

1 **Title:** Mean annual precipitation predicts primary production resistance and resilience to extreme
2 drought

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49 **Abstract**

50 Extreme drought is increasing in frequency and intensity in many regions globally, with
51 uncertain consequences for the resistance and resilience of ecosystem functions, including
52 primary production. Primary production resistance, the capacity to withstand change during
53 extreme drought, and resilience, the degree to which production recovers, vary among and within
54 ecosystem types, obscuring generalized patterns of ecological stability. Theory and many
55 observations suggest forest production is more resistant but less resilient than grassland
56 production to extreme drought; however, studies of production sensitivity to precipitation
57 variability indicate that the processes controlling resistance and resilience may be influenced
58 more by mean annual precipitation (MAP) than ecosystem type. Here, we conducted a global
59 meta-analysis to investigate primary production resistance and resilience to extreme drought in
60 64 forests and grasslands across a broad MAP gradient. We found resistance to extreme drought
61 was predicted by MAP; however, grasslands (positive) and forests (negative) exhibited opposing
62 resilience relationships with MAP. Our findings indicate that common plant physiological
63 mechanisms may determine grassland and forest resistance to extreme drought, whereas
64 differences among plant residents in turnover time, plant architecture, and drought adaptive
65 strategies likely underlie divergent resilience patterns. The low resistance and resilience of dry
66 grasslands suggests that these ecosystems are the most vulnerable to extreme drought – a
67 vulnerability that is expected to compound as extreme drought frequency increases in the future.

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69 **Keywords (max 6):** forest, grassland, extreme drought, primary productivity, resistance,
70 resilience

71

72 **1. Introduction**

73 The frequency and intensity of extreme droughts are predicted to increase throughout the century
74 in many regions across the globe (IPCC, 2013), with widespread effects on ecosystem
75 functioning anticipated but poorly quantified or understood (Bahn et al., 2014; Easterling et al.,
76 2000; Ingrisch and Bahn, 2018). Ecosystem sensitivity to climate extremes is commonly
77 characterized as *resistance* and *resilience*: *resistance* quantifies the immediate change in
78 ecosystem functioning (e.g., primary production) following a perturbation; and *resilience* is the
79 extent to which ecosystem functioning returns to pre-event levels (Lloret et al., 2011;
80 MacGillivray et al., 1995). Global understanding of how these measures of drought sensitivity
81 relate to one another is limited, with most studies examining resistance or resilience to drought,
82 but not both (Donohue et al., 2016). Moreover, whether grasslands and forests within the same
83 geographic regions follow similar, or unique, patterns of primary production resistance and
84 resilience within the same climate space is unknown, but essential in order to generalize the
85 stability of ecosystem functioning across the global climatic continuum.

86 Ecological theory (Grime, 2001) and observations (Petraakis et al., 2016; Schwalm et al.,
87 2012; Zhao et al., 2015) suggest a tradeoff between the resistance and resilience of primary
88 production, with the different life and evolutionary histories of resident grassland and forest plant
89 species portending different functional responses to extreme drought. Forests, containing
90 assemblages of long-lived woody species completing life cycles over decades to centuries, are
91 expected to be more resistant and less resilient because of the increased energetic cost and time
92 associated with rebuilding biomass prior to reproduction (MacGillivray et al., 1995). Conversely,
93 grassland plant species with annual turnover of production may be less resistant but more
94 resilient, exhibiting greater immediate vulnerability to extreme drought but capable of rapid re-

95 establishment, growth, and reproduction by resident plants (Hoover et al., 2014). Forest drought
96 resistance has been attributed to mechanisms that limit water loss, increase water supply
97 (hydraulic lift), or increase water-use efficiency (WUE) (Baldocchi et al., 2004; Wolf et al.,
98 2013). Additionally, trees generally maintain root systems that access deep soil water (Jackson et
99 al., 1996) while grasslands have shallower root systems and maintain high evapotranspiration
100 rates during drought, depleting soil moisture at a faster rate (Teuling et al., 2010; Wolf et al.,
101 2013).

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

111 In order to bridge the gap between ecological theory and empirical observations of
112 production sensitivity and functional response, we conducted a global meta-analysis of primary
113 production resistance and resilience to extreme drought in forests and grasslands across a broad
114 gradient of mean annual precipitation (MAP) (230 mm to 2467 mm yr⁻¹). The goals of this meta-
115 analysis were 1) to evaluate where different ecosystems exhibit shared or divergent responses
116 across a common precipitation continuum, 2) test the theory that forests are more resistant, but

117 less resilient, than grasslands, and 3) observe whether traditional resistance-resilience trade-off
118 theory applies at the ecosystem scale.

