

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

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3 György Kröel-Dulay^{1,*,#}, Johannes Ransijn^{2,#}, Inger Kappel Schmidt², Claus Beier³, Paolo De
4 Angelis⁴, Giovanbattista de Dato⁴, Jeffrey S. Dukes^{5,6}, Bridget Emmett⁷, Marc Estiarte^{8,9},
5 János Garadnai¹, Jane Kongstad², Edit Kovács-Láng¹, Klaus Steenberg Larsen², Dario
6 Liberati⁴, Romà Ogaya^{8,9}, Torben Riis-Nielsen², Andrew Smith¹⁰, Alwyn Sowerby⁷, Albert
7 Tietema¹¹, Josep Penuelas^{8,9}

8 ¹Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4,
9 Vácrátót, 2163-Hungary

10 ²Univ Copenhagen, Dept Geosci & Nat Resources, DK-1958 Frederiksberg, Denmark

11 ³Center for Catchments and Urban Water Research NIVA, Gaustadalléen 21, NO-0349 OSLO,
12 Norway

13 ⁴Dept. for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Via San
14 Camillo de Lellis, snc - 01100 Viterbo, Italy

15 ⁵Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West
16 Lafayette, IN 47907 USA

17 ⁶Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, IN
18 47907 USA

19 ⁷Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor,
20 Gwynedd, UK, LL57 2UW.

21 ⁸CSIC, Global Ecology Unit, CREAF-CSIC-Universitat Autònoma de Barcelona, Cerdanyola del
22 Vallès 08193, Catalonia, Spain

23 ⁹CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain

24 ¹⁰School of Environment, Natural Resources, and Geography, Bangor University, Deiniol Road,
25 Bangor, Gwynedd, UK, LL57 2UW

26 ¹¹Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94240,
27 1090 GE Amsterdam, The Netherlands

28

29 * Corresponding author; e-mail: kroel-dulay.gyorgy@okologia.mta.hu

30 # These authors contributed equally to this work.

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 disturbances¹. This is particularly true today, as increasing human domination of the
56 biosphere² pushes many ecosystems towards a more dynamic, early successional state.
57 Although Odum³ 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^{4,5}, but it remains
61 unclear whether an ecosystem's dynamic state determines its sensitivity to climatic changes.
62 Grime et al.⁴ 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^{6,7}, 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^{8,9} and multi-site and gradient studies across climatically different regions^{10,11}.
70 Each approach has its own merits and limitations^{7,12}, 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^{13,14,15}. Also, long-term experiments have often detected an altered pattern of response
75 over time, including linear increases¹⁶, dampening^{17,18}, and reversals^{19,20}. 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^{21,22}, provide multiple ecosystem services²³ 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 use²⁴. Expanding
82 shrublands and other types of woody vegetation have been estimated to be among the largest

83 carbon sinks in the US²⁵. 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 plants¹³. 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; 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^{4,26}, including a meta-
143 analysis¹⁰. 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 systems²⁶,
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 unaffected²⁷. This fits the pattern previously suggested in a hierarchical
151 response framework²⁸.

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 before¹⁶, another study¹⁷ 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^{19,20}. 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 tundra²⁹, tall-
163 grass steppe³⁰, calcareous grassland³¹, and arid shrubland³², 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 warming³³) at a multi-decadal (50
170 years) timescale and are similar to treatments in many other climate change experiments^{6,13,19}.

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 modelling³⁴ and
176 experimental studies³⁵ show that an unrealistic abrupt change in CO₂ 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^{36,37,38}. 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^{39,40}. 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 temperature³¹ or a 30% decrease/increase in precipitation³², 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^{6,7,13}; 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 sunset⁴¹. 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 day⁴². A study comparing different methods concluded that the passive night-time warming
241 approach is one of the most realistic and applicable⁴³. Although the warming effect obtained
242 with this technique is greatest during the night, there is also some carry-over effect into the
243 day⁴⁴. 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 changes³³ 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 effects⁴¹. 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 m² plots except at
254 DK-B, which had six replicates and a plot size of 9.1 m². 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 experiments²⁶ 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* package⁴⁵ in *R*⁴⁶ to identify treatment effects on total
277 cover, species richness, and compositional change. Compositional change was assessed with
278 the Bray-Curtis dissimilarity⁴⁷ 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* package⁴⁸ 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* package⁴⁹. 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 μ_{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_{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.

