

Long-term resistance to simulated climate change in an infertile grassland

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Climate shifts over this century are widely expected to alter the structure and functioning of temperate plant communities. However, long-term climate experiments in natural vegetation are rare and largely confined to systems with the capacity for rapid compositional change. In unproductive, grazed grassland at Buxton in northern England (U.K.), one of the longest running experimental manipulations of temperature and rainfall reveals vegetation highly resistant to climate shifts maintained over 13 yr. Here we document this resistance in the form of: (i) constancy in the relative abundance of growth forms and maintained dominance by long-lived, slow-growing grasses, sedges, and small forbs; (ii) immediate but minor shifts in the abundance of several species that have remained stable over the course of the experiment; (iii) no change in productivity in response to climate treatments with the exception of reduction from chronic summer drought; and (iv) only minor species losses in response to drought and winter heating. Overall, compositional changes induced by 13-yr exposure to climate regime change were less than short-term fluctuations in species abundances driven by interannual climate fluctuations. The lack of progressive compositional change, coupled with the long-term historical persistence of unproductive grasslands in northern England, suggests the community at Buxton possesses a stabilizing capacity that leads to long-term persistence of dominant species. Unproductive ecosystems provide a refuge for many threatened plants and animals and perform a diversity of ecosystem services. Our results support the view that changing land use and overexploitation rather than climate change *per se* constitute the primary threats to these fragile ecosystems.

calcareous grassland | climate manipulation | global change | multivariate analysis | vegetation

The rapidly developing consensus among environmental scientists concerning the prospect of worldwide, anthropogenic changes of climate over the present century (1–3) is now pressing upon ecologists the urgent need to identify the ecosystems that are most vulnerable to climate change. Although climate manipulations in natural vegetation remain rare, most studies have reported rapid community and ecosystem responses to warming and precipitation changes. For example, simulation of temperature regimes expected at the end of this century had immediate and persisting effects on community composition and structure in arctic (4, 5) and alpine communities (6, 7) and have altered ecosystem processes such as carbon storage (8). Short-term experimental shifts in precipitation regimes altered the diversity, productivity, and trophic relationships of seasonally water-limited systems such as Mediterranean grasslands (9–11). Although a few systems have proven unresponsive to new climate regimes after 1–5 yr (10, 12), there remains the overwhelming suggestion that, ultimately, plant communities will see major shifts in composition and structure with long-term changes in temperature and rainfall (3), which may have dire consequences for species conservation (13) and the delivery of ecosystem services (14).

Grime and colleagues (12) compared the 5-yr responses of two contrasted but species-rich, annually grazed grassland sites on shallow, calcareous soils in northern (Buxton) and southern (Wytham) England (U.K.) to identical manipulations of temperature and rainfall. At Buxton the experimental plots were located on ancient, steeply sloping, unfertilized grassland dominated by long-lived, slow-growing evergreen species. The grassland at Wytham was in an early successional state in which an ex-arable field, with soil still containing fertilizer residues, supported a mixture of productive perennial grasses and forbs. After 5 yr, the vegetation at Wytham was found to be substantially altered by the climate manipulations (12). In contrast, with the exception of reductions in the abundance of some sedges and shallow-rooted forbs in droughted plots, the Buxton vegetation remained remarkably unaffected (12, 15). The broad distinction between resistant and labile vegetation suggested by these data, if confirmed, has several intriguing implications. Under future climatic conditions, will the dynamic and “open” (*sensu* ref. 16) condition of the productive and disturbed ecosystems of urban landscapes and intensively-managed farmland become a pathway for rapid community and ecosystem changes, such as the spread of resident and alien invaders (17, 18)? In contrast, will more unproductive ecosystems, such as those occupying much of upland Europe, prove more resistant to climate shifts, thereby ensuring the survival of the large number of rare plants and animals that exploit them?

Although support for the Wytham experiment was discontinued after 5 yr, climate manipulations and annual species surveys have continued at the Buxton Climate Change Experiment for >13 yr, making it one of the longest-running studies of climate change impacts on natural vegetation. Here we describe the community trajectories at Buxton in response to climate treatments from 1994 to 2006. Our primary objective is to build upon the 5-yr comparison of the Buxton and Wytham studies (12) and evaluate whether the Buxton community continues to exhibit resistance to long-term climate regime shifts of winter warming (3°C over ambient), summer drought, and enhanced summer rainfall (consistent maintenance of 20% above the long-term average). Our approach centers on two alternative hypotheses: (i) Was the greater apparent resistance to change at the unproductive Buxton site after 5 yr due to processes that beget long-term stability in the face of climate shifts? or (ii) Do the slower population dynamics associated with infertile conditions merely slow down vegetation response, such that the communities exhibit slow but progressive change that will ultimately alter their structure and functioning? This distinction is a crucial feature of the assessment of climate change impact on