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120 **2. Methods**

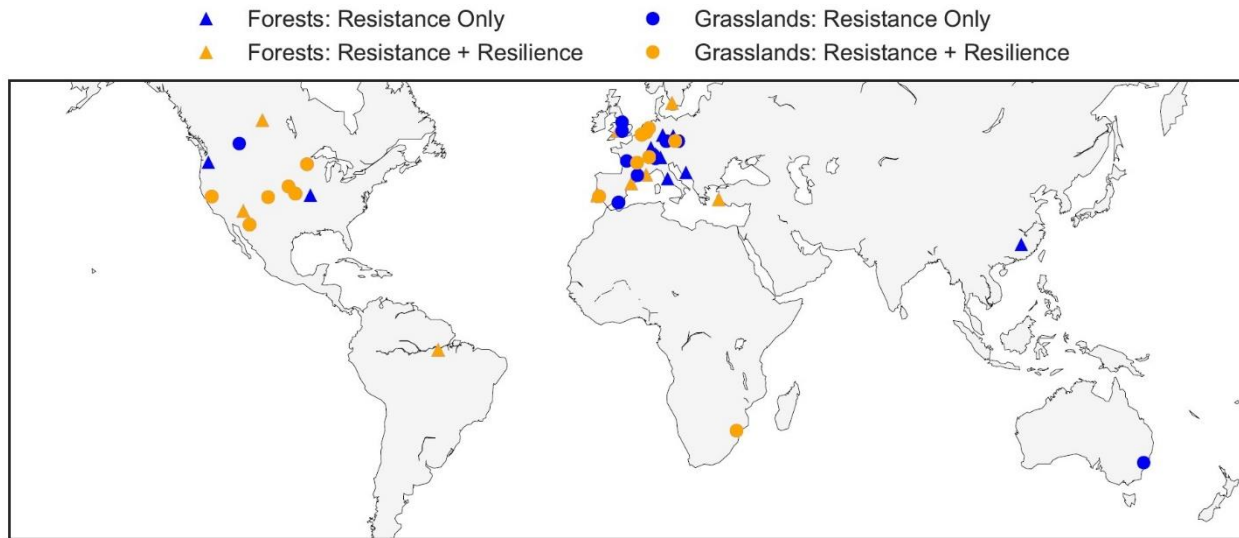
121 *2.1 Study criteria*

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

132 For the resistance analysis, only studies based on terrestrial ecosystems that justified the
133 drought as “extreme” and reported primary productivity from a true control, or a full reference
134 year prior to the event, were included. Post-event productivity one year following the event was
135 required for inclusion in the resilience analysis. Justification of extremity could include: 1) time-
136 scales (Girard et al., 2012; Rondeau et al., 2013; Schwalm et al., 2012), 2) drought return time
137 (Kreyling et al., 2008), 3) standardized precipitation-evapotranspiration index (SPEI) (Cavin et
138 al., 2013; Falk et al., 2008), or 4) >60% decrease in annual precipitation (Hoover et al., 2015).
139 Acceptable metrics of primary production included net primary production (NPP), gross primary
140 production (GPP) (Litton et al., 2007), basal area increments (BAI) (for functional types in

141 which BAI is significantly correlated with productivity) (Lempereur et al., 2015), and cover (in
142 arid and semi-arid ecosystems only) (Zhang et al., 2016). All 64 forest and grassland sites were
143 used in the resistance analysis, while 10 forests and 22 grasslands were included in the resilience
144 analysis.

145



146

147 **Fig. 1.** Global map displaying site locations included in the analyses. Blue circles indicate use in
148 the resistance model only while orange circles represent sites used in both the resistance and
149 resilience models.

150

151 *2.2 Extremity validation*

152 For natural events only, modelled standardized precipitation-evapotranspiration index
153 (SPEI) for each site served as an independent check on author-reported drought extremity.
154 Modelled SPEI values were extracted from DroughtNet using the Precipitation Trends Tool
155 (drought-net.org). Author assessments of extreme drought and modelled SPEI agreed in >90% of
156 the cases. The remaining 10% fell in higher latitudes where the SPEI model generates higher
157 uncertainty (Nathan Lemoine, direct correspondence). To avoid potential experimental bias,

158 analyses were run twice: once including all sites (experimental and natural) and then, including
159 only natural cases that agreed with modelled SPEI.

