

1 **Increased sensitivity to climate change in disturbed ecosystems**

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31

32 **Title**  
33 **Increased sensitivity to climate change in disturbed ecosystems**  
34

35 **Abstract**

36 Human domination of the biosphere includes changes to disturbance regimes, which push  
37 many ecosystems towards early-successional states. Ecological theory predicts that early-  
38 successional ecosystems are more sensitive to perturbations than mature systems, but little  
39 evidence supports this relationship for the perturbation of climate change. Here we show that  
40 vegetation (abundance, species richness, species composition) across seven European  
41 shrublands is quite resistant to moderate experimental warming and drought, and  
42 responsiveness is associated with the dynamic state of the ecosystem, with recently disturbed  
43 sites responding to treatments. Furthermore, most of these responses are not rapid (2-5 years)  
44 but emerge over a longer term (7-14 years). These results suggest that successional state  
45 influences the sensitivity of ecosystems to climate change, and that ecosystems recovering  
46 from disturbances may be sensitive to even modest climatic changes. A research bias towards  
47 undisturbed ecosystems might thus lead to an underestimation of the impacts of climate  
48 change.

49

50 **Introduction**

51 In climate change experiments, the vegetation at a study site is typically viewed as a system  
52 that is stable or close to equilibrium. A common objective is to assess whether a climatic  
53 treatment can push the system away from this hypothesized stable state. Most ecosystems,  
54 however, are not in equilibrium. Rather, they change over time, and are often recovering from  
55 past disturbances<sup>1</sup>. This is particularly true today, as increasing human domination of the  
56 biosphere<sup>2</sup> pushes many ecosystems towards a more dynamic, early successional state.  
57 Although Odum<sup>3</sup> suggested in 1969 that early-successional ecosystems are more sensitive to

58 perturbation than late-successional ones, this feature of ecosystems is rarely taken into  
59 account in climate change research. Single-site climate change experiments have reported that  
60 disturbed or recovering systems were sensitive to climate manipulations<sup>4,5</sup>, but it remains  
61 unclear whether an ecosystem's dynamic state determines its sensitivity to climatic changes.  
62 Grime et al.<sup>4</sup> found that a stable, late-successional grassland was more resistant to the same  
63 climatic manipulations than a dynamic, early-successional grassland. Several authors have  
64 suggested that successional state and disturbance history could modulate responses to climatic  
65 change<sup>6,7</sup>, but a lack of data has prevented direct investigations of these relationships.

66

67 In addition to experimental field manipulation of climatic conditions, two other major field-  
68 based approaches can assess the effects of climate change on ecosystems: long-term  
69 observations<sup>8,9</sup> and multi-site and gradient studies across climatically different regions<sup>10,11</sup>.  
70 Each approach has its own merits and limitations<sup>7,12</sup>, but the combination of these approaches  
71 can be particularly valuable. For example, contrasting results from experiments conducted in  
72 different climatic regions may highlight shifting sensitivities, such as a positive warming  
73 effect on aboveground biomass in cold regions and negative effects in water-limited  
74 regions<sup>13,14,15</sup>. Also, long-term experiments have often detected an altered pattern of response  
75 over time, including linear increases<sup>16</sup>, dampening<sup>17,18</sup>, and reversals<sup>19,20</sup>. Despite the added  
76 value of combined approaches, long-term multi-site experiments are rare.

77

78 Shrublands constitute an important component of global and European terrestrial  
79 vegetation<sup>21,22</sup>, provide multiple ecosystem services<sup>23</sup> and are strongly affected by ongoing  
80 environmental changes. The encroachment of shrubs has been observed in many arid and  
81 semiarid regions of the world, mostly attributed to changes in land use<sup>24</sup>. Expanding  
82 shrublands and other types of woody vegetation have been estimated to be among the largest

83 carbon sinks in the US<sup>25</sup>. As long-lived woody plants, shrubs differ from herbaceous plants in  
84 their life history, ecophysiology, biomass allocation, and sensitivity to disturbance, suggesting  
85 a potentially different sensitivity to changing climate. A global meta-analysis found that  
86 shrubs respond to warming more strongly than other woody and herbaceous plants<sup>13</sup>. All these  
87 considerations suggest that shrubs and shrublands deserve special attention in climate change  
88 impact research.

