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Reference:

Kreyling Juergen, Dengler Jürgen, Walter Julia, Velez Nikolay, Ugurlu Emin, Sopotlieva Desislava, Ransijn Johannes, Picon-Cochard Catherine, Nijs Ivan, Hernandez Pauline,- Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment
Ecology letters - ISSN 1461-023X - 20:11(2017), p. 1405-1413
Full text (Publisher's DOI): <https://doi.org/10.1111/ELE.12848>
To cite this reference: <https://hdl.handle.net/10067/1466430151162165141>

1 **Title: Species richness effects on grassland recovery from drought depend on community**
2 **productivity in a multi-site experiment**

3
4 **Type of article: Letter**

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34 **Running title: Diversity and ecological stability to drought**

35 **Keywords:**

36 Asynchrony, diversity-stability relationship, resilience, insurance hypothesis, extreme event
37 ecology, coordinated distributed experiment

38 **Number of words:** Abstract: 150; Main text: 3903; no text boxes

39 **Number of references:** 52

40 **Number of figures:** 4; **number of tables:** 2

41 **Statement of authorship**

42 A.J., C.W. and J.K. conceived the project; all authors developed the project at a workshop; J.D.,
43 A.J. and J.K. coordinated the experiment across sites; S.B., H.J.D.B., I.N. contributed
44 experimental data for site BE; I.A., D.S., N.V., contributed experimental data for site BG; C.B.,
45 J.D., P.v.G., A.J., M.A.S.A.K, J.K., J.R., J.W. contributed experimental data for site DE; C.P.C. and
46 P.H. contributed experimental data for site FR.; Y.A., E.U., B.G. contributed experimental data
47 for site TR; J.K. assembled and analysed the data; and J.K. wrote the paper, with substantial
48 input from J.M.G.B. and contributions from all authors.

49

50 **Data accessibility statement**

51 Should the manuscript be accepted, the data supporting the results will be archived in an
52 appropriate public repository and the data DOI will be included at the end of the article.

53 **Abstract**

54 Biodiversity can buffer ecosystem functioning against extreme climatic events, but few experiments have
55 explicitly tested this. Here, we present the first multi-site biodiversity×drought manipulation experiment
56 to examine drought resistance and recovery at five temperate and Mediterranean grassland sites.
57 Aboveground biomass production declined by 30% due to experimental drought (standardized local
58 extremity by rainfall exclusion for 72-98 consecutive days). Species richness did not affect resistance but
59 promoted recovery. Recovery was only positively affected by species richness in low productive
60 communities, with most diverse communities even showing overcompensation. This positive diversity
61 effect could be linked to asynchrony of species responses. Our results suggest that a more context-
62 dependent view considering the nature of the climatic disturbance as well as the productivity of the
63 studied system will help identify under which circumstances biodiversity promotes drought resistance or
64 recovery. Stability of biomass production can generally be expected to decrease with biodiversity loss
65 and climate change.

66

67 **Introduction**

68 Loss of biodiversity (Butchard *et al.* 2010) and climate change (e.g. via increasing
69 frequency and magnitude of extreme climatic events; Schär *et al.* 2004; IPCC 2013) can both
70 adversely affect ecosystem functioning (e.g. Cardinale *et al.* 2012; Reichstein *et al.* 2013). The
71 role of biodiversity for the stability of ecosystem functioning in the face of climatic disturbance
72 is therefore of utmost importance.

73 Resistance (*sensu* Pimm 1984) and recovery (*sensu* Hodgson *et al.* 2015) are two
74 important facets of ecological stability (Pimm 1984; Hodgson *et al.* 2015; Donohue *et al.* 2016).
75 Studies which have empirically evaluated diversity effects on these two facets of the stability of
76 ecosystems subjected to extreme climatic events, however, report mixed results. Species
77 richness may increase (Tilman & Downing 1994; Mulder *et al.* 2001; Kahmen *et al.* 2005; Isbell *et*
78 *al.* 2015), not affect (Wardle *et al.* 2000; Pfisterer & Schmid 2002; Caldeira *et al.* 2005; Kahmen
79 *et al.* 2005; DeClerck *et al.* 2006; Wang *et al.* 2007; van Ruijven & Berendse 2010), or even
80 decrease (Pfisterer & Schmid 2002; Allison 2004; Vogel *et al.* 2012) ecosystem resistance. Here,
81 we consider resistance as the lack of instantaneous impact of exogenous disturbance on a
82 system (Hodgson *et al.* 2015) or, more explicitly, the degree to which ecosystem productivity
83 remains unchanged. Likewise, species richness has been found to increase (Allison 2004;
84 DeClerck *et al.* 2006; Vogel *et al.* 2012), decrease (Pfisterer & Schmid 2002), or have no effect
85 (Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015) on recovery. Here,
86 recovery is understood as the endogenous processes that pull the disturbed system back
87 towards an equilibrium (Hodgson *et al.* 2015), or the degree to which ecosystem characteristics
88 return to control or pre-disturbance levels after a disturbance. These mixed findings go beyond

89 simple methodological differences among studies (e.g. artificial versus natural communities;
90 Wardle & Palmer 2016) and call for a better understanding of the biotic and abiotic conditions
91 that affect the biodiversity-stability relationship within ecosystems.

92 Positive effects of biodiversity on ecosystem functioning have previously been attributed
93 to selection effects or complementarity (Tilman et al. 1997; Loreau & Hector 2001). In addition,
94 more diverse systems are expected to be more stable against perturbations and extreme events
95 (*sensu* the Insurance Hypothesis, Yachi & Loreau 1999). Complementarity of species' responses
96 to extreme events can induce such an insurance, i.e. improve stability in more diverse
97 communities (Isbell *et al.* 2009; Loreau & Mazancourt 2013; Mazancourt *et al.* 2013; Gross *et al.*
98 2014). However, functional group diversity may be another important driver of ecosystem
99 functioning (Tilman et al. 2007). For example, presence of key functional groups, such as
100 legumes in grasslands, which are known to over-proportionally affect biomass production
101 (Spehn *et al.* 2002), also have the potential to modulate drought responses of co-existing
102 species (Arfin Khan *et al.* 2014).

103 Experiments manipulating both biodiversity and extreme events are ideally suited to test
104 for resistance to and recovery from disturbance, because they control for confounding effects
105 by the direct comparison between experimentally-induced climatic treatments and the control.
106 Such experimental designs can be particularly useful to analyse non-equilibrium systems as they
107 do not depend on metrics of ecological stability that relate performance after disturbance to
108 performance before disturbance (e.g. Lloret *et al.* 2011; Isbell *et al.* 2015). Controlled
109 experiments minimise noise due to temporal effects such as inherent micro-successional
110 dynamics or weather dynamics. Furthermore, coordinated distributed experiments (Fraser *et al.*

111 2013) which consist of identical setups at multiple sites have the advantage of allowing
112 biodiversity effects to be disentangled from effects of climatic disturbance in the bioclimatic
113 context of different sites.

114 Here, we present results from the first coordinated distributed biodiversity experiment
115 testing for interactions between different components of biodiversity and drought on model
116 grassland systems across a continental biogeographic and climatic gradient. We examined the
117 resistance and recovery of aboveground biomass production after prolonged drought across
118 five sites in Europe and the Near East in field mesocosms. This unique setup allowed us to test
119 for the generality of observed effects. We expected that the drought resistance of biomass
120 production would increase with increasing biodiversity irrespective of biotic (e.g. plant species
121 composition, soil biotic community, productivity) and abiotic (e.g. climate, soil substrate) site
122 conditions. Similarly, we also expected improved recovery with increasing biodiversity across
123 sites in the year after the drought. Biodiversity, here, comprised species richness, functional
124 group richness, and presence of key functional groups such as legumes.

