Increased sensitivity to climate change in disturbed ecosystems

Kröel-Dulay, G.; Ransijn, J.; Schmidt, I.K.; Beier, C.; De Angelis, P.; de Dato, G.; Dukes, J.S.; Emmett, B.; Estiarte, M.; Garadnai, J.; Kongstad, J.; Kovács-Láng, E.; Larsen, K.S.; Liberati, D.; Ogaya, R.; Riis-Nielsen, T.; Smith, A.R.; Sowerby, A.; Tietema, A.; Penuelas, J.

DOI
10.1038/ncomms7682

Publication date
2015

Document Version
Final published version

Published in
Nature Communications

Citation for published version (APA):
Kröel-Dulay, G., Ransijn, J., Schmidt, I. K., Beier, C., De Angelis, P., de Dato, G., Dukes, J. S., Emmett, B., Estiarte, M., Garadnai, J., Kongstad, J., Kovács-Láng, E., Larsen, K. S., Liberati, D., Ogaya, R., Riis-Nielsen, T., Smith, A. R., Sowerby, A., Tietema, A., & Penuelas, J. (2015). Increased sensitivity to climate change in disturbed ecosystems. Nature Communications, 6, [6682]. https://doi.org/10.1038/ncomms7682

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (https://dare.uva.nl)
Increased sensitivity to climate change in disturbed ecosystems

György Kroel-Dulay1,*, Johannes Ransijn2,*, Inger Kappel Schmidt2, Claus Beier3, Paolo De Angelis4, Giovanbattista de Dato4, Jeffrey S. Dukes5,6, Bridget Emmett7, Marc Estiarte8,9, János Garadnai1, Jane Kongstad2, Edit Kovács-Láng1, Klaus Steenberg Larsen2, Dario Liberati4, Romà Ogaya8,9, Torben Riis-Nielsen2, Andrew R. Smith10, Alwyn Sowerby7, Albert Tietema11 & Josep Penuelas8,9

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 and 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.

1Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmanyi u. 2-4, 2163 Vacratot, Hungary. 2Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark. 3Norwegian Institute for Water Research, NIVA, Gaustadallén 21, NO-0349 Oslo, Norway. 4Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Via San Camillo de Lellis snc, 01100 Viterbo, Italy. 5Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, Indiana 47907, USA. 6Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, Indiana 47907, USA. 7Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor LL57 2UW, UK. 8CSIC, Global Ecology Unit, CREAFCsic-UABUniversitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193 Barcelona, Spain. 9CREAF, Cerdanyola del Vallès, 08193 Barcelona, Spain. 10School of Environment, Natural Resources, and Geography, Bangor University, Deiniol Road, Bangor LL57 2UW, UK. 11Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, The Netherlands. * These authors contributed equally to this work. Correspondence and requests for materials should be addressed to G.K.-D. (email: kroel-dulay.gyorgy@okologia.mta.hu).
n 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. This is particularly true today, as increasing human domination of the biosphere pushes many ecosystems towards a more dynamic, early-successional state. Although Odum 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, but it remains unclear whether an ecosystem’s dynamic state determines its sensitivity to climatic changes. Grime et al. found that a stable, late-successional grassland was more resistant to the same climatic manipulations as a dynamic, early-successional grassland.

Several authors have suggested that successional state and disturbance history could modulate responses to climatic change, but a lack of data has prevented direct investigations of these relationships.

In addition to the experimental field manipulation of climatic conditions, two other major field-based approaches can assess the effects of climate change on ecosystems: long-term observations and multi-site and gradient studies across climatically different regions. Each approach has its own merits and limitations, 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. Also, long-term experiments have often detected an altered pattern of response over time, including linear increases, dampening and reversals. 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 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. Expanding shrublands and other types of woody vegetation have been estimated to be among the largest carbon sinks in the United States. 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. 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 and 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 and 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
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 | 52°24′N | 55°53′N | 56°23′N | 46°53′N | 41°18′N | 40°36′N |
| Soil type (FAO) | Peaty Podzol | Haplic Arenosol | Sandy Podzol | Sandy Podzol | Calcaric Arenosol | Petrocalcic Calcixerepts | Luvisol and Leptosol |
| Growing season | April–September | October | April–September | September | January–May, October–December | January–May, October–December |
| Dominant species | Calluna vulgaris | Calluna vulgaris | Calluna vulgaris | Calluna vulgaris | Festuca | Globularia alpina | Helichrysum italicum |
| Site code | DK-B, Denmark at Brandbjerg; DK-M, Denmark at Mols; HU, Hungary; IT, Italy; NL, Netherlands; SP, Spain; UK, United Kingdom. |

MAP, mean annual precipitation; MAT, mean annual temperature. MATs and 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.