89

90 Here we investigated the responses of vegetation (abundance, species richness, species  
91 composition) to experimental warming and drought in a standardized field experiment across  
92 seven shrubland sites in Europe over 7-14 years (Fig. 1; Table 1; [www.increase.ku.dk](http://www.increase.ku.dk); UK:  
93 United Kingdom, NL: The Netherlands, DK-M and DK-B: Denmark, HU: Hungary, SP:  
94 Spain, IT: Italy ). Our results show that the studied shrublands are generally quite resistant to  
95 long-term experimental warming and drought, with no across-site responses and few  
96 responses within individual sites. However, sites that respond to treatments are all recovering  
97 from disturbance; vegetation does not respond to treatments in sites that are in a steady state  
98 (as assessed by long-term trend in vegetation abundance in the control plots at each site). This  
99 suggests that sensitivity to climate change may be related to the successional state of  
100 ecosystems, and that ecosystems recovering from disturbances may be sensitive to even  
101 modest climatic changes.

102

## 103 **Results**

104 **Responses to warming and drought treatments.** Neither warming nor drought affected total  
105 vegetation abundance or species richness across all sites averaged after 7-14 years of  
106 experimental manipulation (long-term responses) (Figs. 2 and 3). We found that, across sites,  
107 the change in vegetation composition was marginally affected by both warming ( $p=0.061$ ;

108 Fig. 4a) and drought ( $p=0.072$ ; Fig. 4b). Within the individual sites, warming decreased  
109 species richness at SP but had no significant effect on the other vegetation parameters at any  
110 of the sites (Figs. 2a, 3a, 4a). Drought decreased total cover at NL ( $p=0.02$ ; Fig. 2b) and  
111 species richness at SP ( $p=0.001$ ; Fig. 3b). Drought also induced a greater vegetation change at  
112 DK-M ( $p=0.011$ ) and SP ( $p=0.044$ ) than in the respective control plots (Fig. 4b).

113

114 We found even fewer responses when we performed the same set of analyses for years 2-5  
115 after onset of the experimental manipulation (short-term responses) (Supplementary Figs. 1-  
116 3). Warming increased total vegetation abundance at the cross-site level ( $p=0.035$ ;  
117 Supplementary Fig. 1), but this effect disappeared in the long term (Supplementary Fig. 4a).  
118 The only individual-site level response to appear over the short term occurred at SP, where  
119 drought reduced species richness ( $p=0.011$ ). In the four additional site-level variables that  
120 displayed long-term (but not short-term) responses, effect sizes increased over time  
121 (Supplementary Fig. 4).

122

123 **The effect of the dynamic state on vegetation sensitivity.** To quantify the dynamic state of  
124 the sites, we investigated the change in vegetation abundance in the control plots during the  
125 study period. Total vegetation abundance significantly increased over time in the control plots  
126 at NL (6.3% per year;  $p<0.01$ ), SP (3.8% per year;  $p<0.01$ ) and DK-M (2.7% per year;  
127  $p<0.01$ ), but did not change significantly at the other four sites (Fig. 5). The climatic  
128 manipulations thus led to significant responses only at sites (NL, SP, and DK-M) that showed  
129 significant successional changes in the control plots. In addition, the dynamic state of the sites  
130 (as assessed by the trend in vegetation abundance in the control plots) was related to treatment  
131 responses of the vegetation (effect sizes of the treatment effects on Bray-Curtis dissimilarity)  
132 for both warming ( $p=0.04$ ) and, marginally, drought ( $p=0.07$ ; Fig. 6). In contrast, these effect

133 sizes of the warming and drought treatments were not related to mean annual temperature  
134 (MAT) ( $p=0.57$  and  $0.97$ , respectively) or mean annual precipitation (MAP) ( $p=0.36$  and  $0.43$ ,  
135 respectively) at the sites.