125

126 **Material and Methods**

127 *Experimental Design*

128 An *in situ* coordinated biodiversity × drought experiment was implemented using buried field
129 mesocosms at five sites across Europe and the Near East (BE: Belgium, BG: Bulgaria, DE:
130 Germany, FR: France, TR: Turkey; Table 1). At each of the five sites, grassland communities were
131 planted at three species richness levels (1/3/6), also systematically altering functional group

132 richness (FGR: 1/2/3) and the presence of legumes. Twelve locally-frequent, native species
133 which naturally occur together on the local target substrate were selected from the local
134 species pool at each site. Study species included three functional groups (forbs, grasses,
135 legumes) with four species representing each functional group per site (Table S1) and comprised
136 different ecological strategy types at each site (Table S1). FGR was nested within species
137 richness, so that its effects could be statistically tested (Scherer-Lorenzen 2008; Table S2). Per
138 site and diversity level, 12 different species compositions were created (considered as replicates
139 for the species richness levels). Each of these 180 unique species compositions (5 sites \times 3
140 species richness levels \times 12 species compositions) was set up once in the control and once in the
141 drought treatment (see below). All plants were grown from seed under standardized conditions
142 at each site and planted into field mesocosms in early spring 2014 (>three months before the
143 start of the drought manipulation). Seeds were collected from autochthonous populations close
144 to the study sites (relying on expert knowledge).

145 Each mesocosm consisted of a PVC tube of 30 cm diameter and 50 cm height. The base
146 of mesocosms was closed with root matting, permeable for water but impermeable for roots.
147 Mesocosms were buried in the soil to ensure natural temperature and drainage patterns, and
148 filled with local soil substrate (homogenized, sieved to 2 cm). Mesocosms were planted with 18
149 pre-grown plant individuals in a systematic arrangement, avoiding con-specific neighbours, and
150 ensuring that edge/centre ratios were similar for each species. Each species occurred at
151 comparable frequencies within each species richness level. Non-target species were weeded out
152 at a monthly interval. No fertilization was applied. Upon planting, plants were cut to a height of

153 6 cm above ground level as standardization. Mortality was checked regularly and dead
154 individuals were replaced during the first month after planting.

155 *Drought manipulations*

156 We simulated a pulsed-drought event by using rain-out shelters with 100% rainfall reduction for
157 specific periods during the local growing season. A randomized block design was applied at each
158 site with two or three blocks (with each block containing both a rain-out shelter and a control).
159 Mesocosms were completely randomized within each drought treatment-block combination,
160 with each single species composition occurring twice (i.e. once per treatment). Drought length
161 was standardized across sites and intended to be extreme on the basis that such events will
162 become common in the future (Schär *et al.* 2004). Drought length was calculated for each site as
163 150% of the statistical 1000-year recurrence of consecutive days with <2.5 mm precipitation
164 based on local precipitation series in daily resolution (median series length: 30 years), and
165 constrained within the local growing season (months with mean temperature >5°C and
166 precipitation sum [mm] >2 x mean temperature [°C]). Thus, the extremity of the manipulation is
167 directly comparable for all sites. Ecologically, this is a more meaningful standardization of
168 drought length than simply applying the same drought length to systems under different
169 climatic conditions and, consequentially, different evolutionary adaptation of species and plant
170 traits. The drought treatment started after the second fifth of the growing season (see Table 1
171 for dates and duration per site). In case of natural drought outside the drought manipulation
172 period, all mesocosms were irrigated in order to avoid drought stress (DE: 7 x 10 mm; FR: 16 x
173 10 mm; TR: 5 x 10 mm). In case of natural drought during the manipulation period, control plots
174 were irrigated (DE: 4 x 10 mm; FR: 15 x 10 mm; TR: 4 x 10 mm). The drought manipulations were

175 ended by irrigating the droughted mesocosms with 20 mm and the control mesocosms with 5
176 mm, in order to ensure a temporal synchrony between the post-manipulation rainfall events.

177 *Biomass production*

178 Aboveground biomass (B) was harvested at four dates during the experiment: (B₀) two weeks
179 before the start of the drought treatment ('before drought'), to allow for a standardized
180 quantification of biomass production during the drought period; (B₁) directly at the end of
181 drought ('end of drought'); (B₂) at the end of the first growing season (except for TR, where (B₁)
182 and (B₂) were identical and BG where no regrowth was observed between (B₁) and (B₂)); (B₃) at
183 peak biomass in the following growing season ('peak following year', used for assessing recovery
184 after drought). Note that low values for this harvest in TR are explained by harvesting midway
185 through the growing season since peak biomass in this Mediterranean system usually occurs at
186 the end of the growing season, whereas peak biomass in temperate systems usually occurs in
187 the middle of the growing season. Biomass was always harvested at 3 cm above ground, and
188 included all plant material rooted inside the mesocosms. Species-specific biomass harvests were
189 conducted directly after the drought (harvest B₁) and at the peak of the following year (harvest
190 B₃; BG and DE only). Community biomass harvests were conducted at all other points in time
191 (B₀, B₂).

192 *Facets of ecological stability*

193 We used relative measures of resistance and recovery in order to infer different facets of
194 ecological stability (Pimm 1984; Donohue *et al.* 2016). Both metrics are dimensionless, and thus
195 directly comparable between sites and communities with different levels of productivity. Within
196 each experimental site and block, the single different species compositions occurred both under

197 control and drought treatment. Consequently, we calculated resistance and recovery to drought
198 for each unique species composition by comparing biomass production between drought
199 treatment and control as:

200

$$201 \quad \text{Resistance} = \frac{(B_1)_{Drought}}{(B_1)_{Control}}$$

$$202 \quad \text{Recovery} = \frac{(B_3)_{Drought}}{(B_3)_{Control}}$$

203 where (B₁) is the biomass of each community at the end of the drought period and (B₃) is the
204 biomass of each community at the peak of biomass production in the following year. The
205 resistance index equals 1 for complete resistance and 0 for no resistance (no biomass
206 production during drought). The recovery index equals 1 for complete recovery and is <1 for
207 incomplete recovery. Values >1 indicate overcompensation. Community compositions with less
208 than 1.5 g dry weight per mesocosm under control conditions (3% of all cases) were disregarded
209 because of their high relative uncertainty (e.g. incremental differences in cutting height can
210 have strong relative effects) and their potential to over-proportionally inflate errors (grand
211 mean over all measurements is 37.2 ± 2.9 (SE) g per mesocosm).

212 *Statistical analyses*

213 We used linear mixed effects models to test whether biomass production for each single time
214 step (from harvest to harvest) depended on ‘species richness’ and ‘drought’ treatments (testing
215 for main effects and their interaction; Fig. 1). The blocked structure of the experimental design
216 was acknowledged by nesting ‘blocks’ within ‘sites’ in the formulation of the random effects.

217 Resistance and recovery to drought were tested with similarly structured mixed models with the
218 fixed effects 'species richness', 'productivity under control conditions', and their interaction
219 combined with the same formulation of random effects as described above (Fig. 2). 'Species
220 richness' was introduced into the model as linear numeric variable, but note that log-linear and
221 factorial response produced qualitatively the same results in all models. 'Productivity under
222 control conditions' (B1 for resistance and B3 for recovery) was also analysed as linear numeric
223 variable (again, log-linear response did not affect the outcome). For further visualization,
224 communities were subsequently separated into low productive and high productive using the
225 respective 70% percentile as split (400 g m⁻² control biomass for resistance and 700 g m⁻²
226 control biomass for recovery, respectively; Fig. 2C-F).

