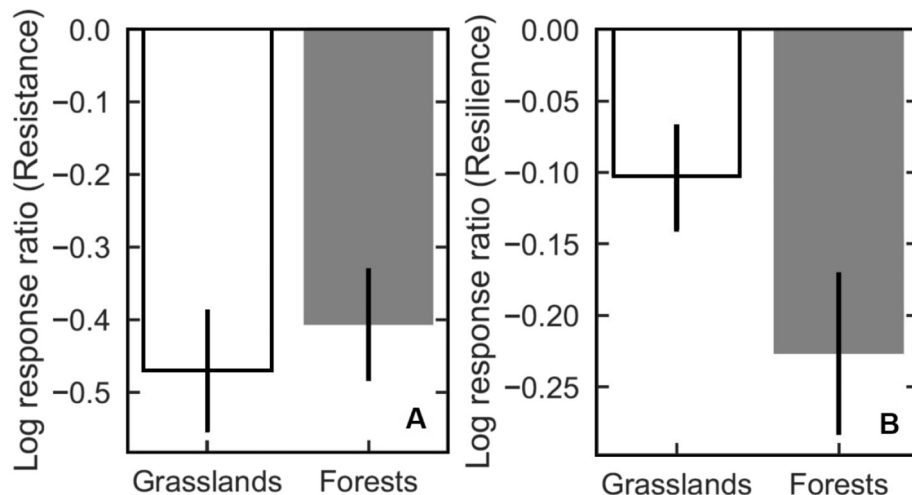
Fig. 3. Forest versus grassland contrasts of resistance (a) and resilience (b) following extreme drought (±standard deviation).
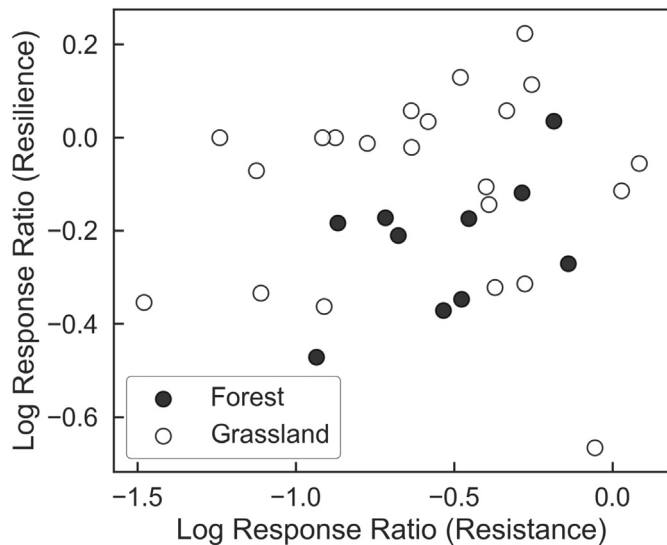
Fig. 4. The resistance and resilience of forest and grassland primary productivity following extreme drought. Open circles represent grasslands and closed circles represent forests.

those findings may reflect the forest plant functional type observed (Beer et al., 2009) rather than inherent differences between ecosystem type (i.e. grassland versus forest). Strengthening this idea further, a WUE synthesis across a range of ecosystems and plant functional types found that WUE was higher for broad-leaf forests compared to needleleaf forests, but generally did not differ between forests and grasslands (Beer et al., 2009).

Opposing relationships between forest and grassland resilience with MAP could potentially be explained by differences among predominant resident plant species in drought adaptations, plant architecture and anatomy, and turnover time life history. Dry-adapted woody species may be more drought tolerant than their wetter counterparts, and, therefore recover more rapidly and fully following extreme drought (Anderegg and Hillerislambers, 2016; Bannister, 1986; Gazol et al., 2017; López et al., 2016; Wright et al., 2013). Additionally, increased mortality events noted in drier forest ecosystems following extreme drought (Allen et al., 2010, 2015) may decrease competition for water and other resources, allowing surviving individuals to rapidly compensate when precipitation returns (Bottero et al., 2017; Reed et al., 2014). Such mortality production compensation has been noted following other heterogeneous mortality events (Stuart-Haëntjens et al., 2015). Since mesic forests are more resistant to extreme drought, less mortality may occur, dampening this compensatory growth that contributes to resilience. When mortality does occur, the degree of the growth response due to reduced inter-tree competition for water could be of lesser magnitude since mesic ecosystems are less likely to be water-limited (Huxman et al., 2004).

Grasslands, having evolved in more variable and often drier climates than forests, and being prone to frequent, biomass reducing disturbance regimes such as grazing, mowing or burning, likely possess a higher prevalence of traits that support rapid re-establishment and regrowth following perturbation (Ingrisch et al., 2017; Stampfli et al., 2018). Since grasses do not maintain tall woody structures, but often senesce when extremely water-stressed (Moran et al., 2014), the majority of aboveground biomass must regenerate following drought alleviation. Mesic grasslands often rapidly regrow when water availability returns, sometimes overshooting pre-drought productivity (Carter and Blair, 2012; Hofer et al., 2016; Stampfli et al., 2018), while dry grasslands recover more slowly, likely due to a general water-limitation (Reich, 2014; Schwalm et al., 2017) or because droughts cause higher plant mortality in dry than in mesic biomes.

Our findings are not without limitations, and particularly expose the need to evaluate extreme drought responses in underrepresented ecosystem types and geographic regions. Our meta-analysis could not robustly assess the resistance and resilience of shrublands and woodlands because sample sizes were low (4 of each ecosystem). However, these intermediary ecosystem types, occurring between forests and grasslands along precipitation continua, may display different resistance and resilience patterns (Ma et al., 2016; Peñuelas et al., 2007; Pereira et al., 2007). Similarly, the majority of studies incorporated in our analysis were temperate (64%) and most derive from temperate North America or Europe (92%), with Asia, South and Central Americas, Australia, and Africa representation disproportionally lower. This concentrated distribution and representation of ecosystems in the literature highlights a need for broader investigation of primary production resistance and resilience to extreme drought.

5. Conclusions

Our findings offer new insights into global patterns of resilience and resistance, while raising new questions about the mechanisms underlying our observations. The congruent resistance behaviors of grasslands and forests across the precipitation gradient could be explained by a shared cross-ecosystem continuum of physiological adaptations that maximize water-use efficiency within a common precipitation climate domain (Ponce Campos et al., 2013). In contrast, the divergent resilience patterns of grasslands and forests may be caused by differences in mean plant turnover time, with regrown grassland species recovering to pre-drought biomass levels more rapidly than woody forest plant species (Grime, 2001). The low primary production resistance and resilience of dry grasslands indicates that these ecosystems could be the most vulnerable to forecasted intensification of climate extremes with changing climate (Cook et al., 2014). Moreover, though beyond the scope of our analysis, our findings reinforce those suggesting cumulative effects of repeated extreme events may be most profound for these ecosystems (Schwalm et al., 2017). The low resilience of mesic forests suggests greater vulnerability of these large carbon sinks to recurrent drought extremes (Saatchi et al., 2013), while the higher than expected resilience of dry forests could prompt a reconsideration of the vulnerability of these forests types. Climate extremes are major drivers of the global carbon cycle (Reichstein et al., 2013), making it essential to consider these divergent ecosystem responses when estimating the future impact of extreme droughts on biogeochemical cycling and climate feedbacks.

Competing financial interests

Authors declare no competing financial interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.04.290.

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