136

## 137 **Discussion**

138 While the cross-site pattern of responses we found suggested an important and rarely explored  
139 relationship between recovery from disturbance and sensitivity to climate, we found that  
140 vegetation in most sites was resistant to treatments, and site-specific outcomes were  
141 consistent with results from other ecosystems. The negative response of total vegetation  
142 abundance to drought at NL is similar to findings in other studies<sup>4,26</sup>, including a meta-  
143 analysis<sup>10</sup>. Note that vegetation abundance was increasing at this site (Fig. 5), thus the  
144 negative drought effect does not imply a decline but rather a reduced increase. The negative  
145 effect of drought on species richness at SP agrees with other studies in semiarid systems<sup>26</sup>,  
146 and is most likely related to reduced colonisation due to water stress. The fact that  
147 compositional change was the parameter with most of the significant responses (two sites)  
148 suggests that plant community composition is among the most sensitive ecosystem properties  
149 to climatic change, and can respond even when ecosystem characteristics like total vegetation  
150 abundance are unaffected<sup>27</sup>. This fits the pattern previously suggested in a hierarchical  
151 response framework<sup>28</sup>.

152

153 Most responses detected in the long term (7-14 years) were not present in the short term (2-5  
154 years), and effect sizes increased over time. Although an increasing effect size over time has  
155 been found before<sup>16</sup>, another study<sup>17</sup> lists examples of effects fading within ten years due to  
156 acclimation, species re-ordering, or new limiting factors. It has also been found that short-

157 term changes in community composition can be reversed within a few years due to species  
158 interactions<sup>19,20</sup>. This volatility highlights the risk in basing conclusions on short-term studies.

159

160 Although we found a few site-level responses, the overall resistance of the studied shrublands  
161 to 7-14 years of experimental warming and drought is noteworthy. Resistance to long-term  
162 climatic manipulation has been reported for various ecosystems, such as arctic tundra<sup>29</sup>, tall-  
163 grass steppe<sup>30</sup>, calcareous grassland<sup>31</sup>, and arid shrubland<sup>32</sup>, indicating a generally widespread  
164 ecosystem resistance to climatic change.

165

166 The lack of responses to experimental climate change observed in our shrubland ecosystems  
167 may be related to the relatively moderate treatment regimes applied (an average 0.43 K  
168 increase in temperature and 22% reduction in annual precipitation). However, our treatments  
169 are in line with recently observed decadal changes (0.13 K warming<sup>33</sup>) at a multi-decadal (50  
170 years) timescale and are similar to treatments in many other climate change experiments<sup>6,13,19</sup>.

171 Although the treatments are not that strong, consistent moderate warming and drought for 8-  
172 14 years may be an extreme situation, which is supported by the finding that most responses  
173 emerged only in the long run. Experiments that impose larger treatment magnitudes have a  
174 greater chance to exceed thresholds and thus may provide important insights into ecosystem  
175 sensitivity, but are also more likely to have artefacts. For example, both modelling<sup>34</sup> and  
176 experimental studies<sup>35</sup> show that an unrealistic abrupt change in CO<sub>2</sub> concentration  
177 overestimates ecosystem sensitivity compared to a gradual change to the same level. Mild  
178 treatments, on the other hand, may not immediately push the environment beyond observed  
179 levels of inter-annual variation, but may allow the detection of effects that accumulate slowly  
180 or result from interacting factors. In our case, the relatively mild treatments allowed us to

181 detect differences in sensitivity that seem to be related to successional states and disturbance  
182 events.

183

184 All sites that responded to the treatments had vegetation that was increasing in abundance  
185 following a disturbance. NL was recovering from a previous cutting-management  
186 intervention, SP was recovering from a fire prior to the start of the experiment, and DK-M  
187 was affected by a severe outbreak of heather beetles (and consequent mowing) during the first  
188 study year (1999). The observed treatment effects at these sites suggest an altered recovery in  
189 the drought plots compared to the control plots. In contrast, at the four sites that did not  
190 respond to treatments, vegetation abundance did not change over time, suggesting that the  
191 vegetation was in a relatively steady state. These results indicate that the dynamic state of  
192 ecosystems may be an important predictor of sensitivity to climate change.

