Increased sensitivity to climate change in disturbed ecosystems

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Title

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Abstract

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

Introduction

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

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

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

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

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

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

Results

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

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

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

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

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

Discussion

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

Most responses detected in the long term (7-14 years) were not present in the short term (2-5 years), and effect sizes increased over time. Although an increasing effect size over time has been found before[16], another study[17] lists examples of effects fading within ten years due to 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

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

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

Methods

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

Experimental manipulations. We used the same experimental technology for the three treatments (warming, drought, and control) at each study site. The warming plots received passive warming at night; the plots were automatically covered with curtains that reflected outgoing radiation after sunset[41]. The warming curtains were automatically withdrawn during rain events. The night-time warming approach is in accordance with reports that in the ongoing global warming there is a higher rate of warming during the night than during the day[42]. A study comparing different methods concluded that the passive night-time warming approach is one of the most realistic and applicable[43]. Although the warming effect obtained with this technique is greatest during the night, there is also some carry-over effect into the day[44]. The warming treatment was applied year-round and resulted in an average temperature increase of 0.43 K (range: 0.2-0.9 K, Table 2). This is relatively modest but is in line with 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.

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

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

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

We calculated the effect sizes of the treatments as Hedges's g[50]:

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

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

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

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

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

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

All analyses where done in R[46].

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Acknowledgements

This study was supported by the INCREASE infrastructural project funded by the EC FP7-Infrastructure-2008-1 grant agreement 227628 and by the participating institutions. G.K.-D. was supported by the Hungarian Scientific Research Fund (OTKA K112576), and JP and ME research was supported by Spanish government grant CGL2013-48074-P, Catalan government grant SGR 2014-274, and European Research Council grant ERC-2013-SyG-610028 IMBALANCE-P. We thank all the people that have been involved with the maintenance of the various experimental sites and with the collection of data.

Author contributions

C.B. designed the experiment and J.P. designed the vegetation assessment. C.B. and I.K.S. 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.-D. coordinated the research at individual sites. J.R. performed the data analysis. G.K-D coordinated the data synthesis and wrote the manuscript with major input from J.R., I.K.S., JSD, and J.P. All authors contributed to data collection, data synthesis, and final manuscript writing.

Additional information

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

Competing financial interest

The authors declare no competing financial interests.

Figure legends:

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

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

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

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

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

Table 1: Characteristics of the study sites.

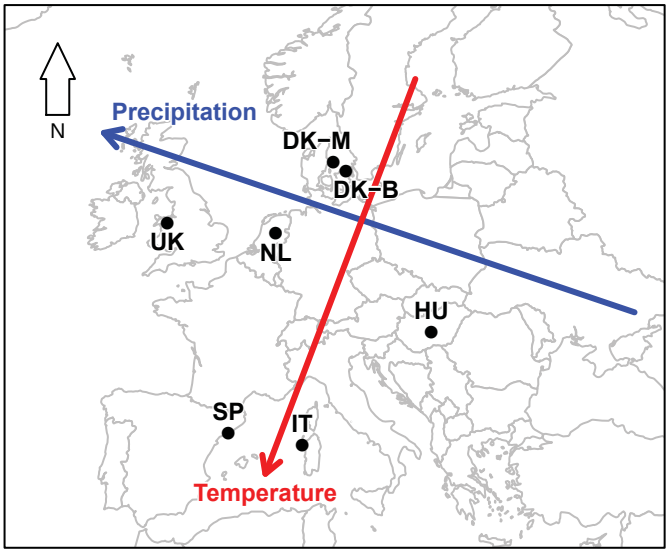
Site code	**UK**	**NL**	**DK-B**	**DK-M**	**HU**	**SP**	**IT**
Country	United Kingdom	The Netherlands	Denmark	Denmark	Hungary	Spain	Italy
Site name	Clocaenog	Oldebroek	Brandbjerg	Mols	Kiskunság	Garraf	Capo Caccia
Coordinates	53°03′N 3°28′W	52°24′N 5°55′E	55°53′N 11°58′E	56°23′N 10°57′E	46°53′N 19°23′E	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*