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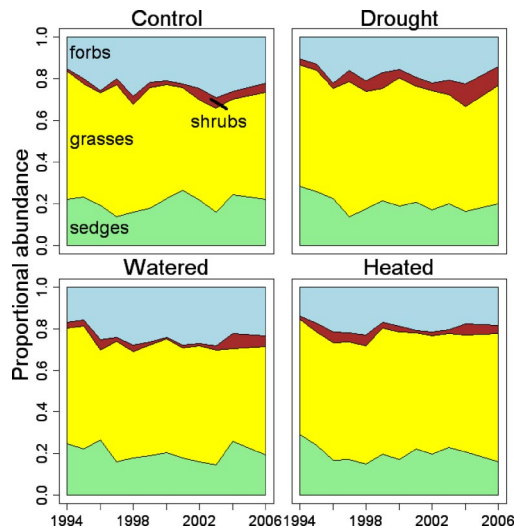


Fig. 1. Proportional abundance of life form groups in controls and three main climate treatments over the 13-yr course of the experiment. Group membership was restricted to species of non-trivial abundance over the course of the experiment, including 4 sedges (*Carex* spp.), 10 grasses, 2 low-growing shrubs (*Helianthemum nummularium* and *Thymus polytrichus*), and 11 forbs.

ecosystems. Processes such as local adaptation (19) could confer long-term stability to community structure in the face of climate shifts and explain the historical persistence of some communities (20, 21). Alternatively, unproductive ecosystems like Buxton may simply respond slowly to climate shifts. Although such responses would be difficult to detect in short-term studies, they would nonetheless suggest widespread displacement of plants and animals in the decades to come, regardless of ecosystem productivity.

Results

Shifts in temperature and rainfall regimes over the 13 yr of the Buxton study have had little effect on vegetation structure and physiognomy. Fig. 1 compares the relative abundance of broadly defined species groups based on life form in control and climate-manipulated plots from 1994, the year climate manipulations began, until 2006. The main feature of these results is the close similarity between data from control and treated plots. Only the drought treatment was sufficient to induce significant responses in life-form groups, where prostrate shrubs (esp. *Thymus polytrichus*) increased and forbs (esp. *Potentilla erecta*) decreased (MANOVA of four species groups in response to main climate treatments; shrub, $F = 4.9$, $P < 0.01$; forb, $F = 5.1$, $P < 0.01$). Across all treatments, there were decreases in the abundance of sedges and grasses over time (MANOVA year response, sedges, $F = 18.5$, $P < 0.0001$; grasses, $F = 21.2$, $P < 0.0001$), most likely associated with the restoration of annual grazing at the onset of the experiment in 1993.

Chronic summer drought for more than a decade also significantly influenced the diversity and productivity of the Buxton grassland, but plots were otherwise largely insensitive to climate manipulations (Fig. 2). To test for persistent effects of climate treatments on annual production, living aboveground biomass was harvested from each plot after 11 yr in 2004, a year in which the drought treatment was not applied. Reduction of biomass by 35% (Fig. 2, Upper) in response to drought in part indicates compositional shifts toward more drought-tolerant, less productive species (including *Thymus polytrichus* and the xeromorphic grass *Festuca ovina*). Production losses in plots subjected to both summer drought and winter heating (+H-W) were not significantly different from controls, and neither winter heating, maintenance of enhanced summer rainfall, nor their combina-