193

194 Disturbances are likely to modulate ecosystem responses to climatic change because different  
195 life stages of individual plants and successional stages of plant communities differ in their  
196 sensitivity to environmental conditions (e.g., drought stress). Regeneration of the previously  
197 dominant vegetation after a disturbance can be affected by a climatic change that would  
198 hardly affect established mature vegetation because early life stages of plants are often more  
199 sensitive to environmental changes than mature plants<sup>36,37,38</sup>. Changing environmental  
200 conditions may not directly lead to an ecosystem state shift, but may just reduce the resilience  
201 of an ecosystem (ability to recover from a perturbation), thus making it more prone to state  
202 shift, but only when disturbed<sup>39,40</sup>. This implies that the resistance of some ecosystems to  
203 long-term and severe manipulations of climatic factors, such as a 3 K increase in  
204 temperature<sup>31</sup> or a 30% decrease/increase in precipitation<sup>32</sup>, does not necessarily hold after the  
205 occurrence of a major natural or anthropogenic disturbances. The results of our study hint that



206 climatic change reduces the resilience of the studied shrubland ecosystems, even though the  
207 imposed treatments had few effects in the absence of disturbances.

208

209 The results of this study highlight the potential importance of successional state, which has  
210 mostly been overlooked in climate change studies. There are several important implications  
211 for the planning and interpretation of climate-change impact research. The sensitivity of an  
212 ecosystem to climatic change is likely to be critically determined by its ability to recover after  
213 a disturbance. This implies, that new experiments should account for site history and quantify  
214 successional state or should ideally deliberately include disturbances in the experimental set-  
215 up. In addition, meta-analyses should include the dynamic state of study systems. Finally,  
216 researchers should recognize that many results from climate change experiments to date come  
217 from relatively stable near-natural ecosystems<sup>6,7,13</sup>; disturbed, early-successional systems are  
218 often avoided. This bias towards relatively stable ecosystems, coupled with the short time  
219 frame covered by most studies may lead to a broad underestimation of ecosystem sensitivity  
220 to climate change.

221

222 **Methods**

223 **Study sites.** We studied seven sites (Fig. 1) that spanned different climatic regions within  
224 Europe (Table 1). MAT at the sites ranged from 7.4 to 16.1 °C, and MAP ranged from 544 to  
225 1263 mm (Table 1). The sites contained the major types of shrubland that occur in temperate  
226 Europe: Atlantic heathland (UK - United Kingdom, NL - The Netherlands, DK-M, and DK-B  
227 - Denmark), continental forest steppe (HU - Hungary), and Mediterranean machia/garrigue  
228 (SP - Spain and IT - Italy). The sites were established in 1998 (UK, NL, DK-M, and SP),  
229 2001 (HU and IT), or 2004 (DK-B). We used climatic data recorded in the control plots of  
230 each experimental site to obtain the climate characteristics of each site. The treatment effect at  
231 each site was calculated as the average difference in measured temperature, precipitation, and  
232 soil moisture between control and treatment plots.

233

234 **Experimental manipulations.** We used the same experimental technology for the three  
235 treatments (warming, drought, and control) at each study site. The warming plots received  
236 passive warming at night; the plots were automatically covered with curtains that reflected  
237 outgoing radiation after sunset<sup>41</sup>. The warming curtains were automatically withdrawn during  
238 rain events. The night-time warming approach is in accordance with reports that in the  
239 ongoing global warming there is a higher rate of warming during the night than during the  
240 day<sup>42</sup>. A study comparing different methods concluded that the passive night-time warming  
241 approach is one of the most realistic and applicable<sup>43</sup>. Although the warming effect obtained  
242 with this technique is greatest during the night, there is also some carry-over effect into the  
243 day<sup>44</sup>. The warming treatment was applied year-round and resulted in an average temperature  
244 increase of 0.43 K (range: 0.2-0.9 K, Table 2). This is relatively modest but is in line with  
245 observed past changes<sup>33</sup> at a multi-decadal (50 years) time scale.

246 During rain events, transparent waterproof sheets automatically covered the drought plots,  
247 excluding the rain. Note that these sheets covered the drought plots only for the duration of  
248 the rain events, thus avoiding warming effects<sup>41</sup>. The timing and duration of the experimental  
249 drought differed among the sites, dependent on seasonality and regional climatic predictions  
250 (Table 2). We excluded an average of 22% of precipitation (range: 8-49%, Table 2), and rain  
251 exclusion resulted in an average soil moisture decline of 36% (range 23-47%, Table 2) by the  
252 end of the drought periods. Control plots had the same metallic scaffolding as the treated  
253 plots, but without curtains and sheets. Each treatment had three replicate 20 m<sup>2</sup> plots except at  
254 DK-B, which had six replicates and a plot size of 9.1 m<sup>2</sup>. Replicate numbers were limited by  
255 logistical and financial constraints associated with such complex field experiments. Replicates  
256 were grouped in blocks consisting of a control, a warming, and a drought plot. There was no  
257 blocking of control and warming plots at the NL site.