227 A second model formulation was used to test also for the effects of 'FGR' and 'presence of
228 legumes' on resistance and recovery, by adding both terms as fixed effects after the fixed effect
229 'species richness' and the same random effect formulation as described above (Table 2). For all
230 models, the response variable was log(x+1.1)-transformed (Hector *et al.* 2002) to meet model
231 assumptions (homoscedasticity and normal distribution of residuals). Models were fit with the
232 lmer-function in the lme4 package (version 1.1-12) in R (R Core Team 2016), and results were
233 extracted with the anova-function in the lmer.test package (version 2.0-33) in R.

234 Observed diversity effects were partitioned into complementarity effects and selection
235 effects according to Loreau and Hector (2001). This partitioning was done by the addpart-
236 function in the package pdiv (version 1.4.1) in R and provides these effects in original units of
237 the response parameter (here: g biomass per area). Further statistical analysis of

238 complementarity and selection effects was done using mixed effects models as described above
239 for biomass production.

240 Asynchrony in species responses to drought was assessed according to Loreau and de
241 Mazancourt (2008) as $1 -$ the degree of synchrony in species biomass production between
242 control and drought treatment for each species composition, i.e. comparing changes in biomass
243 between treatment and control, which do not have a temporal component. Specifically,
244 community-level variances within each species composition and treatment were compared to
245 species-level variance of the same species composition between the treatments (drought versus
246 control), resulting in one value for each species composition. Asynchrony ranges from 0 (perfect
247 synchrony) to 1 (perfect asynchrony). Synchrony was extracted by the synchrony-function of the
248 package *codyn* (version 1.1.0) in R. Further statistical analysis on asynchrony values was done by
249 mixed effects models as described above for biomass production. As species-specific biomass
250 data was not available for all sites and times, two separate models were applied, one over all
251 sites for harvest B1 ('end of drought') with site and species richness as fixed effects; and another
252 one for BG and DE only for harvests B1 and B3 ('peak next season') with harvest year, site, and
253 species richness as fixed effects. Note that species asynchrony increases (as we use $1 -$
254 synchrony) with species richness (Loreau and de Mazancourt 2008). These authors show that, in
255 the special case of independent species responses, synchrony should decline by $1/S$, which
256 approximately fits for our data. Therefore, we focus the interpretation of our data on site
257 differences and changes in asynchrony from the event year to the year after the event.

258 **Results**

259 Species richness increased biomass production irrespective of measurement date (Fig.
260 1). Drought reduced biomass production by 30% on average across diversity treatments and
261 sites (Fig. 1B). Species richness had no significant effect on drought resistance of biomass
262 production ($p = 0.580$; Fig. 2A). Overall, recovery values showed that the most species-rich
263 communities (6 species) overcompensated for biomass reduction recorded during the drought
264 period (mean recovery = 1.19 ± 0.10 (SE)). In contrast, monocultures and low diversity
265 communities (3 species) only reached recovery values of 0.85 ± 0.07 and 0.82 ± 0.10 respectively
266 within one year after the experimental drought ($p = 0.002$; Fig. 2B).

267 Observed recovery effects were driven by productivity (interaction between species
268 richness and productivity: $p = 0.014$; Fig. 2B). The richness effect on recovery was only
269 significant for low productive communities (Fig. 2D) but not for high productive communities
270 (Fig. 2F). No such productivity-dependent differentiation was observed for resistance (Fig. 2 C
271 and E). Neither functional group richness nor presence of legumes had a significant effect on
272 resistance or recovery (Table 2).

273 The positive richness effect on recovery after drought appeared to be driven by
274 asynchrony of species responses to drought. Asynchrony in species performance between
275 drought and control increased from the end of the drought to the peak biomass of the following
276 year (year: $p = 0.002$; Fig. 3). Asynchrony did not differ between sites (both models with no
277 significant site effect or any interaction with site).

278 Complementarity had a greater influence on observed diversity effects on aboveground
279 biomass production compared with selection effects (Fig. 4). Drought reduced the magnitude of

280 these complementarity effects on the end-of-drought harvest ($p < 0.001$). Higher species
281 richness (six versus three species) tended to increase complementarity in both harvests ($p =$
282 0.051 and $p = 0.058$, respectively) while it reduced the (already negative) selection effect in the
283 harvest one year after the drought ($p = 0.008$). The selection effect was not affected by the
284 drought treatment (Table 2).

285

286 **Discussion**

287 Species richness improved the drought recovery of biomass production in our multi-site
288 experiment. This positive richness effect was driven by community productivity. Recovery was
289 high irrespective of species richness in our high-productive plots while it depended on species
290 richness in the low-productive communities where only diverse communities reached full
291 recovery within one year (Fig. 2 D and F). This is consistent with the idea that conservative,
292 slow-growing species characteristic of low-productivity communities are less able to take
293 advantage of increased resource availability after the end of the drought (Lepš *et al.* 1982;
294 Grime *et al.* 2000; Májeková *et al.* 2014; Reich 2014). Our species pool covered a wide gradient
295 of plant strategy types, including slow- and also fast-growing species and productivity levels
296 ranged from 2 g m^{-2} to 7 kg m^{-2} (peak biomass in control plots in the second study year, 1st
297 quartile: 165 g m^{-2} , median: 435 g m^{-2} , 3rd quartile: 897 g m^{-2}). Taken together, the advantages
298 of high species richness (and an increased range in species traits) may be greater for recovery of
299 biomass production after drought where productivity is low.

300 Community productivity has been reported to negatively affect resistance to drought
301 irrespective of species richness (Wang *et al.* 2007). Furthermore, van Ruijven & Berendse (2010)

302 show that a positive diversity-resistance effect to a natural drought depends negatively on
303 productivity, while recovery after drought increases with diversity independent of productivity.
304 The positive effect of species richness on recovery, at least in low productive communities,
305 observed in the present study is generally consistent with previous studies showing a positive
306 relationship between diversity and recovery after extreme events (Allison 2004; DeClerck *et al.*
307 2006; van Ruijven & Berendse 2010; Vogel *et al.* 2012). In contrast with some previous grassland
308 studies (e.g., Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015), we did
309 not observe significant diversity effects on resistance of biomass production across sites. This
310 may be due to our short gradient in species richness (1-6 species). Meta-analyses on
311 biodiversity-stability and biodiversity-ecosystem functioning studies, however, show strongest
312 diversity effects right in the range of species richness covered by our experiment (Cardinale *et*
313 *al.* 2006; Isbell *et al.* 2015). Species resistance to sudden pulse events (our study) may be
314 different compared with chronic press events such as prolonged natural drought events (e.g.,
315 Tilman & Downing 1994; van Ruijven & Berendse 2010; Isbell *et al.* 2015) which usually include
316 small rainfall events even during the dry periods (Knapp *et al.* 2017). The latter offers greater
317 options for community resistance through asynchrony of species responses, promoting
318 subordinate and stress-tolerant species, which are usually less productive under regular climatic
319 conditions (Mariotte *et al.* 2013). Such a reordering of community dominance patterns,
320 however, requires time and was not observed during our drought experiment (Fig. 3).
321 Therefore, we suggest that biodiversity effects are more likely to occur after rather than during
322 sudden pulse events, affecting recovery rather than resistance. This expectation is confirmed by
323 increased asynchrony between drought and control over time following our experimental
324 drought. It is noteworthy that the drought-induced reduction in biomass production in our

325 study was comparable in effect size to severe natural drought events such as the Central
326 European heat wave in summer 2003 (Ciais *et al.* 2005), as well as to other studies on diversity-
327 stability relations (Pfisterer & Schmid 2002; van Ruijven & Berendse 2010; Isbell *et al.* 2015).
328 Significant increase in senescence due to drought at all sites (Fig. S2) indicated drought stress
329 for our plants.