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 ± s.e., n = 3). DK-B, Denmark at Brandbjerg; DK-M, Denmark at Mols; HU, Hungary; IT, Italy; NL, Netherlands; SP, Spain; UK, United Kingdom.

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 ± s.e., n = 3). NL was omitted from this analysis due to its single-species vegetation. DK-B, Denmark at Brandbjerg; DK-M, Denmark at Mols; HU, Hungary; IT, Italy; SP, Spain; UK, United Kingdom.

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 studies4,26, including a meta-analysis10. 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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the

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, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the negative effect of drought on species richness at SP agrees with other studies in semiarid systems, and is most likely related to reduced colonization due to water stress. The fact that compositional change was the parameter with most of the
increase in precipitation does not necessarily hold after the factors, such as a 3 K increase in temperature or a 30% decrease/increase in precipitation, does not necessarily hold after the occurrence of a major natural or anthropogenic disturbance. 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, 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 1,263 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 macha/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. The warming curtains were automatically withdrawn during rain events. The night-time warming approach is one of the most realistic and applicable. Although the warming effect obtained with this technique is greatest during the night, there is also some carry-over effect into the day. 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 at a multi-decadal (50 years) timescale.

During rain events, transparent waterproof sheets automatically covered the drought plots, excluding the rain. Note that these sheets covered the drought plots only for the duration of the rain events, thus avoiding warming effects. The timing and duration of the experimental drought differed among the sites, dependent on seasonality and regional climatic predictions (Table 2). We excluded an average of 22% of precipitation (range: 8–49%, Table 2), and rain exclusion resulted in an average soil moisture decline of 36% (range 23–47%, Table 2) by the end of the drought periods. Control plots had the same metallic scaffolding as the treated plots, but without curtains and sheets. Each treatment had three replicate 20 m² plots except at DK-B, which had six replicates and a plot size of 9.1 m². Replicate numbers were limited by logistical and financial constraints associated with such complex field experiments. Replicates were grouped in blocks consisting of a control, a warming and a drought plot. There was no blocking of control and warming plots at the NL site.

Sampling of vegetation. We used the point-intercept method to measure plant cover and composition. At each site, 300 permanent positions were sampled per plot per sampling year, except for DK-M (200 positions) and DK-B (50 positions per plot in six replicate plots). The points were arranged either along lines (HU, SP, IT and NL) or in grids per experimental plot (DK-M, DK-B and UK). Vegetation sampling was conducted at least 50 cm from the plot edge to avoid edge effects. Pin hits for all vascular plant species were recorded. Only the first hit was recorded at IT where the vegetation was open. The vegetation was sampled annually following the start of the experiments, but the sampling years varied subsequently: UK: 1998–2000, 2002–2003 and 2007–2012; NL: 1998–2003, 2005, 2008, 2009 and 2012; DK-M:1998–2001, 2003, 2006 and 2009–2012; DK-B: 2004 and 2006–2012; HU: 2001–2012; SP: 1999–2012; 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 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 to identify treatment effects on total cover, species richness and compositional change. Compositional change was assessed with the Bray–Curtis dissimilarity of the plant community in a specific year compared with the plant community at the beginning of the experiment at the same plot (pretreatment 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. We applied separate models to analyse 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).
Table 2 | Experimental manipulations at the study sites.

| Site code | UK | NL | DK-B | DK-M | HU | SP | IT |
|-----------|----|----|------|------|----|----|----|
| Start of the experiment (pretreatment year) | 1998 | 1998 | 2004 | 1998 | 2001 | 1998 | 2001 |
| First treatment year | | | | | | | |
| Drought Timing | May-September | May-September | April-July | May-June | May-July | May-June | October-November |
| 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 | 0.2 | 0.9 | 0.4 | 0.6 |

DK-B, Denmark at Brandbjerg; DK-M, Denmark at Mols; HU, Hungary; IT, Italy; MAT, mean annual temperature; NL, Netherlands; SP, Spain; UK, United Kingdom.