258

259 **Sampling of vegetation.** We used the point-intercept method to measure plant cover and  
260 composition. At each site, 300 permanent positions were sampled per plot per sampling year,  
261 except for DK-M (200 positions) and DK-B (50 positions per plot in six replicate plots). The  
262 points were arranged either along lines (HU, SP, IT, and NL) or in grids per experimental plot  
263 (DK-M, DK-B, and UK). Vegetation sampling was conducted at least 50 cm from the plot  
264 edge to avoid edge effects. Pin hits for all vascular plant species were recorded. Only the first  
265 hit was recorded at IT where the vegetation was open. The vegetation was sampled annually  
266 following the start of the experiments, but the sampling years varied subsequently: UK: 1998-  
267 2000, 2002-2003, and 2007-2012; NL: 1998-2003, 2005, 2008, 2009, and 2012; DK-M: 1998-  
268 2001, 2003, 2006, and 2009-2012; DK-B: 2004 and 2006-2012; HU: 2001-2012; SP: 1999-  
269 2012; and IT: 2001-2004 and 2010-2012.

270 We used the number of hits per 100 pins as a proxy for plant or vegetation abundance, as  
271 typical in multi-year climate-change experiments<sup>26</sup> where the experimental plots are too small  
272 for the regular harvesting of biomass.

273

274 **Data analysis.** The cover of vascular plants for years 7-14 was used to assess the mid- to  
275 long-term responses of shrubland plant communities to experimental manipulations. We used  
276 linear mixed models from the *lme4* package<sup>45</sup> in *R*<sup>46</sup> to identify treatment effects on total  
277 cover, species richness, and compositional change. Compositional change was assessed with  
278 the Bray-Curtis dissimilarity<sup>47</sup> of the plant community in a specific year compared to the plant  
279 community at the beginning of the experiment at the same plot (pre-treatment year or first  
280 year at SP). The Bray-Curtis dissimilarity was calculated for each plot in all sampling years  
281 with the *vegdist* function in the *vegan* package<sup>48</sup> in *R*. Values of total cover, species richness,  
282 and compositional change were averaged across available years (7-14 for long term responses  
283 and 2-5 years for short term responses) for each plot to avoid temporal pseudo-replication.  
284 We calculated *p*-values for fixed-effect parameters with an analysis of variance using the  
285 Satterthwaite estimation of the degrees of freedom with the *lmerTest* package<sup>49</sup>. We applied  
286 separate models to analyze the effects of the warming and drought treatments and used *site*  
287 and *site:block* as random factors for the cross-site tests; block was a random factor in the site-  
288 specific analyses (the warming effect in NL was analysed with a linear model, since warming  
289 and control plots were not blocked).

290

291 Data were log-transformed (ln) to obtain normality and homoscedasticity in the cross-site  
292 analyses. NL was excluded from all tests related to species richness and Bray-Curtis  
293 dissimilarity because it only had one vascular plant species.

294

295 We calculated the effect sizes of the treatments as Hedges's  $g^{50}$ :

$$296 \quad g = J \frac{\mu_{\text{treatment}} - \mu_{\text{control}}}{s^*} \quad (1)$$

297 Where  $\mu_{\text{treatment}}$  and  $\mu_{\text{control}}$  are the average values in treatment and control plots.  $s^*$  is the  
298 pooled standard deviation of both control and treatment plots, calculated as follows:

$$299 \quad s^* = \sqrt{\frac{(n_{\text{control}} - 1) \sigma_{\text{control}}^2 + (n_{\text{treatment}} - 1) \sigma_{\text{treatment}}^2}{n_{\text{control}} + n_{\text{treatment}} - 2}} \quad (2)$$

300 Where  $n_{\text{control}}$  and  $n_{\text{treatment}}$  are the number of replicates and  $\sigma_{\text{control}}^2$  and  $\sigma_{\text{treatment}}^2$  are the  
301 variances of control and treatment plots. Finally,  $J$  is a factor to correct for bias (related to  
302 small sample size) in the estimated effect size:

$$303 \quad J \approx 1 - \frac{3}{4(n_{\text{control}} + n_{\text{treatment}}) - 9} \quad (3)$$