330 Mixed results on diversity-stability (*sensu* Pimm 1984; Donohue *et al.* 2016) effects in
331 the literature may generally reflect (i) characteristics of the climate extremes, (ii) characteristics
332 of the studied communities, and (iii) metrics of ecological stability.

333 (i) In addition to potential differences in diversity-stability effects among pulse and chronic
334 events (see above), the extremity of the event could affect the outcome. Drought duration
335 defined by rainfall exclusion relative to local climate series should not be directly interpreted as
336 evidence for extreme ecological drought effects (Smith 2011; Kreyling *et al.* 2016). Biodiversity-
337 stability studies will benefit from objective and relative quantification of extremity (Smith 2011)
338 and rigorous testing along gradients of extremity to uncover potential thresholds and non-
339 linearities (Kreyling *et al.* 2014).

340 (ii) Characteristics of the target communities can affect biodiversity effects on resistance to and
341 recovery from disturbance. Our data implies that such diversity effects depend on the
342 productivity of the study systems. Furthermore, the successional state of ecosystems and age of
343 individuals may also need to be taken into account when evaluating their response to climate
344 extremes. It has been suggested that ecological stability of early successional state plant
345 communities is driven by recovery while stability of late successional state communities is
346 driven by resistance to drought (Lepš *et al.* 1982). Still, the importance of plant community age

347 for the stability of grassland ecosystem processes remains unknown (Bloor & Bardgett 2012)
348 and research focusing on undisturbed, late-successional ecosystems might consequently lead to
349 an underestimation of instantaneous climate change impacts (Kröel-Dulay *et al.* 2015). Likewise,
350 studies on young or recently disturbed ecosystems may overestimate direct impacts while
351 emphasizing potential for recovery. Studying such non-equilibrium systems further emphasizes
352 the need for controlled designs to allow for sound quantification of the drought resistance and
353 recovery by directly comparing performance under drought and control conditions. Generally,
354 diversity effects in controlled, artificially created, and randomized species compositions might
355 differ from effects of non-random species loss in nature (Wardle & Palmer 2016). This, however,
356 does not explain the mixed results in biodiversity-stability studies as the vast majority of those
357 studies artificially generated their communities.

358 (iii) Terminology on components of ecological stability, such as resilience, resistance and
359 recovery, is ambiguous in the scientific literature (Holling 1973; Pimm 1984; Grimm & Wissel
360 1997; Hodgson *et al.* 2015; Donohue *et al.* 2016). Here, we focused on the ratio between
361 biomass production in the drought treatment and control conditions for defined periods of time
362 (the drought period for resistance and the year after drought for recovery), thereby obtaining
363 more direct estimates of resistance and recovery than observational surveys, which rely on
364 comparisons with previous years, and usually include biomass produced before or after the
365 drought. Adapting stability indices commonly used in observational time series (Isbell *et al.*
366 2015) to our controlled design, we find no significant effects of species richness on resistance
367 and resilience (Figure S3). While the shifting baseline in a controlled design (control during the
368 drought year versus control after the drought year) controls for confounding effects in non-

369 equilibrium systems, it also hampers direct comparisons to observational studies (see Appendix
370 S3 for details). Still, the main difference to our recovery index is that the resilience index *sensu*
371 Isbell *et al.* (2015) focuses only on stability and does not allow for a separation between
372 overcompensation and incomplete recovery (see Appendix S3 for details). While this is a sound
373 definition from the perspective of stability theory, we argue that overcompensation, as
374 observed in our study, is of high ecological and economical importance.

375 Recovery in our most species-rich communities (6 species) indicated overcompensation
376 of biomass production in the year following experimental drought. Asynchrony in species
377 responses to the drought (compared with species performance under control conditions)
378 increased from the end of the drought period, when species richness had no effect on
379 resistance, through to the following year, when species richness resulted in the positive effect
380 on recovery. This is consistent with the Insurance Hypothesis (Yachi & Loreau 1999), which
381 states that more diverse communities are more likely to contain species with unique strategies
382 to cope with perturbations. It has been suggested that insurance effects may occur
383 predominantly in the absence of positive diversity-productivity relationships before the
384 perturbation (van Ruijven & Berendse 2003; Allison 2004). This was not the case in our study
385 where a positive diversity-productivity relationship was observed both before and also at the
386 end of the drought period and throughout the recovery period across sites. Positive effects of
387 species richness on ecosystem functioning during recovery after drought can be explained by
388 higher complementarity or resource partitioning associated with the nutrient flush caused by
389 rewetting (with resource supply during the moment of rewetting having been greater for

390 droughted than for non-droughted communities) (DeClerck *et al.* 2006; Bloor & Bardgett 2012;
391 Roy *et al.* 2016).

392 Generally, our results confirm the positive biodiversity–ecosystem functioning
393 relationship (e.g. Cardinale *et al.* 2012). Our coordinated, distributed experimental study
394 suggests that species richness, but not functional group richness or presence of legumes,
395 underlies these observed positive diversity effects (Table 2). Moreover, complementarity, rather
396 than selection (*sensu* Loreau & Hector 2001), explained the positive diversity effects. Drought
397 reduced the positive complementarity effect (Fig. 4), which is in agreement with recent findings
398 from other grassland field studies (Craven *et al.* 2016). Contrary to expectations (Spehn *et al.*
399 2002; Arfin Khan *et al.* 2014), presence of legumes did not affect resistance to or recovery from
400 drought.

401 Our study demonstrates that species richness has positive effects on ecosystem
402 functioning by supporting recovery of biomass production after drought in low-productive, and
403 presumably slow-growing, communities. The most diverse communities even overcompensated
404 for the negative drought effect during recovery by reordering community composition, as
405 indicated by increased asynchrony of species responses to drought. No diversity effect was
406 found for resistance against pulsed, prolonged drought. We suggest that a more context-
407 dependent view (e.g. considering pulsed versus chronic events, extremity of the event,
408 productivity and successional stage of the studied system) will help identify which
409 circumstances promote drought resistance or recovery. Restoring and protecting biodiversity in
410 times of increasing climatic extremity, nevertheless, can generally be expected to improve

411 ecological stability, thereby ensuring ecosystem productivity and also productivity-dependent
412 ecosystem services.

413

414 **Acknowledgements**

415 This work is part of the project SIGNAL which is funded by the ERA-Net BiodivERsA
416 (<http://www.biodiversa.org>; Funding ID 01LC1201, Jentsch *et al.* 2013), with the national
417 funders Belgian Federal Science Policy Office (BELSPO), German Federal Ministry of Education
418 and Research (BMBF), Bulgarian Science Found and Ministère de l'Écologie, du Développement
419 durable et de l'Énergie (France) as part of the 2011–2012 BiodivERsA call for research proposals.
420 For site FR we thank P. Pichon, A. Salcedo, J. Pottier, M.E. Lefranc, M. Michaux, A. Vernay and G.
421 Zannin for help during the course of the experiment.

422 We thank three anonymous referees for insightful and constructive comments on an earlier
423 version of this manuscript.