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.

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 the Bray-Curtis dissimilarity because it only had one vascular plant species.

We calculated the effect sizes of the treatments as Hedges’s $g^2$:

$$g = \frac{\bar{x}_\text{treatment} - \bar{x}_\text{control}}{s'},$$

Where $\bar{x}_\text{treatment}$ and $\bar{x}_\text{control}$ are the average values in treatment and control plots, respectively, and $s'$ is the pooled s.d. of both control and treatment plots, calculated as follows:

$$s' = \sqrt{\frac{s_\text{control}^2 + s_\text{treatment}^2 - 2}{N}}$$

Where $s_\text{control}$ and $s_\text{treatment}$ are the number of replications and $s_\text{control}^2$ and $s_\text{treatment}^2$ 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:

$$J = 1 - \frac{3}{4(N_\text{control} + N_\text{treatment}) - 9}$$

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^66.

References

1. Pickett, A. T. & White, P. S. The Ecology of Natural Disturbances and Patch Dynamics (Elsevier, 1985).
2. Haberl, H. et al. Quantifying and mapping the human appropriation of net primary production in earth’s terrestrial ecosystems. Proc. Natl Acad. Sci. USA 104, 12942–12947 (2007).
3. Odum, P. The strategy of ecosystem development. Science 164, 262–270 (1969).
4. Grime, J. P. et al. The response of two contrasting limestone grasslands to simulated climate change. Science 289, 762–765 (2000).
5. Prieto, P., Penuelas, J., Lloret, F., Llorens, L. & Estiarte, M. Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean shrubland. Ecosystems 32, 623–636 (2009).
6. Rustad, L. E. et al. A meta-analysis of the response of soil respiration, net N mineralisation, and above-ground plant growth to experimental ecosystem warming. Oecologia 126, 543–562 (2001).
7. Beier, C. et al. Precipitation manipulation experiments – challenges and recommendations for the future. Ecol. Lett. 8, 899–911 (2012).
8. Aono, Y. & Kazui, K. Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. Int. J. Climatol. 28, 905–914 (2008).
9. Ovaskainen, O. et al. Community-level phenological response to climate change. Proc. Natl Acad. Sci. USA 110, 13434–13439 (2013).
10. Lang, S. I. et al. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Glob. Change Biol. 18, 1096–1107 (2012).
11. Kova´cs-Láng, E. et al. Changes in the composition of sand grasslands along a climatic gradient in Hungary, and implications for climate change. Phytoecologa 30, 385–407 (2000).
12. Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T. & Ferrier, S. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl Acad. Sci. USA 110, 9374–9379 (2013).
13. Lin, D., Xia, J. & Wan, S. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. New Phytol. 188, 187–198 (2010).
14. Wu, Z., Dijkstra, P., Koch, G. W., Penuelas, J. & Hungrate, B. A. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob. Change Biol. 17, 927–942 (2011).
15. Penuelas, J. et al. Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Glob. Change Biol. 13, 2563–2581 (2007).
16. Elmendorf, S. C. et al. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol. Lett. 15, 164–175 (2012a).
17. Leuzinger, S. et al. Do global change experiments overestimate impacts on terrestrial ecosystems? Trends Ecol. Evol. 26, 236–241 (2011).
18. Barbeta, A., Ogaya, R. & Penuelas, J. Dampening effects of long-term experimental drought on growth and mortality rates of a Holm oak forest. Glob. Change Biol. 19, 3133–3144 (2013).
19. Suttle, K. B., Thomsen, M. A. & Power, M. E. Species interactions reverse grassland responses to changing climate. Science 315, 640–642 (2007).
20. Li, G., Liu, Y., Frelich, L. E. & Sun, S. Experimental warming induces degradation of a Tibetan alpine meadow through trophic interactions. J. Appl. Ecol. 48, 659–667 (2011).
21. Specht, R. L. (ed.) Heathlands and Related Shrublands. Ecosystems of the World 9 (Elsevier, 1979).
22. Di Castri, F., Goodall, D. W. & Specht, R. L. (eds) Mediterranean-type Shrublands of the world. Ecosystems of the World 11 (Elsevier, 1981).
23. McKell, C. M. Shrub – a neglected resource of arid lands. Science 187, 803–809 (1975).
