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Increased sensitivity to climate change in disturbed ecosystems

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1

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[1]. This is particularly true today, as increasing human domination of the

56 biosphere[2] pushes many ecosystems towards a more dynamic, early successional state.

57 Although Odum[3] 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 increases[16], 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 services[23] 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[24]. Expanding

82   shrublands and other types of woody vegetation have been estimated to be among the largest

83 carbon sinks in the US[25]. 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[13]. 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;

4

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   analysis[10]. 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[26],

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[27]. This fits the pattern previously suggested in a hierarchical

151   response framework[28].

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[16], another study[17] 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 tundra[29], tall-

163   grass steppe[30], calcareous grassland[31], and arid shrubland[32], 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[33]) 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 modelling[34] and

176   experimental studies[35] show that an unrealistic abrupt change in CO_2 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 temperature[31] or a 30% decrease/increase in precipitation[32], 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 sunset[41]. 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[42]. A study comparing different methods concluded that the passive night-time warming

241 approach is one of the most realistic and applicable[43]. 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[44]. 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[33] 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[41]. 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^2 plots except at

254   DK-B, which had six replicates and a plot size of 9.1 m^2. 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[26] 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[45] 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 dissimilarity[47] 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[48] 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[49]. 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     $$g = J \, \frac{\mu_{treatment} - \mu_{control}}{s^*} \tag{1}$$

297   Where $\mu_{treatment}$ and $\mu_{control}$ 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     $$s^* = \sqrt{\frac{(n_{control} - 1) \, \sigma^2_{control} + (n_{treatment} - 1) \, \sigma^2_{treatment}}{n_{control} + n_{treatment} - 2}} \tag{2}$$

300   Where $n_{control}$ and $n_{treatment}$ are the number of replicates and $\sigma^2_{control}$ and $\sigma^2_{treatment}$ 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     $$J \approx 1 - \frac{3}{4 \, (n_{control} + n_{treatment}) - 9} \tag{3}$$

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 where done in R[46].

315

316

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434

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

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 ±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 ±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 ± 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	Clocaenog	Oldebroek	Brandbjerg	Mols	Kiskunság	Garraf	Capo Caccia
Coordinates	53°03′N 3°28′W	52°24′N 5°55′E	55°53′N 11°58′E	56°23′N 10°57′E	46°53′N 19°23′E	41°18′N 1°49′E	40°36′N 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	*Calluna vulgaris*	*Calluna vulgaris*	*Calluna vulgaris Deschampsia flexuosa*	*Calluna vulgaris Deschampsia flexuosa*	*Populus alba Festuca vaginata*	*Erica multiflora Globularia alypum*	*Cistus monspeliensis Helichrysum italicum Dorycnium pentaphyllum*

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

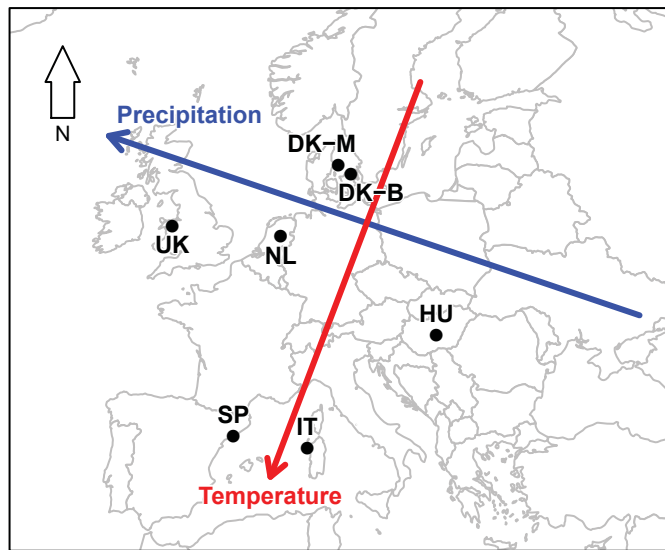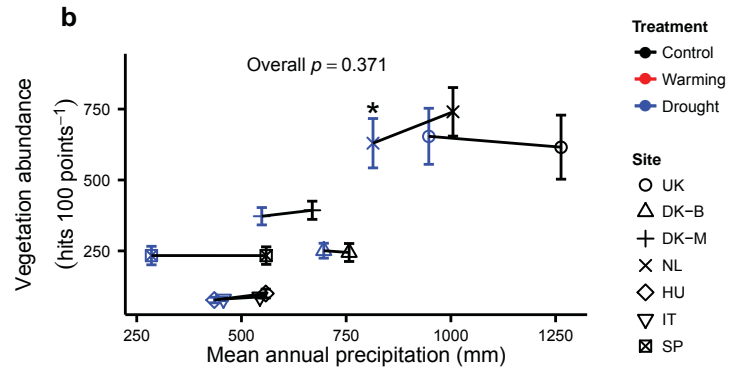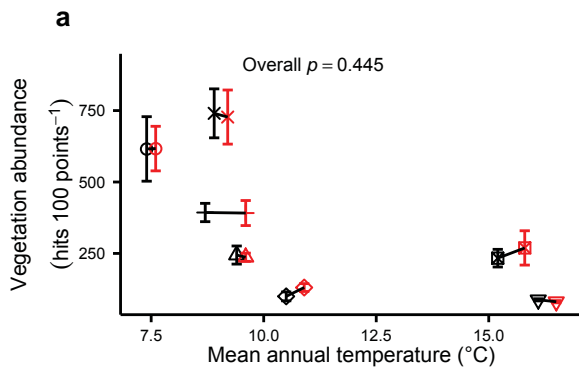501   study period are listed as dominant species.