160

161 *2.3 Metrics of resistance and resilience*

162 Using previously published metrics, resistance was quantified as the change in ecosystem
163 functioning following drought, and resilience the extent to which ecosystem functioning returned
164 to pre-event levels one year post-drought (Gazol et al., 2017; Hoover et al., 2014; Lloret et al.,
165 2011; MacGillivray et al., 1995; Nimmo et al., 2015; Pretzsch et al., 2013). To standardize site
166 comparison, we calculated the log response ratio effect sizes of primary production resistance,
167 quantified as production during drought divided by control (or pre-drought) production, and
168 resilience, production one-year post drought divided by control (or pre-drought) production, for
169 each site.

170

171 *2.4 Statistical analysis*

172 Data were analyzed using two separate Bayesian analysis of covariance models, one for
173 each response variable (resistance and resilience). Each model included ecosystem type (forest,
174 grassland) as a categorical predictor, author-reported MAP as a continuous predictor, and the
175 interaction between ecosystem type and MAP. We placed weakly informative priors [$N(0, 1)$] on
176 all parameter estimates (Lemoine et al., 2016). These conservative priors state that it is unlikely
177 that a one standard deviation change in MAP would yield a change of > 1 log response ratio unit,
178 thereby guarding against overestimated effect sizes with small datasets (Button et al., 2013;
179 Lemoine et al., 2016). Models were allowed a warm-up of 5,000 iterations for each of four
180 Markov Chain Monte Carlo (MCMC) chains, and the next 5,000 iterations from each chain were

181 saved as posterior parameter estimates (20,000 total estimates). Convergence was checked using
182 posterior density and trace plots.

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

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

197 To account for potentially confounding variables, we tested for, but found no support for,
198 significant differences between the resistance and resilience of: author-reported natural versus
199 experimentally imposed drought events; managed versus unmanaged ecosystems; extreme
200 drought events only versus extreme drought events with heatwaves; use of pre-event versus
201 control production derivation of resistance/resilience; and GPP versus NPP metrics of production
202 (SI Table 1). Similarly, we found no significant difference between the resistance and resilience
203 of pulse (<2-year duration) versus press (>2-year duration) drought events (*sensu* Hoover et al.

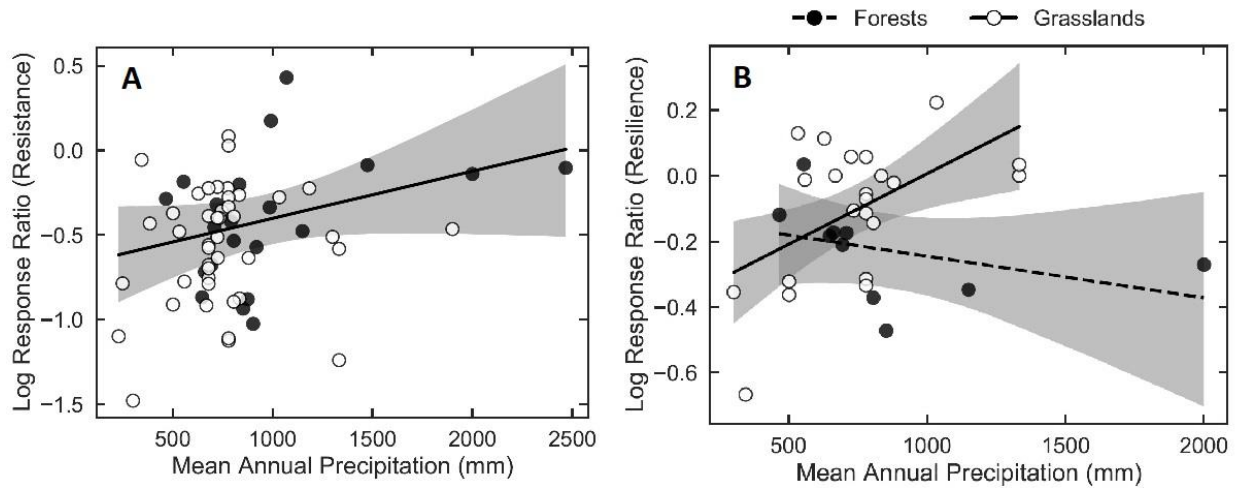
204 2015). We found no correlation between modelled SPEI and resistance or resilience (SI Fig. 1).
205 Sample sizes were too low to compare resistance and resilience of plant functional types within
206 ecosystem functional types (see site characteristics in SI Table 1; examples include C3 versus C4
207 grasslands evergreen needleleaf versus deciduous broadleaf for forests).