24. Schlesinger, W. H. et al. Biological feedback in terrestrial ecosystems? Science 247, 1043–1048 (1990).
25. Pacala, S. W., Hurtt, G. C. & Baker, D. Consistent land- and atmosphere-based estimates on U.S. carbon sink estimates. Science 292, 2316–2320 (2001).
26. Báez, S., Collins, S. L., Pockman, W. T., Johnson, J. E. & Small, E. E. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. Ecol. Lett. 14, 1117–1127 (2011).
27. Hoepner, S. S. & Dukes, J. S. Interactive responses of old-field plant growth and competition to warming and precipitation. Glob. Change Biol. 18, 1754–1768 (2012a).
28. Smith, M. D., Knapp, A. K. & Collins, S. L. A framework for assessing ecosystem dynamics in response to chronic resource alternations induced by global change. Ecology 90, 3279–3289 (2009).
30. Collins, S. L. et al. Stability of tallgrass prairie during a 19-year increase in growing season precipitation. *Punct. Ecol.* **26**, 1450–1459 (2012).
31. Christensen, J. H. et al. Long-term responses to simulated climate change in an infertile grassland. *Proc. Natl Acad. Sci. USA* **105**, 10028–10032 (2008).
32. Tielborger, K. et al. Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment. *Nat. Commun.* **5**, 5102 (2014).
33. Christensen, J. H. et al. in Climate Change 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Solomon, S. et al.) Chapter 11 (Cambridge Univ. Press, 2007).
34. Luo, Y. & Hui, D. in *Real World Ecology, Large-Scale and Long-Term Case Studies and Methods* (eds Miao, S., Carstenn, S. & Nungesser, M.) 267–292 (Springer, 2009).
35. Klironomos, J. N. et al. Abrupt rise in atmospheric CO₂ overestimates community response in a model plant-soil system. *Nature* **433**, 621–624 (2005).
36. Harper, J. L. *Population Biology of Plants* (Academic Press, 1985).
37. Luo, L. & Chen, Y. H. Observations from old forests underestimate climate change effects on tree mortality. *Nat. Commun.* **4**, 1655 (2013).
38. Anderson-Teixeira, K. J. & Beier, C. Novel approaches to study climate change effects on terrestrial ecosystems in the field - drought and passive night time warming. *Ecosystems* **7**, 583–597 (2004).
39. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656 (2003).
40. Beier, C. et al. Improved the performance of infrared reflective night curtains for warming field plots. *Agric. Forest Meteorol.* **149**, 1791–1799 (2009).
41. Bruehl, D. et al. Improving the performance of infrared reflective night curtains for warming field plots. *Agric. Forest Meteorol.* **173**, 53–62 (2009).
42. Bates, D., Maechler, M. & Bolker, B. *lme4: Linear mixed-effects models using S4 classes*. R package version 1.0-6. Available at http://CRAN.R-project.org/package=lme4 (2014).
43. R Development Core Team. *R: A Language and Environment for Statistical Computing*. R (Foundation for Statistical Computing, 2013).
44. Bruhn, D. *Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality*. *Agric. Forest Meteorol.* **149**, 1791–1799 (2009).
45. Oksanen, J. et al. *Vegan: community ecology package*. R package version 2.0-10. Available at http://CRAN.R-project.org/package=vegan (2013).
46. Hedges, L. V. & Olkin, I. *Statistical Methods for Meta-Analysis* (Academic Press, 1985).

**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 J.P.’s and M.E.’s research was supported by Spanish government grant CGL2013–48074-P, Catalan government grant SGR 2014–274 and European Research Council grant ERC-2013-8400028 IMBALANCE-P. We thank all the people who 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.D.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., J.S.D. and J.P. All authors contributed to data collection, data synthesis and final manuscript writing.

**Additional information**

Supplementary Information accompanies this paper at http://www.nature.com/naturecommunications

Competing financial interests: The authors declare no competing financial interests.

Reprints and permission information is available online at http://npg.nature.com/reprintsandpermissions.

**How to cite this article**: Kröl-Dulay, G. et al. Increased sensitivity to climate change in disturbed ecosystems. *Nat. Commun.* 6:6682 doi: 10.1038/ncomms7682 (2015).