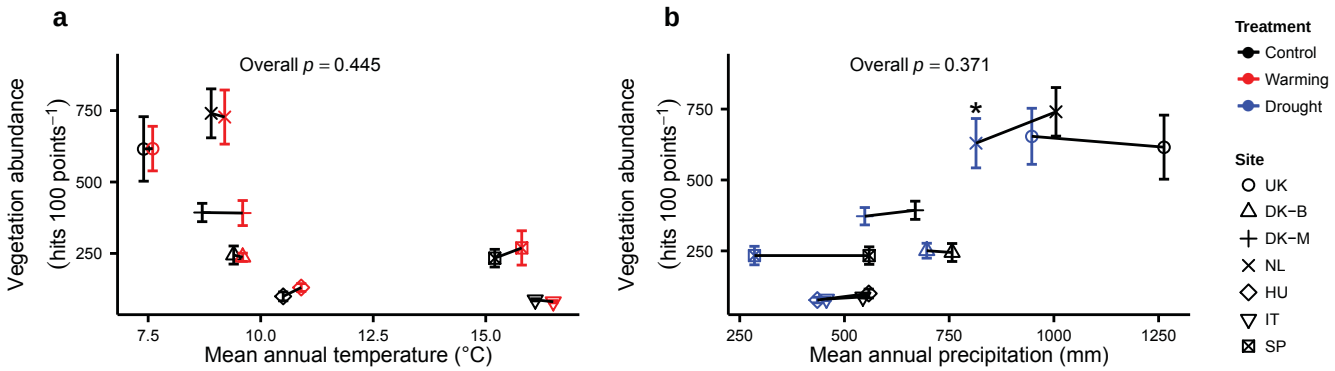
Mean annual temperatures (MATs) and mean annual precipitations (MAPs) apply to the study period (see Table 2). Species with relative cover above 10% in the control plots during the study period are listed as dominant species.

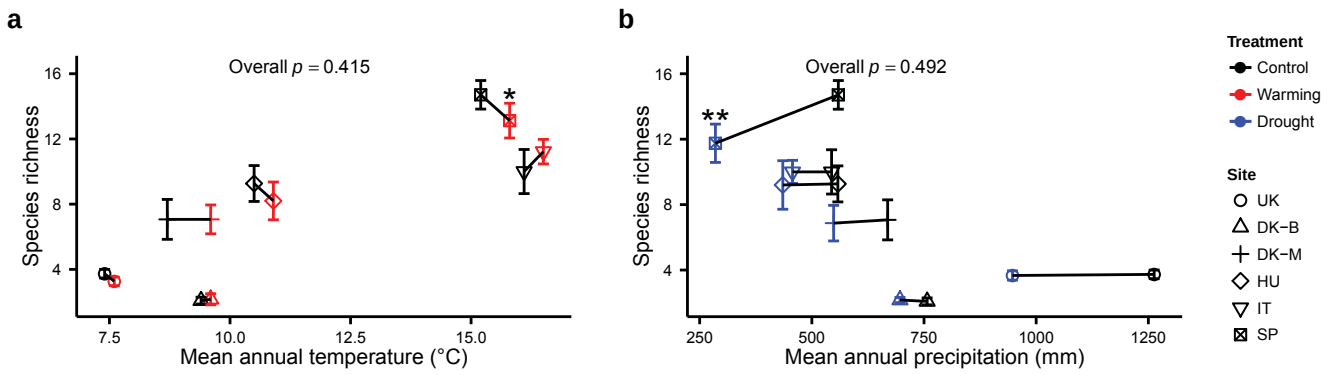
Table 2: **Experimental manipulations at the study sites**.

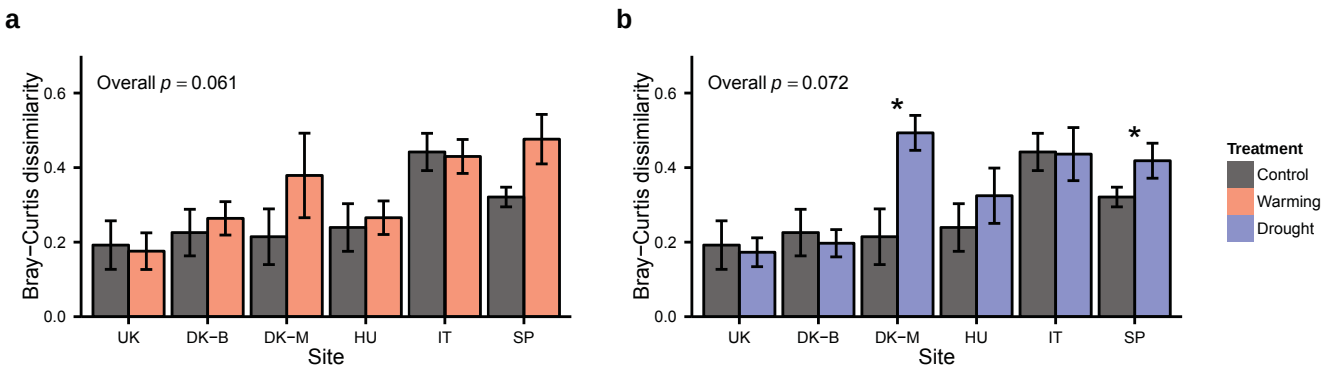
Site code	**UK**	**NL**	**DK-B**	**DK-M**	**HU**	**SP**	**IT**
Start of the experiment (pre-treatment year)	1998	1998	2004	1998	2001	1998	2001
First treatment year	1999	1999	2006	1999	2002	1999	2002
Drought							
timing	May-Sep	Apr-Jul	May-Jun	May-Jul	May-Jun	May-Jun, Oct-Nov	Apr-Oct
precipitation excluded (% 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