208

209 **3. Results**

210 *3.1 Resistance*

211 We found that the resistance of both forests and grasslands increased along a common
212 continuum of MAP [Probability of an effect: $\Pr(\text{MAP slope} > 0) = 0.95$] (Fig. 2A, SI Table 2).
213 Contrary to theoretical expectations, forests and grasslands exhibited the same trend across a
214 MAP gradient of > 2000 mm [$\Pr(\text{Interaction}) = 0.70$]. Forest and grassland sites with low MAP
215 exhibited similarly low primary production resistance, and thus were more likely to decline
216 following extreme drought irrespective of ecosystem type, whereas forest and grassland sites
217 with higher MAP were more resistant. Similar trends were found when MAI was substituted for
218 MAP (SI Fig. 2, SI Table 3). Forests were, on average, wetter than grasslands and thus had
219 higher average resistance [$\Pr(\text{Forests} > \text{Grasslands}) = 0.96$] (Fig. 3A, SI Table 4). However, the
220 lack of an interaction suggests that forests and grasslands exhibited similar resistance across an
221 overlapping range of MAP (Fig. 2A). Our findings demonstrate that mean differences in the
222 resistance of forests and grasslands is attributed to their distribution in climate space rather than
223 unique resistance sensitivities (i.e., slopes) across MAP.



224

225 **Fig. 2.** Resistance (A) and resilience (B) of forest (closed circles) and grassland (open circles)

226 primary production following extreme drought against mean annual precipitation. Resistance

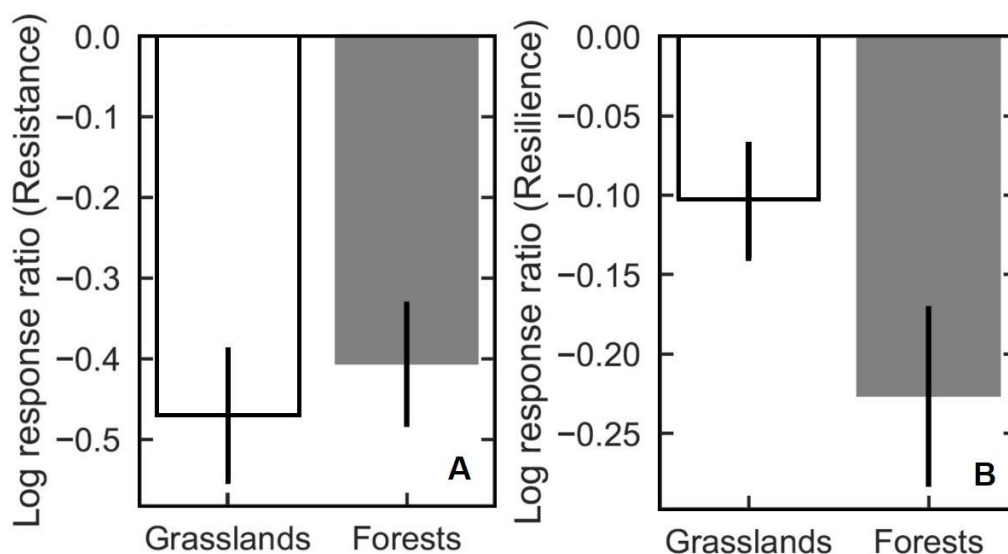
227 was calculated as the log response ratio of drought productivity divided by pre-drought

228 productivity. Resilience was calculated as the log response ratio of post-drought productivity

229 divided by pre-drought productivity. The shaded area depicts the 95% Bayesian credible interval

230 of the regression.

231



232

233 **Fig. 3.** Forest versus grassland contrasts of resistance (a) and resilience (b) following extreme
234 drought (\pm standard deviation).