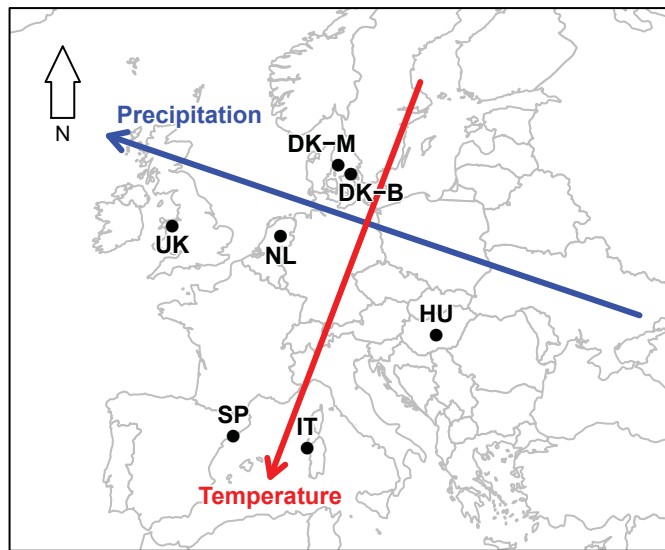
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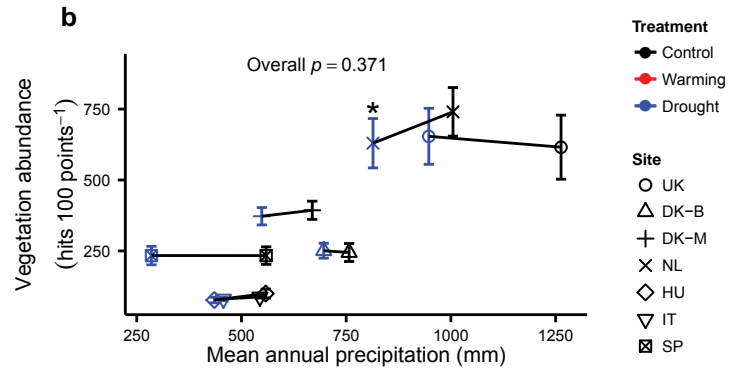
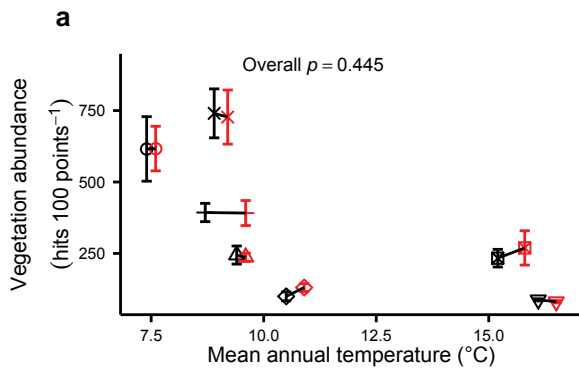
503 **Table 2: Experimental manipulations at the study sites.**

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

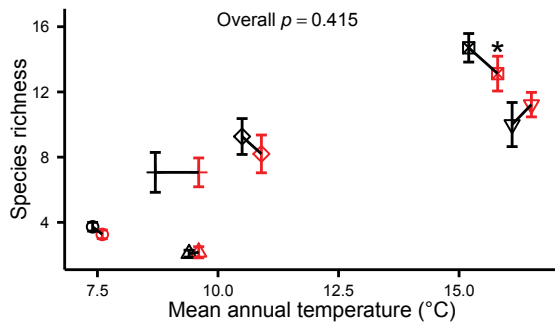
504 Drought and warming effects are averages from the first year of the treatments to 2012. Soil

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

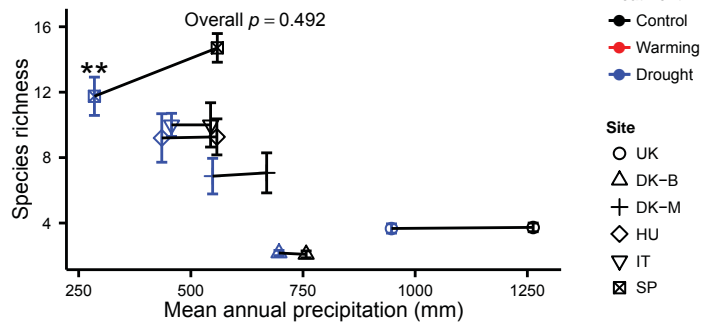




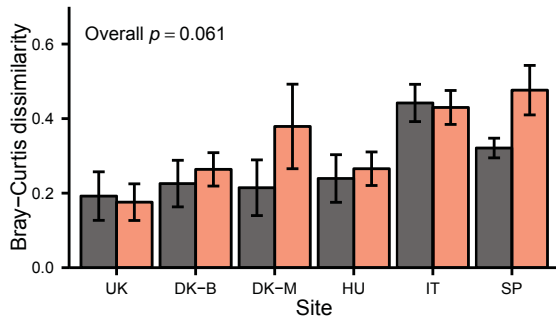
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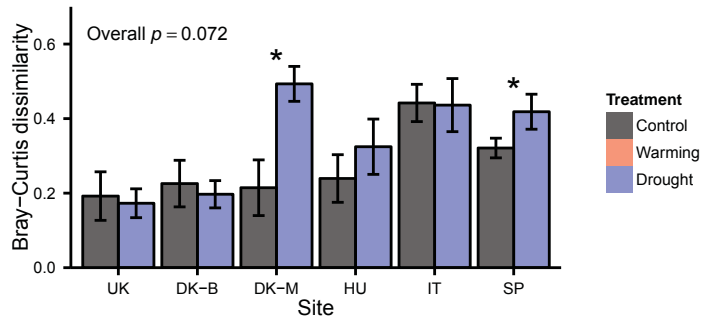
b



a



b



Treatment
Control
Warming
Drought