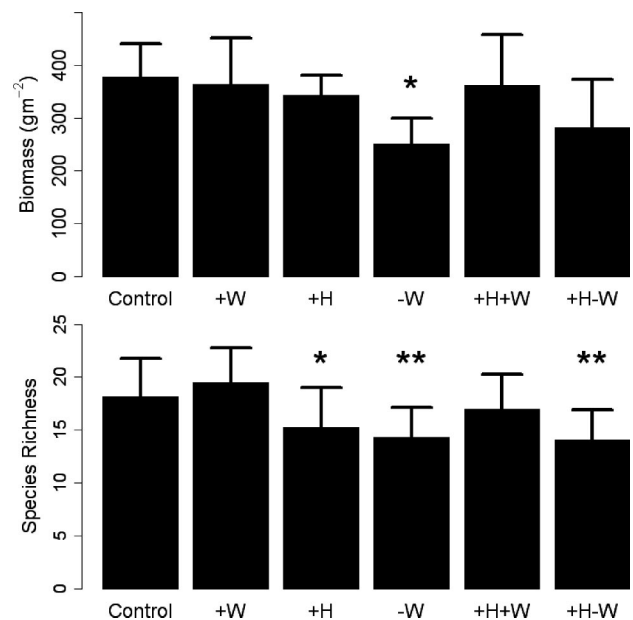


Fig. 2. Mean (\pm SE) aboveground biomass (Upper) and species richness (Lower) responses to climate treatments of watering (+W), winter heating (+H), summer drought (-W), and combinations of watering and heating (+H+W) and drought and heating (+H-W). Asterisks indicate significant treatment differences from controls in ANOVA (*, $P < 0.05$; **, $P < 0.01$). Biomass was harvested after 11 yr in 2004, a year in which the drought (-W) treatment was suspended. Species richness was measured in 120 100-cm² quadrats in 2006.

tion (+H+W) were sufficient to induce productivity responses after 11 yr.

Species richness was measured in plot subquadrats after 13 yr in 2006, where controls averaged 17 species per 100 cm² (Fig. 2 Lower). Although watered plots did not exhibit changes in richness over this period, minor but significant species losses were detected in both heated and droughted plots, and their combination (Fig. 2). Drought sensitive species included shallow-rooted sedges (*Carex pulicaris*, *C. panicea*) and several dicots of high leaf transpiration potential (*Lotus corniculatus*, *Potentilla erecta*, *Viola riviniana*). Only two species, the early-season grass *Briza media* and the subshrub *Helianthemum nummularium*, declined consistently in response to winter heating.

The overall response of community composition to climate treatments was established by year 1 (1994) and has remained relatively stable during the subsequent 13 yr. Fig. 3 shows the difference in composition between treatments and controls over the course of the experiment. Enhanced summer rainfall caused abundance shifts in several species in year 1, but remained stable thereafter except for the 1996 survey that followed the major late-summer drought of 1995. Minor compositional differences from winter warming have stabilized since 1996 and show no tendency for progressive increase. Droughted plots, including those combined with winter heating (+H-W), showed greatest compositional differences from controls in 2003 and 2004, but then in 2006 reverted back to the differences established in year 1 (comparison of year 1 and year 13, $t = -1.13$, $df = 8$, $P > 0.2$). With the exception of the droughted plots, there was no tendency for compositional differences to increase over time in response to climate manipulation (Fig. 3).

Multivariate analysis of species composition over time with respect to climate treatment confirms that the annual drift of composition in all plots was of greater magnitude than compositional differences driven by treatment (Fig. 4). We calculated three separate estimates of the relative effect sizes of treatment

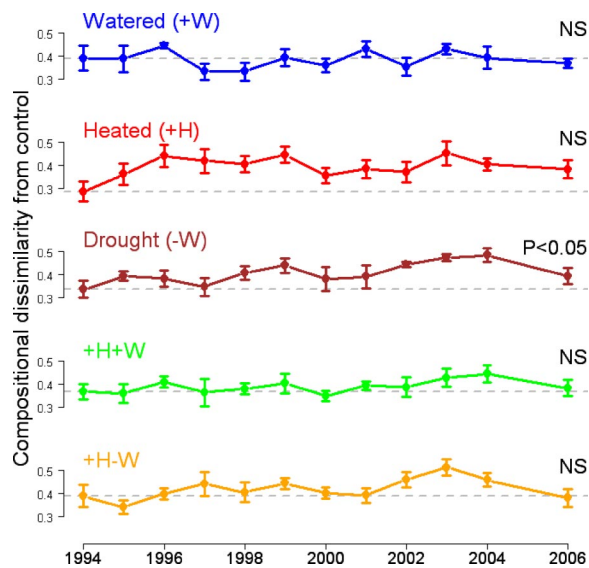


Fig. 3. Mean (\pm SE) dissimilarity of treatment and control species composition for each year of the Buxton experiment. Dissimilarity was measured by Sørensen distance estimated separately within each replicate ($n = 5$ per treatment-year). Dashed lines indicate mean dissimilarity in year 1 of the experiment. Statistics indicate whether treatment dissimilarity progressively increased over time based on linear autoregressive models (see *Statistical Analysis*).

and year based on different multivariate techniques. Multivariate analysis of the Sørensen distance matrix confirmed significant effects for treatment and year, but revealed an effect size for year twice as great as that of climate treatment (year partial $R^2 = 0.086$, treatment partial $R^2 = 0.047$). Similar analysis addressing the correlation of compositional dissimilarity to climate treatment dissimilarity, here defined as the Euclidean distance of treatment