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549 environment: The insurance hypothesis. *Proc Nat Acad Sci USA*, 96, 1463–1468.

550

551 **Tables and figures**

552

553 Table 1: Site characteristics. Mean annual temperature (MAT) and mean annual precipitation
 554 (MAP) from www.worldclim.org (Hijmans *et al.* 2005). Drought duration was standardized to
 555 local precipitation series in order to be comparable across sites (see text for details).

Site	Country	Latitude (°)	Longitude (°)	Altitude (m a.s.l.)	MAT (°C)	MAP (mm)	Start of drought	Duration (d)
BE	Belgium	51.24917	4.6717	13	9.9	792	19.06.2014	88
BG	Bulgaria	42.6468	23.2981	650	10.1	597	23.06.2014	85
DE	Germany	49.9219	11.5819	365	8.0	674	25.06.2014	76
FR	France	45.7191	3.0166	890	9.7	687	15.07.2014	72
TR	Turkey	38.6765	27.3010	70	15.4	725	05.02.2015	98

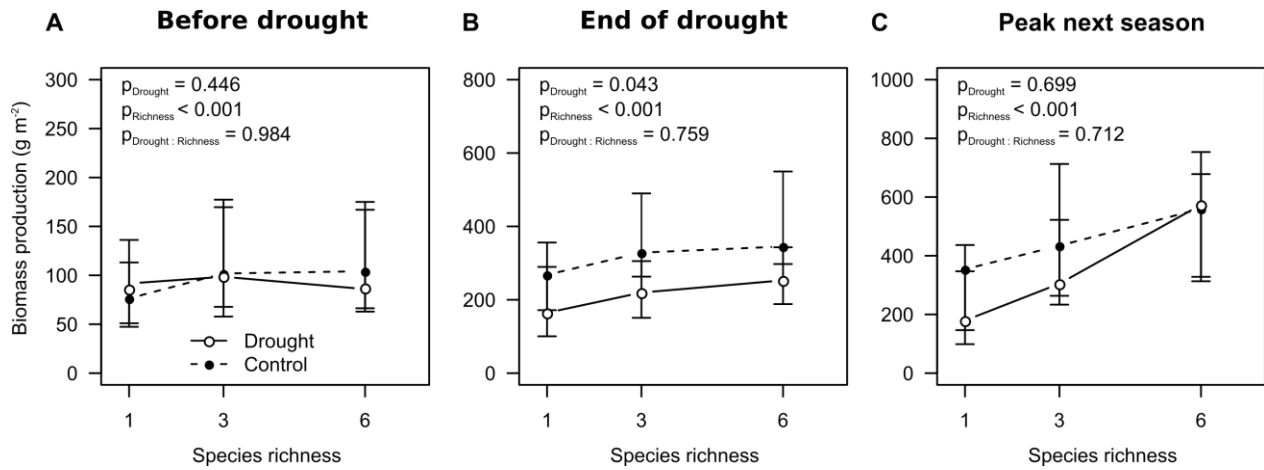
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558 Table 2: Biodiversity parameters affecting the resistance and recovery of biomass production in
 559 response to drought periods. Results are from mixed-model ANOVA with the single species
 560 compositions nested in treatment blocks further nested in study site as random effects. Both
 561 response variables were $\log(x+1.1)$ -transformed. Satterthwaite approximation is given for
 562 denominator degrees of freedom. Superscripts represent the respective p-values.

Fixed effects	Resistance	Recovery
Species richness	$F_{156.8} = 1.11^{0.293}$	$F_{136.5} = 6.67^{0.011}$
Legume presence	$F_{154.8} = 2.13^{0.146}$	$F_{135.9} = 0.40^{0.524}$
Functional group richness	$F_{157.4} = 0.01^{0.922}$	$F_{136.5} = 0.36^{0.528}$

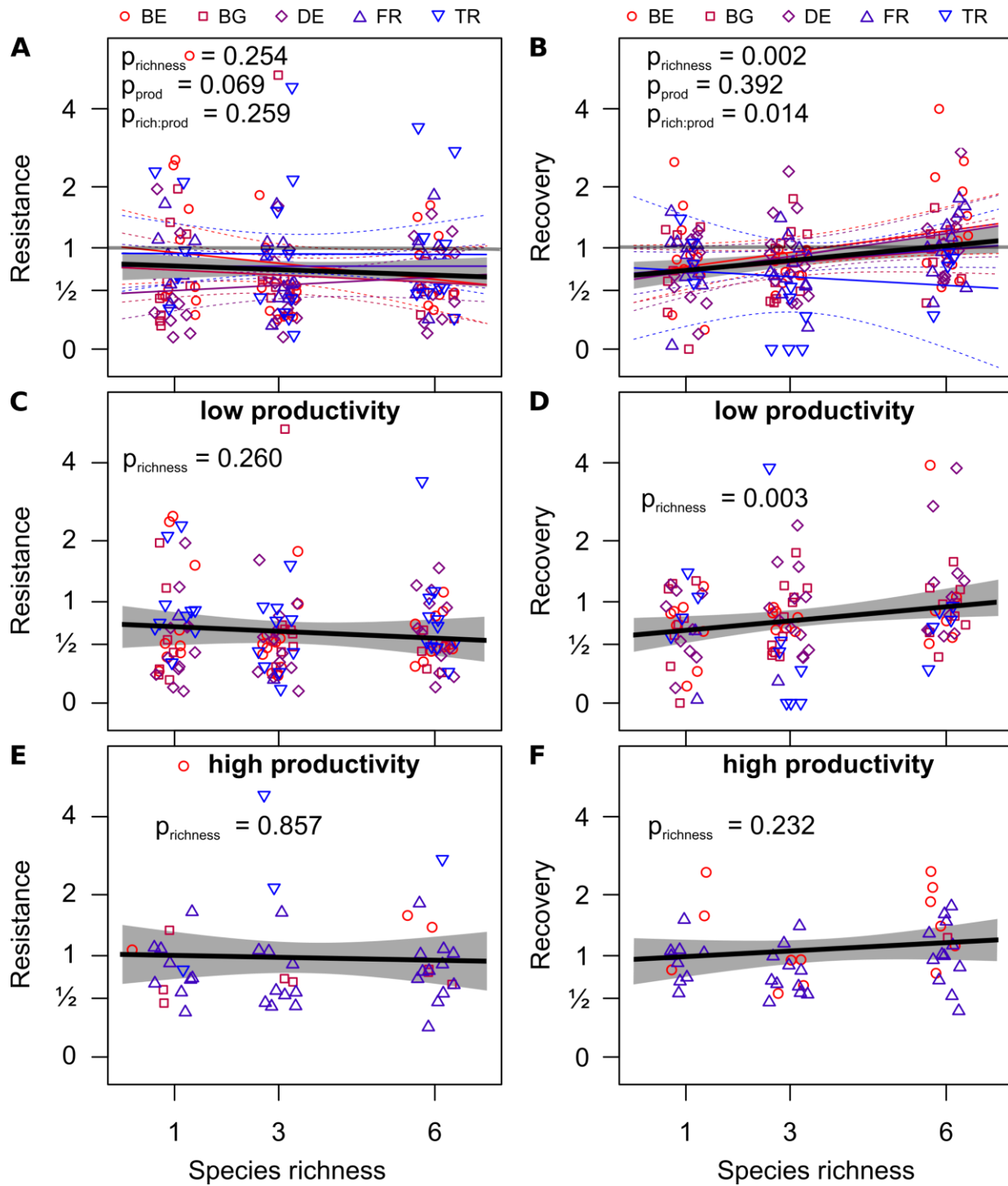
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564

565 Figure 1: Biomass production across sites (median and quartiles, n=60 per point) between the
566 previous and the specified time step. Fixed effects from mixed-model ANOVA analysis are given.
567 Site-specific biomass production is provided in Fig. S1. Note that 'before drought' and 'end of
568 drought' data stem from the same year; their sum being equivalent to the harvest at peak next
569 season in terms of time covered per growing season.