304

305 For variables with a significant treatment response in either the short or the long term, we  
306 calculated the effect size over time. The successional status of the various sites was  
307 determined by linear regression of vegetation abundance (relative to the vegetation abundance  
308 at the start of the experiment) in the control plots over time. The slope estimates from these  
309 linear regressions (average annual change) were used as a measure of the dynamic status or  
310 successional trend for each site, with higher values indicating more dynamic vegetation. We  
311 investigated whether the effect size of the variable related to plant community composition  
312 (Bray-Curtis dissimilarity) was related to MAT or MAP or the dynamic status of the sites  
313 with linear regression.

314 All analyses were done in  $R^{46}$ .

315

316

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- 434



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443

444 **Author contributions**

445 C.B. designed the experiment and J.P. designed the vegetation assessment. C.B. and I.K.S.  
446 coordinated the cross-site research, and C.B., I.K.S., B.E., A.T., J.P., P.A., E.K.-L. and G.K.-  
447 D. coordinated the research at individual sites. J.R. performed the data analysis. G.K.-D  
448 coordinated the data synthesis and wrote the manuscript with major input from J.R., I.K.S.,  
449 JSD, and J.P. All authors contributed to data collection, data synthesis, and final manuscript  
450 writing.

451

452 **Additional information**

453 Supplementary information is available in the online version of the paper ...

454

455 **Competing financial interest**

456 The authors declare no competing financial interests.

457

458

459 **Figure legends:**

460

461 **Figure 1: Location of the climatic manipulation experiments in Europe.** Arrows depict  
462 broad-scale gradients in precipitation and temperature. DK-B, Denmark at Brandbjerg; DK-  
463 M, Denmark at Mols; HU, Hungary; IT, Italy; NL, Netherlands; SP, Spain; UK, United  
464 Kingdom.

465

466 **Figure 2: Change in vegetation abundance in response to treatments.** Total vegetation  
467 abundance at the seven sites 7-14 years after the start of the experiments in the warming (**a**)  
468 and drought (**b**) treatments. \* indicates a significant difference ( $p<0.05$ ) between treated and  
469 control plots; linear mixed model (mean  $\pm$ SE,  $n=3$ ).

470

471 **Figure 3: Change in species richness in response to treatments.** Species richness at six  
472 sites 7-14 years after the start of the experiments in the warming (**a**) and drought (**b**)  
473 treatments. \* ( $p<0.05$ ) and \*\* ( $p<0.01$ ) indicate significant differences between treated and  
474 control plots; linear mixed model (mean  $\pm$ SE,  $n=3$ ). NL was omitted from this analysis due to  
475 its single-species vegetation.

476

477 **Figure 4: Change in vegetation composition in control and treated plots.** Bray-Curtis  
478 dissimilarity between pre-treatment year and 7-14 years after the start of the experiments in  
479 the warming (**a**) and drought (**b**) treatments. \* indicates a significant difference ( $p<0.05$ )  
480 between treated and control plots; linear mixed model. NL was omitted from this analysis due  
481 to its single-species vegetation (mean  $\pm$  SE,  $n=3$ ).

482

483 **Figure 5: Change in total cover in the control plots over the experimental period.**

484 Average annual change in total cover (TC) in the control plots during the study period,

485 estimated by linear regression of TC over time (\*\*  $p < 0.01$ ). Yearly cover change is expressed  
486 relative to the cover of the pre-treatment year (% of pre-treatment year cover). Error bars are  
487 the standard errors of the estimated trends (n differs per country and ranges from three  
488 replicates times seven years (21 data points) to three replicates times 15 years (45 data  
489 points); see the Methods).

490

491 **Figure 6: Relationships between effect size of vegetation change in response to**  
492 **treatments and successional tendency of the sites.** Relationships between the effect size  
493 (Hedges's  $g$ ) of warming (**a**) and drought (**b**) effects on changes in vegetation composition  
494 relative to the start of the experiment (assessed by Bray-Curtis dissimilarity) and the  
495 successional tendency (calculated as the trend in total cover (relative to pre-treatment total  
496 cover) in the control plots). The  $p$ -values represent the significance of the linear regressions.