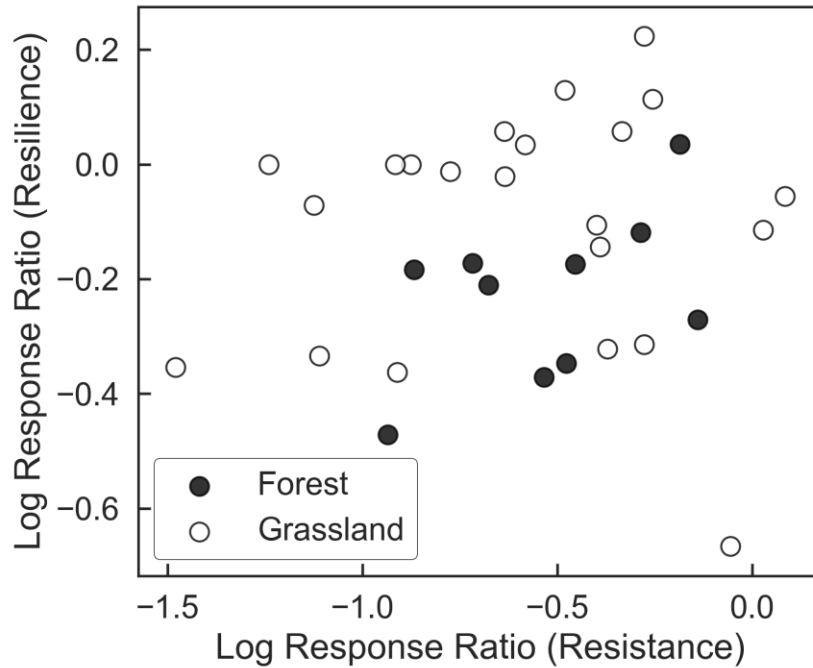
235 *3.2 Resilience*

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

247

248 *3.3 Resistance-Resilience Trade-off Theory*

249 We found no evidence that the theoretical assumption of a tradeoff between functional
250 resistance and resilience applies at the ecosystem scale [$\text{Pr}(> 0) = 0.55$], nor did we find evidence
251 that tradeoffs differed among ecosystem types [$\text{Pr}(\text{Interaction}) = 0.80$] (Fig. 4, SI Table 9).



252

253 **Fig. 4.** The resistance and resilience of forest and grassland primary productivity following
 254 extreme drought. Open circles represent grasslands and closed circles represent forests.

255

256 **4. Discussion**

257 Our findings suggest that the theoretical expectations that forest and grassland
 258 ecosystems, with different life and evolutionary histories, should exhibit tradeoffs in their
 259 primary production resistance and resilience following extreme drought are not supported.
 260 Rather, grasslands and forests displayed a common resistance relationship with MAP but
 261 opposing patterns of resilience. On average, forests were more resistant than grasslands;
 262 however, differences in mean ecosystem resistance were attributed to climate space rather than
 263 inherent differences in sensitivity to precipitation. A common continuum of shifting plant
 264 physiological adaptation to increasingly dry environments, such as control of stomatal
 265 conductance, as well as functional diversity of drought “tolerating” and “avoiding” species

266 (Anderegg and Hillerislambers, 2016; Craine et al., 2012; Dry et al., 2007), may stabilize
267 grasslands and forests equally during periods of extreme drought with a linear decline in function
268 (Huxman et al., 2004). Production of drier ecosystems can be more sensitive to inter-annual
269 precipitation variability (Huxman et al., 2004), suggesting drier ecosystems may operate closer
270 to water limitations, supporting our results. Although some observational studies found forests to
271 have a higher water-use efficiency than grasslands during drought (Baldocchi et al., 2004; Wolf
272 et al., 2013), those findings may reflect the forest plant functional type observed (Beer et al.,
273 2009) rather than inherent differences between ecosystem type (i.e. grassland versus forest).
274 Strengthening this idea further, a WUE synthesis across a range of ecosystems and plant
275 functional types found that WUE was higher for broad-leaf forests compared to needleleaf
276 forests, but generally did not differ between forests and grasslands (Beer et al., 2009).

277 Opposing relationships between forest and grassland resilience with MAP could
278 potentially be explained by differences among predominant resident plant species in drought
279 adaptations, plant architecture and anatomy, and turnover time life history. Dry-adapted woody
280 species may be more drought tolerant than their wetter counterparts, and, therefore recover more
281 rapidly and fully following extreme drought (Anderegg and Hillerislambers, 2016; Bannister,
282 1986; Gazol et al., 2017; López et al., 2016; Wright et al., 2013). Additionally, increased
283 mortality events noted in drier forest ecosystems following extreme drought (Allen et al., 2015,
284 2010) may decrease competition for water and other resources, allowing surviving individuals to
285 rapidly compensate when precipitation returns (Bottero et al., 2017; Reed et al., 2014). Such
286 mortality production compensation has been noted following other heterogeneous mortality
287 events (Stuart-Haëntjens et al., 2015). Since mesic forests are more resistant to extreme drought,
288 less mortality may occur, dampening this compensatory growth that contributes to resilience.

289 When mortality does occur, the degree of the growth response due to reduced inter-tree
290 competition for water could be of lesser magnitude since mesic ecosystems are less likely to be
291 water-limited (Huxman et al., 2004).

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

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

312 distribution and representation of ecosystems in the literature highlights a need for broader
313 investigation of primary production resistance and resilience to extreme drought.

314

315 **5. Conclusions**

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

335

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