570



571

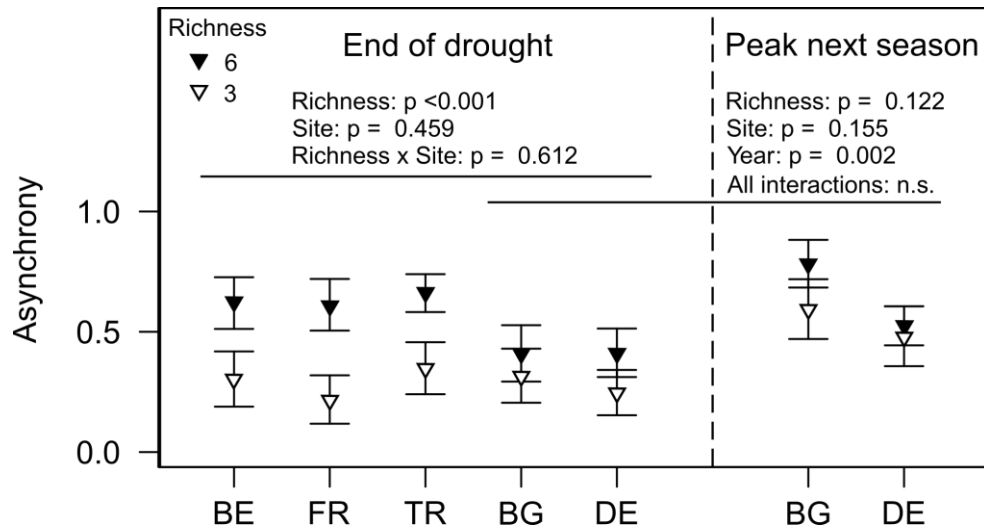
572 Figure 2: Species richness effects on resistance and recovery to drought. Species richness did

573 not affect resistance (i.e. the biomass ratio between drought manipulation and control at the

574 end of drought) (A), irrespective of community productivity (tested as numeric explanatory

575 parameter in (A) and further visualized here as low productivity ($< 400 \text{ g m}^{-2}$ = 0.7-quantile; (C))
576 and high productivity ($> 400 \text{ g m}^{-2}$ (E))). Species richness affected recovery (i.e. the biomass ratio
577 between drought manipulation and control one year after the drought (B)), but this effect
578 depended on productivity (significant interaction in (A)), further visualized by separating into
579 low (i.e. communities with a productivity of $< 700 \text{ g m}^{-2}$ (= 0.7-quantile) in the year after the
580 drought manipulation) and high productivity plots (F) (i.e. communities with a productivity of $>$
581 700 g m^{-2}). Black solid lines are mixed-effects model fits, grey shades represent their respective
582 95% confidence intervals. P-values are given for the fixed species richness effect, the fixed
583 productivity effect (p_{prod}) and their interaction ($p_{\text{rich:prod}}$) in (A) and (B). Values on the y-axis are
584 unitless. X-axis values are jittered around the applied levels of species richness to improve
585 visibility of single points ($n = 12$ per site and species richness level in (A) and (B)). Colours and
586 symbols code the single sites with their respective linear model fits (solid lines) and 95%
587 confidence intervals (dotted lines). Note that no single-site linear model yielded statistical
588 significance. Grey horizontal lines represent complete resistance (A) and recovery (B). For the
589 latter, values above 1 represent overcompensation.

590



591

592

593

Figure 3: Asynchrony in species responses to the drought manipulation (mean ± SEM, n=12 per

594 point) expressed as 1 - synchrony according to Loreau and de Mazancourt (2008) between

595 species variances in control and drought manipulation at the end of the drought period and at

596 peak biomass in the following year. Asynchrony ranges from 0 (perfect synchrony) to 1 (perfect

597 asynchrony). ANOVA results are given for two subsets (i) all sites at the end of the drought

598 period and (ii) sites BG and DE at both points in time (subsets are indicated by the solid

599 horizontal lines below each ANOVA result). Species asynchrony being higher in more diverse

600 than in less diverse communities is an inherent effect of the index, which increases (as we use 1-

601 synchrony) with species richness (Loreau and de Mazancourt 2008). These authors show that, in

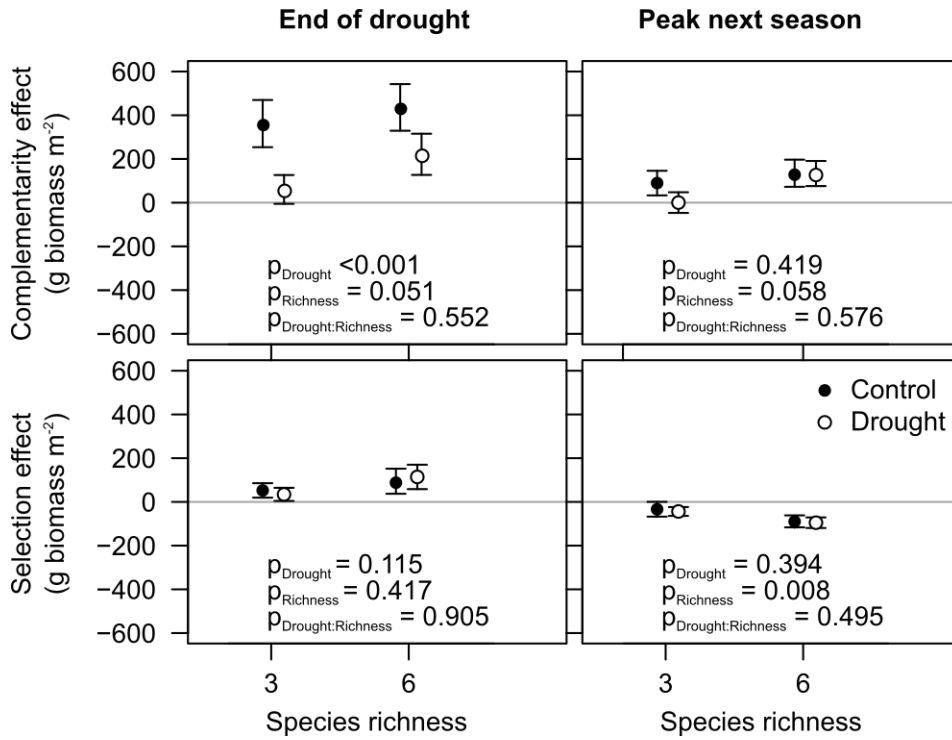
602 the special case of independent species responses, synchrony should decline by 1/S, which

603 approximately fits for our data for end of drought. Based on this, the results emphasize (a) no

604 significant difference in asynchrony among the five sites and (b) an increase in asynchrony from

605 the event year to the year after the event.