497

498 **Table 1: Characteristics of the study sites.**

Site code	UK	NL	DK-B	DK-M	HU	SP	IT
Country	United Kingdom	The Netherlands	Denmark	Denmark	Hungary	Spain	Italy
Site name	Cloacaenog	Oldebroek	Brandbjerg	Mols	Kiskunság	Garraf	Capo Caccia
Coordinates	53°03'N	52°24'N	55°53'N	56°23'N	46°53'N	41°18'N	40°36'N
	3°28'W	5°55'E	11°58'E	10°57'E	19°23'E	1°49'E	8°9'E
Soil type (FAO)	peaty Podzol	haplic Arenosol	sandy Podzol	sandy Podzol	calcaric Arenosol	petrocalcic Calcixerepts	Luvisol and Leptosol
MAT (°C)	7.4	8.9	9.4	8.7	10.5	15.2	16.1
MAP (mm)	1263	1005	757	669	558	559	544
Growing season	Apr-Sep	Apr-Oct	Apr-Sep	Apr-Sep	Apr-Sep	Jan-May Oct-Dec	Jan-May Oct-Dec
Dominant species	<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i>	<i>Calluna vulgaris</i> <i>Deschampsia flexuosa</i>	<i>Calluna vulgaris</i> <i>Deschampsia flexuosa</i>	<i>Populus alba</i> <i>Festuca vaginata</i>	<i>Erica multiflora</i> <i>Globularia alypum</i>	<i>Cistus monspeliensis</i> <i>Helichrysum italicum</i> <i>Dorycnium pentaphyllum</i>

499 Mean annual temperatures (MATs) and mean annual precipitations (MAPs) apply to the study

500 period (see Table 2). Species with relative cover above 10% in the control plots during the

501 study period are listed as dominant species.

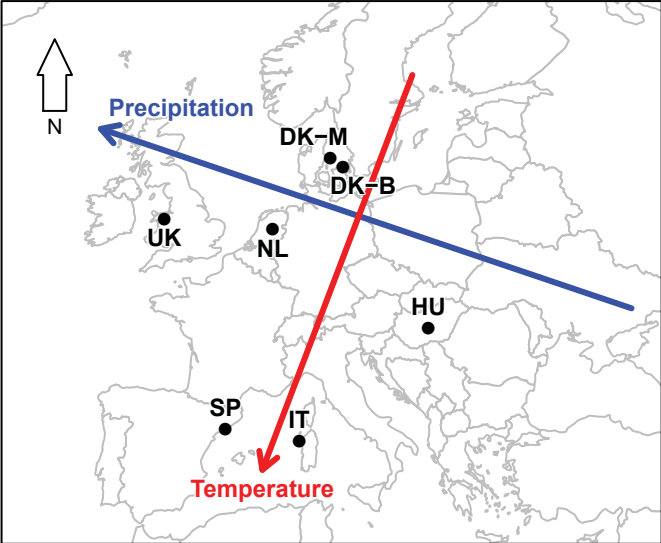
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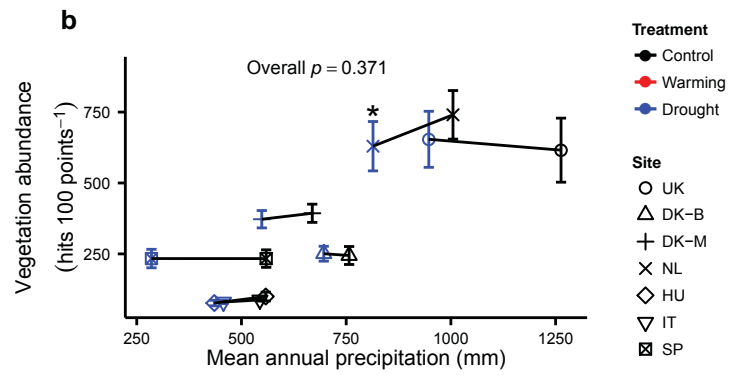
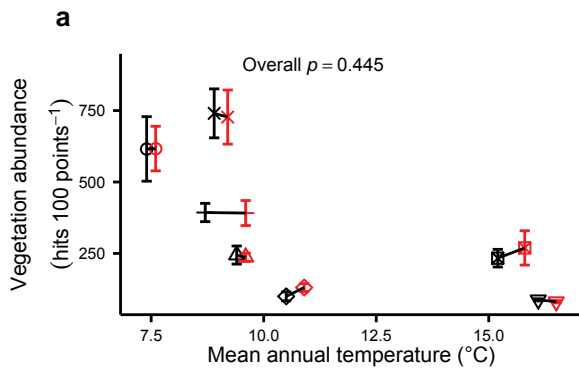
503 **Table 2: Experimental manipulations at the study sites.**