502

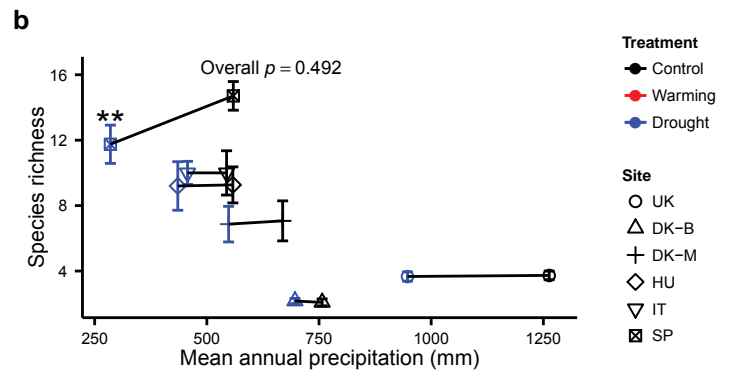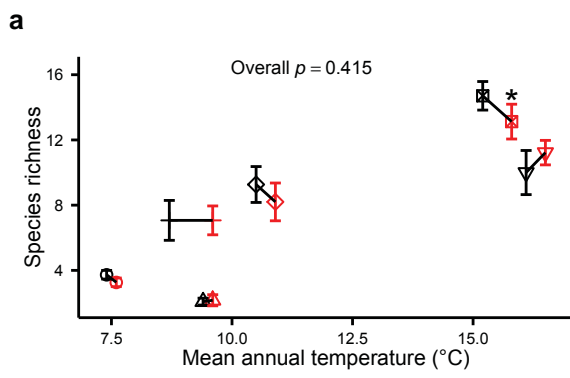503   **Table 2**: **Experimental manipulations at the study sites**.

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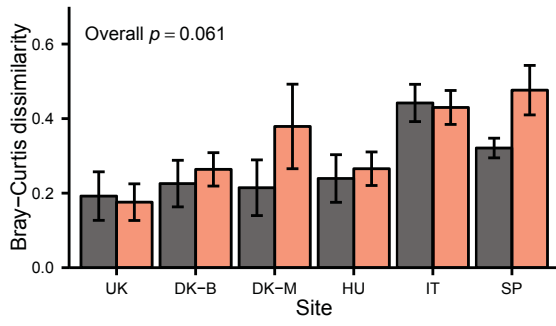
505   moisture reduction applies to the end of the experimental drought period.

a

Overall *p* = 0.415

Species richness

Mean annual temperature (°C)

b

Overall *p* = 0.492

Species richness

Mean annual precipitation (mm)

Treatment
- Control
- Warming
- Drought

Site
- ○ UK
- △ DK–B
- + DK–M
- ◇ HU
- ▽ IT
- ⊠ SP

Trend in vegetation abundance
(% year^{-1})

a

$p = 0.04$ $R^2 = 0.692$

SP

DK−M

DK−B HU

UK

IT

Hedges's *g*

Trend in vegetation abundance in control (%)

b

DK−M

$p = 0.071$ $R^2 = 0.6$

SP

HU

IT

DK−B UK

Hedges's *g*

Trend in vegetation abundance in control (%)