606



607

608 Figure 4: Partitioning the observed diversity effects into complementarity and selection effects

609 according to Loreau and Hector (2001). Displayed are mean \pm SEM for 'end of drought' harvests

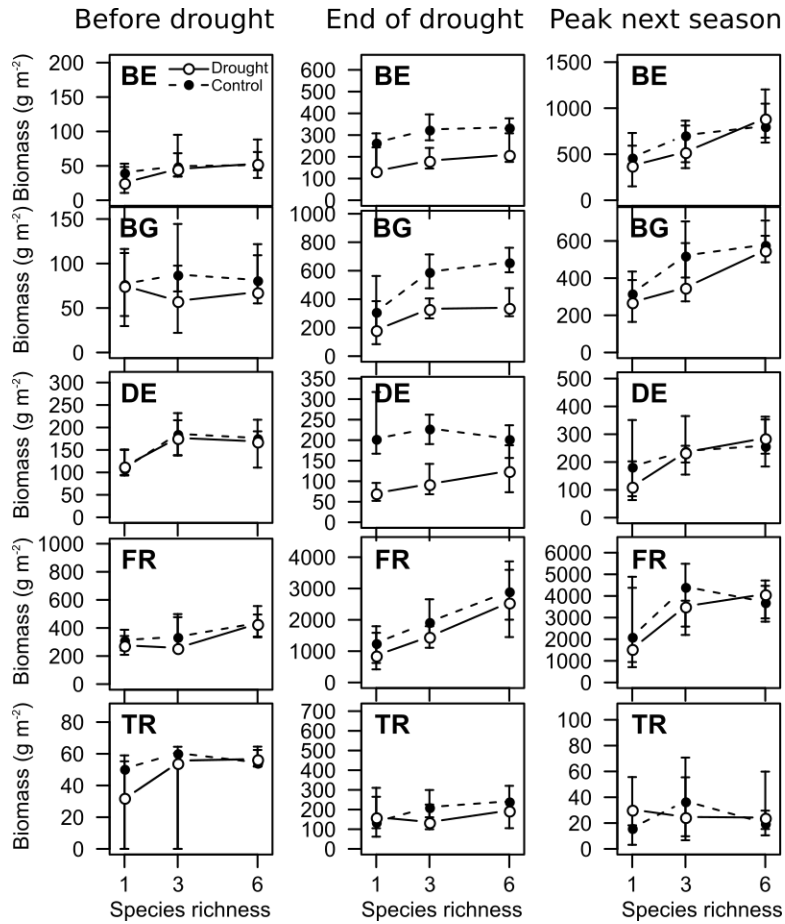
610 (all sites, n=60) and for 'peak next season' harvests (BG and DE only, n = 24). Fixed effects from

611 mixed-model ANOVA analysis are given.

612

613 **Supplementary Information:**

614

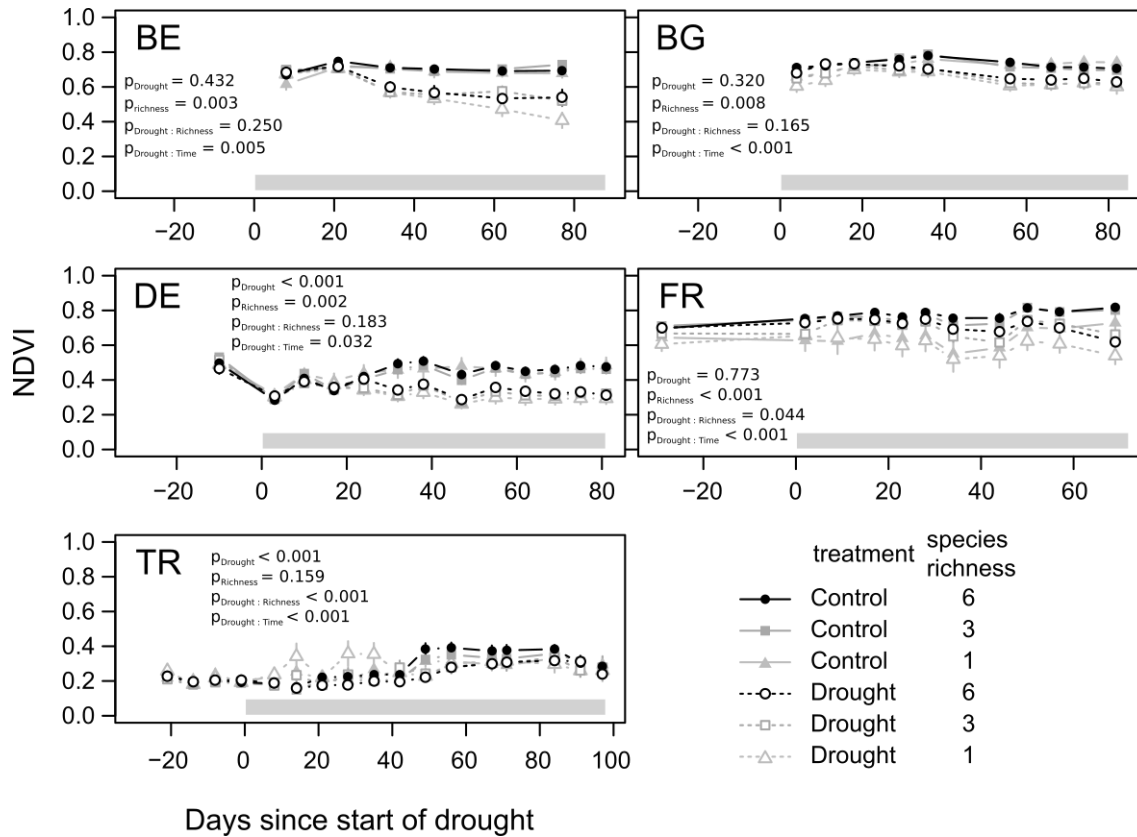


615

616 Figure S1: Biomass (median and quartiles, n=12 per point) produced before drought (harvest
 617 B₀), during the drought until the end of the drought period (harvest B₁), and in the following
 618 year (harvest B₃) for each site.

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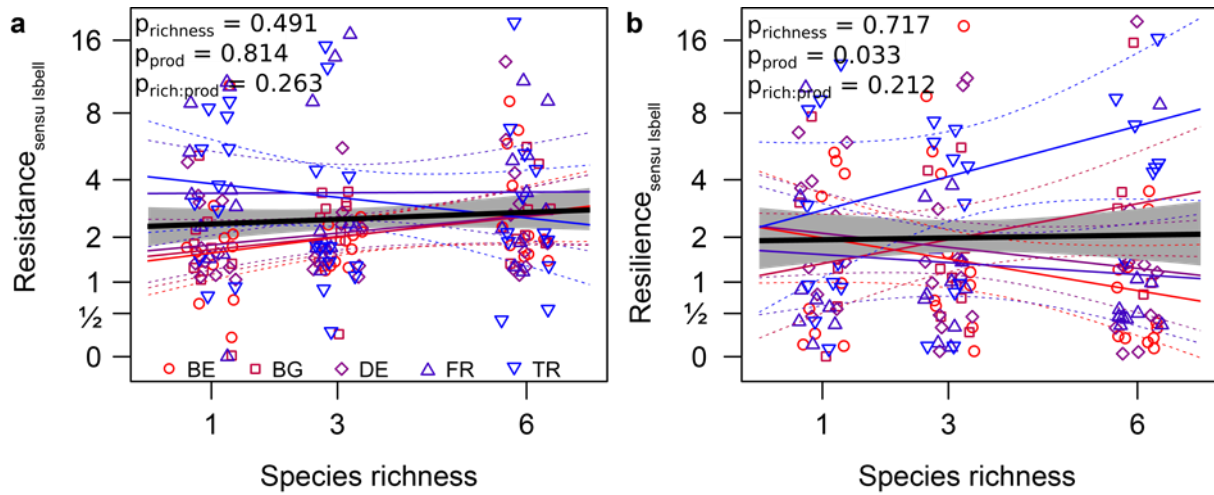
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622 Figure S2: The drought treatments increased senescence at all sites as indicated by significant
623 treatment by time interactions (mixed models ANOVA with fixed effects as specified in the
624 figures and treatment block and time as random effects accounting for the block design and the
625 repeated measures). NDVI is the Normalized Differenced Vegetation Index measured by
626 handheld sensors (“Greenseeker”, Trimble, CA, USA) at each mesocosm ranging from 0 (no
627 green cover) to 1 (abundant and healthy plant cover).