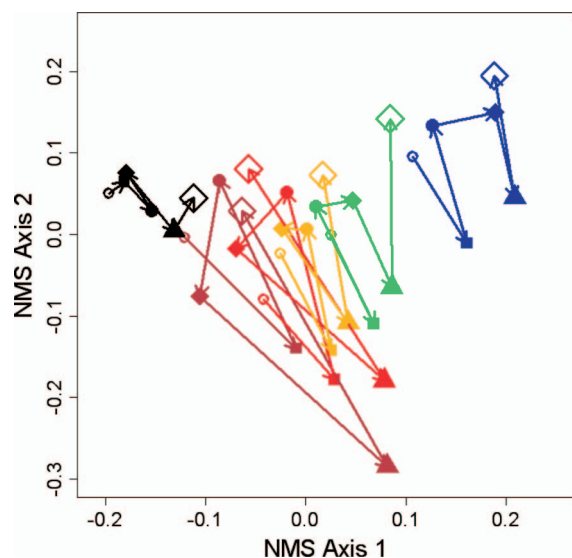


Fig. 4. Compositional drift of climate treatments (colored symbols, corresponding to Fig. 3) over time (arrows) in relation to control plots (black). Points represent the summed abundance of species across replicates in six consecutive 2-yr periods: 1994–1995 (open circles); 1996–1997 (filled squares); 1998–1999 (filled circles); 2000–2001 (filled diamonds); 2002–2003 (filled triangles); and 2004/2006 (open diamonds). Diagram produced with two-axis non-metric multidimensional scaling (NMS) of a Sørensen distance matrix. Multivariate analysis of this distance matrix confirms that treatment and year explained significant ($P < 0.001$) but small ($<10\%$ partial R^2 each) proportions of compositional variance.

water and temperature regimes (+/- heating, +/- water), revealed a correlation between composition and treatment nearly an order of magnitude lower (Mantel $r = 0.03$, $P < 0.001$) than that for species composition and year (Mantel $r = 0.26$, $P < 0.001$). In addition, a nonparametric test of within-group compositional structure [multiresponse permutation procedure (MRPP)], using either climate treatments or years to define groups, documented several-fold higher within-group structure for plots grouped by year than plots grouped by treatment (MRPP “A” statistic, year = 0.082, treatment = 0.015).

Compositional changes over time across treatments were partly the result of large annual climate fluctuations at Buxton over this period. Natural interannual variation in August rainfall from 1994–2006 ranged from 94 mm in 1995 to 339 mm in 2004. Two natural drought episodes in particular, in 1995 and 2003 (122 mm), explain the common trajectory of treatments through compositional space (Fig. 4). Because plant surveys were originally conducted in early summer (June), effects of the 1995 drought were not manifest until 1996 (filled squares), and by 1998 (filled circles) the vegetation had recovered after several years of normal rainfall. In 2003 (triangles), drought effects were detected immediately by a survey in the fall of that year, but the communities had recovered by 2004 (open diamonds) as a result of high 2004 rainfall. Summer rainfall thus accounts for about half of compositional variation through time (Mantel $r = 0.12$, $P < 0.001$). The remainder of the temporal effect on composition is associated with a change in management regime associated with the onset of the experiment, where species such as *Plantago lanceolata* and *Briza media* have increased across treatments in response to the resumption of defoliation by simulated annual grazing. This is seen in Fig. 4 as a general drift of all treatments to the upper right of compositional space over time. Communities were not significantly affected by interannual variation in winter temperatures, despite average January temperature variation from 1.5°C (1996) to 4.8°C (1998), the same magnitude as the winter warming treatment.

Discussion

The 13-yr analysis of community responses to temperature and rainfall manipulation at Buxton portrays an ecosystem with rapid but relatively minor sensitivity to changes in summer rainfall patterns, and generally unresponsive to winter temperature regime change. Changes in the abundance of several species in response to a consistent summer rainfall regime 20% over the long-term Buxton average were apparent in year 1 and persisted for 13 yr without increasing in intensity. In part, this reflects the nature of the treatment as a climate stabilizing force as well as a moderate overall increase in rainfall; its major effect was to allow for the persistence of otherwise drought-sensitive species in a system with poorly developed soils. Drought-induced responses for several species were apparent in both the immediate and long-term effects of the summer drought treatment and in annual compositional fluctuations across all treatments in response to natural drought episodes in 1995 and 2003. The sensitivity of species abundances to water status at Buxton is consistent with well known spatial differences in grassland composition along topographic gradients associated with soil moisture deficit (22, 23). Yet, despite the ecosystem significance of recurrent summer drought, compositional changes induced by recurrent drought have increased only marginally through time and have not produced large changes in vegetation structure. In general, soil moisture gradients in these grasslands more strongly influence local abundance than community membership (24), which further attests to the ability of these communities to persist in their basic structure while still exhibiting fine adjustment to natural rainfall patterns (25). Indeed, most evidence suggests that, since forest clearance, these grasslands have persisted in their basic form and composition over several centuries through periods of considerable climate variation (26, 27).