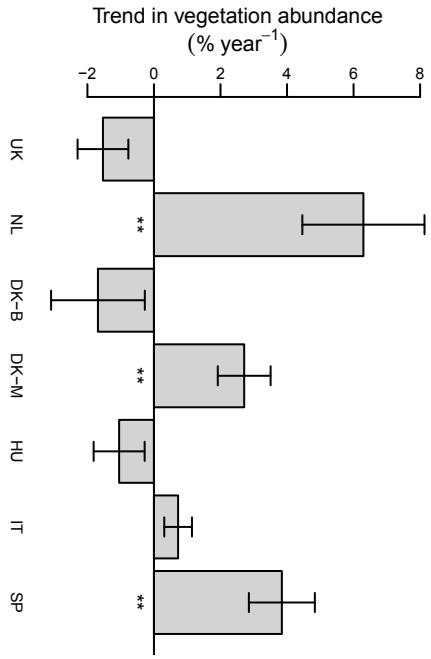
Drought and warming effects are averages from the first year of the treatments to 2012. Soil moisture reduction applies to the end of the experimental drought period.

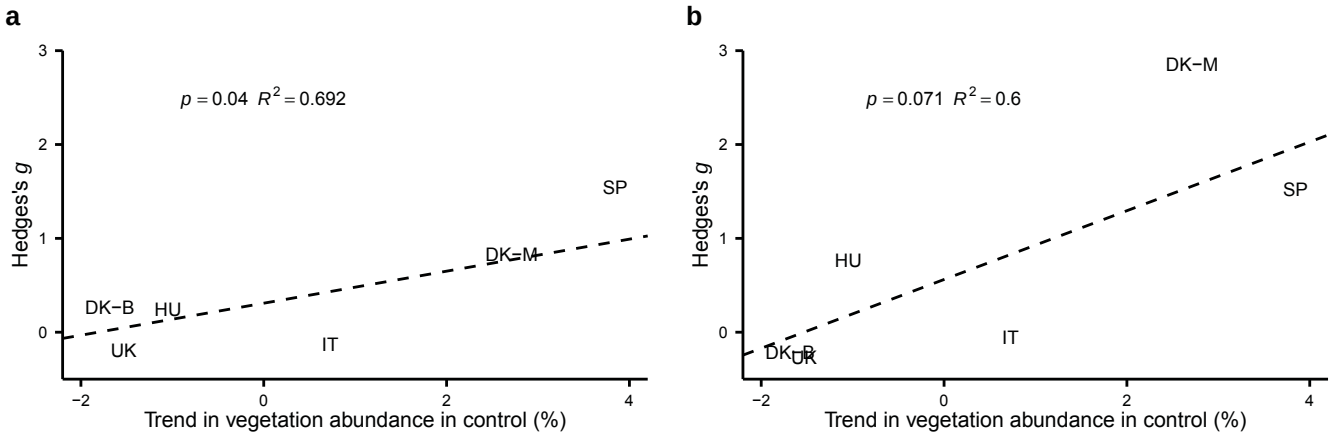

N
Precipitation
DK−M
DK−B
UK
NL
HU
SP
IT
Temperature


a
Overall p = 0.445
Vegetation abundance
(hits 100 points−1)
750
500
250
7.5
10.0
12.5
15.0
Mean annual temperature (°C)
b
Overall p = 0.371
*
Vegetation abundance
(hits 100 points−1)
750
500
250
250
500
750
1000
1250
Mean annual precipitation (mm)
Treatment
Control
Warming
Drought
Site
UK
DK−B
DK−M
NL
HU
IT
SP


a
Overall p = 0.415
Species richness
16
12
8
4
7.5
10.0
12.5
15.0
Mean annual temperature (°C)
*
b
Overall p = 0.492
Species richness
16
12
8
4
250
500
750
1000
1250
Mean annual precipitation (mm)
**
Treatment
Control
Warming
Drought
Site
UK
DK−B
DK−M
HU
IT
SP


a
b
Overall p = 0.061
Overall p = 0.072
Bray–Curtis dissimilarity
0.0
0.2
0.4
0.6
UK
DK–B
DK–M
HU
IT
SP
Site
*
*
Treatment
Control
Warming
Drought


Trend in vegetation abundance
(% year^{-1})
−2
0
2
4
6
8
UK
NL
DK−B
DK−M
HU
IT
SP
**
**
**


a
b
$p = 0.04$ $R^2 = 0.692$
$p = 0.071$ $R^2 = 0.6$
Hedges's g
Trend in vegetation abundance in control (%)
DK−B
HU
UK
IT
DK−M
SP
3
2
1
0
−2
0
2
4