Site code	UK	NL	DK-B	DK-M	HU	SP	IT
Start of the experiment (pre-treatment year)	1998	1998	2004	1998	2001	1998	2001
First treatment year	1999	1999	2006	1999	2002	1999	2002
Drought timing	May-Sep	Apr-Jul	May-Jun	May-Jul	May-Jun	May-Jun, Oct-Nov	Apr-Oct
precipitation excluded (% of yearly total)	25	19	8	18	22	49	16
reduction in soil moisture (% of control, 0-20 cm)	45	43	47	41	23	28	27
Warming timing	year-round	year-round	year-round	year-round	year-round	year-round	year-round
increase in MAT (K)	0.2	0.3	0.2	0.9	0.4	0.6	0.4

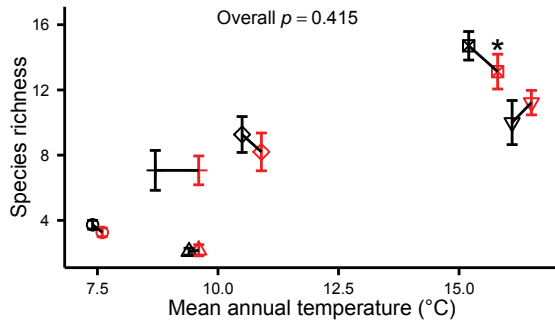
504 Drought and warming effects are averages from the first year of the treatments to 2012. Soil

505 moisture reduction applies to the end of the experimental drought period.

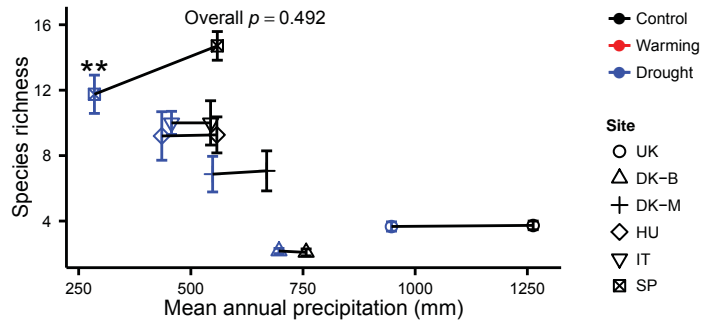




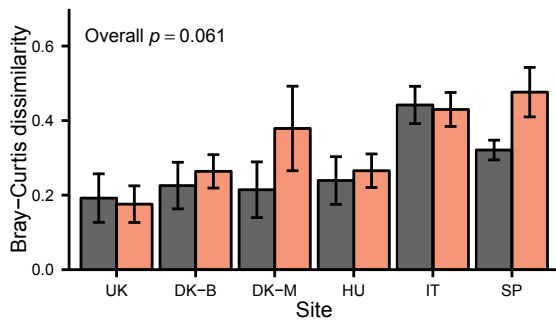
**a**



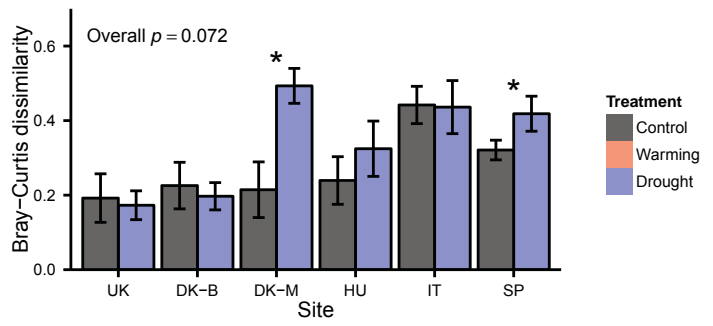
**b**



**a**



**b**



**Treatment**  
Control  
Warming  
Drought