628



629

$$Resistance_{sensu\ Isbell} = \frac{(B_1)_{Control}}{|(B_1)_{Drought} - (B_1)_{Control}|}$$

630

$$Resilience_{sensu\ Isbell} = \frac{|(B_1)_{Drought} - (B_1)_{Control}|}{|(B_3)_{Drought} - (B_3)_{Control}|}$$

631 Figure S3: Resistance and resilience *sensu* Isbell et al. (2015) are not affected by species richness. Black
 632 solid lines are the mixed-effects model fits with their respective p-value, grey shade represent their 95%
 633 confidence intervals. Values on the y-axis are unitless. X-axis values are jittered around the applied levels
 634 of species richness to improve visibility of single points. Colors code the single sites with their respective
 635 linear model fits (solid lines) and 95% confidence intervals (dotted lines). Note that no single-site linear
 636 model yielded statistical significance. The resistance *sensu* Isbell et al. (2015) equals 1 for no resistance
 637 and runs to positive infinite and is undefined for complete resistance. The resilience *sensu* Isbell et al.
 638 (2015) is infinite towards complete resilience, i.e. when biomass production of the drought treatment
 639 approaches control levels in the following year. It is generally larger when the immediate drought effect
 640 is bigger. Note that the approach by Isbell et al. (2015) penalizes overcompensation (identical values if
 641 biomass production drops to 50% during the drought and then reaches 75% or 125%, respectively, in the
 642 following year). We would like to stress that overcompensation in the year after drought, one of the
 643 major findings of our study, cannot be detected by the resilience index of Isbell et al. (2015).

644 Our study design focused on the direct comparison between drought and control over time, i.e. it
645 controls for unavoidable and potentially confounding effects of biotic (ontogeny, natural succession,
646 etc.) and/or environmental change over time (climatic variability, atmospheric deposition, etc.) that are
647 unrelated to the drought treatment (see Figure 2). This issue is particularly important for non-
648 equilibrium systems. The direct comparison to control conditions over time solves the problem of
649 potentially confounding effects and non-equilibrium, and therefore allows for the causal analysis of the
650 treatment effect (here: the drought effect). Unfortunately, such controlled designs are rare in the
651 diversity- stability context. A direct comparison to indices commonly used in time series is therefore
652 limited by the fact that we differ in our definition of “expected ecosystem productivity during normal
653 years (mean across all non-climate event years)” as used in Isbell *et al.* (2015; please consider that this
654 comparison among years implies rather strong assumptions about equilibrium). Here, we instead provide
655 the productivity of the respective control plots, which is uncritical for resistance *sensu* Isbell *et al.* (2015)
656 as this metric only focuses on one point in time, in our case immediately after drought. However, this is
657 problematic for resilience *sensu* Isbell *et al.* (2015), as then the expected productivity is entered in the
658 numerator and in the denominator of the ratio. For the numerator, though, the comparison to the
659 control during the event year and for the denominator the comparison to the control of the year after
660 the event year would logically make sense. Those two control values will differ and thereby affect the
661 outcome of the index while they are identical in the original application by Isbell *et al.* (2015). The results
662 are therefore not directly comparable.

663 Table S1: Target species per functional group and site. Species ID defines the occurrences of the
 664 species in the general experimental design. If available, strategy type according to Grime's CSR
 665 triangle is provided based on Klotz *et al.* (2002) as competitors (C), ruderals (R), stress –
 666 tolerators (S), and their respective combinations, retrieved from the database www.biolflor.de.

Species ID	functional group	BE	BG	DE	FR	TR
1	grass	<i>Anthoxanthum odoratum</i> CSR	<i>Festuca pratensis</i> C	<i>Agrostis capillaris</i> CSR	<i>Festuca arundinacea</i> C	<i>Taeniatherum caput-medusae</i>
2	grass	<i>Festuca rubra</i> agg. C	<i>Cynosurus cristatus</i> CSR	<i>Anthoxanthum odoratum</i> CSR	<i>Trisetum flavescens</i> CSR	<i>Poa timoleontis</i>
3	grass	<i>Dactylis glomerata</i> C	<i>Arrhenatherum elatius</i> C	<i>Arrhenatherum elatius</i> C	<i>Poa pratensis</i> C	<i>Bromus scoparius</i>
4	grass	<i>Holcus lanatus</i> C	<i>Holcus lanatus</i> C	<i>Festuca rubra</i> agg. C	<i>Dactylis glomerata</i> C	<i>Aegilops columnaris</i>
5	forb	<i>Stellaria graminea</i> CS	<i>Lactuca saligna</i> CR	<i>Plantago lanceolata</i> CSR	<i>Cerastium fontanum</i> CSR	<i>Erodium cicutarium</i> R
6	forb	<i>Ranunculus acris</i> C	<i>Prunella vulgaris</i> CSR	<i>Hypochaeris radicata</i> CSR	<i>Plantago lanceolata</i> CSR	<i>Scandix pecten-veneris</i> R
7	forb	<i>Rumex acetosa</i> C	<i>Plantago lanceolata</i> CSR	<i>Knautia arvensis</i> C	<i>Knautia arvensis</i> C	<i>Plantago lagopus</i>
8	forb	<i>Epilobium hirsutum</i> C	<i>Sanguisorba officinalis</i> CS	<i>Leontodon autumnalis</i> CSR	<i>Taraxacum officinale</i> agg. CSR	<i>Crepis foetida</i> CR
a	legume	<i>Trifolium pratense</i> C	<i>Lotus corniculatus</i> CSR	<i>Trifolium pratense</i> C	<i>Lotus corniculatus</i> CSR	<i>Lupinus angustifolius</i> CR
b	legume	<i>Vicia sativa</i> CR	<i>Vicia grandiflora</i> CR	<i>Trifolium dubium</i> R	<i>Trifolium pratense</i> C	<i>Onobrychis caput-galli</i>
c	legume	<i>Lotus corniculatus</i> CSR	<i>Medicago lupulina</i> CSR	<i>Lotus corniculatus</i> CSR	<i>Vicia hirsuta</i> R	<i>Hymenocarpus circinnatus</i>
d	legume	<i>Trifolium dubium</i> R	<i>Trifolium pratense</i> C	<i>Vicia hirsuta</i> R	<i>Trifolium repens</i> CSR	<i>Coronilla parviflora</i>

667 Klotz, S., Kühn, I. & Durka, W. (2002). BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der
 668 Gefäßpflanzen in Deutschland, Schriftenreihe für Vegetationskunde 38. Bundesamt für Naturschutz, Bonn.

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670 Table S2: Experimental design of the biodiversity treatment testing for the effects of species
671 richness and also allowing for quantification of the effect of legume presence and functional
672 group richness (FGR). Numbers show unique species compositions over all five sites. Note that
673 each of these unique species compositions occurred once in the drought treatment and once
674 under control conditions.

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Species richness	FGR = 1	FGR = 2	FGR = 3	Legumes present	Total n
1	60	-	-	20	60
3	15	30	15	40	60
6	-	30	30	40	60

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