Winter warming of 3°C has altered the growth and flowering phenology of several species at Buxton (12) but this has not translated into large abundance shifts, even after 13 yr. It is perhaps significant that warming in a California grassland, in which growth is generally perceived to be strongly nitrogen limited, was also insufficient to induce changes in community structure or productivity after 5 yr (10). Studies of environmental drivers of species composition in the limestone grasslands of the Buxton region for many decades have confirmed their extreme sensitivity to nutrient addition, particularly soil phosphorus (28, 29). Together, these results suggest land-use change in the form of disturbance and eutrophication constitute the primary anthropogenic threats to these ecosystems rather than changes in climate expected by the end of this century, particularly with respect to regional temperature regimes (3).

Why should the unproductive community at Buxton exhibit long-term resistance to large compositional or structural shifts induced by temperature or rainfall shifts, when other grasslands (6, 12) show rapid and persisting change in composition, structure, and functioning? One possibility is that responses of the Buxton grassland to any environmental regime change are very slow, simply because infertile ecosystems are dominated by stress-adapted plants where strategies of nutrient retention and tissue protection are fundamentally associated with slow growth, long individual lifespans, and persistent shoot and root systems capable of withstanding significant seasonal and interannual climate variation (30–33). Historically, opportunities for the establishment of new individuals in these systems have been rare and competitive exclusion slow (34). Such a ‘slow dynamics’ model could lead to the appearance of resistance to environmental change over short durations. Although slow dynamics are an undeniable aspect of the Buxton community, we would expect a gradual magnification of compositional shifts over time in response to climate regime change if this was the sole cause of apparent resistance. To the contrary, the composition of all climate treatments after 13 yr (2006) was more similar to control plots than those after 11 yr (2004) and, with the exception of the drought treatment, did not exhibit progressive shifts over the course of the experiment. From this we conclude that a slow dynamics model cannot be the sole explanation of resistance to climate change at Buxton.

The grassland at Buxton is also an annually grazed system, and annual disturbance should constrain the type of fast compositional changes that are mediated by rapid competitive dominance of species more adapted to new climate regimes (30, 35). However, like many uplands of Western Europe, these grasslands have evolved over hundreds of years in association with intense grazing, and yet they are prone to rapid transformation by other types of environmental shifts such as eutrophication (36). Indeed, the paired climate manipulations at Wytham, a system under the same grazing regime as Buxton, resulted in immediate and significant changes in biomass and composition (12), suggesting that the stability of the Buxton grassland to climate manipulation over 13 yr is not the result of its regular management regime.

Alternatively, particular attributes of the Buxton community could act as stabilizing forces that lead to long-term recalcitrance of community and ecosystem-level properties subjected to climate change. Three such mechanisms may be particularly important at Buxton. First, the long-lived tissues of long-lived individuals tend to be capable of rapid and reversible cellular adjustments (37–39) that maintain viability and function despite seasonal and year-to-year shifts of temperature and soil moisture. Second, the rarity of new establishment opportunities, coupled with a low influx of outside propagules, could allow resident populations to locally adapt to a new climate through the expansion and contraction of particular genotypes (19, 40). Nearly all species at Buxton are out-crossing perennials, and recent investigations of populations of several common Buxton

species at a nearby nature reserve confirm a surprising level of genetic diversity at fine spatial scales (41, 42) that has important ramifications for population- and community-level dynamics (41–43). Third, local edaphic heterogeneity may provide sufficient variance in moisture and nutrient regimes to accommodate species that would be otherwise excluded by climate shifts on homogeneous substrate.

Grasslands of carboniferous limestone on steep slopes like those at Buxton are typified by small rock outcrops in a matrix of shallow soils with intermittent deep crevices and surface leaching, creating a complex mosaic of fine-scale variation in soil moisture, pH, and nutrient availability (44, 45). Both microsite variation and the potential for genetic restructuring at Buxton suggest vegetation responses are occurring at the population level that have thus far been undetected in species-level data.

Although the experiment described here documents high resistance to climate manipulation it remains appropriate to describe ancient, unproductive grasslands as fragile ecosystems. In particular, their low productivity leads to inadequate powers of recovery when subjected to repeated physical damage by overgrazing and fire or rapid displacement by other vegetation types as a consequence of eutrophication (46, 47). On this basis it seems essential, especially in temperate regions, to recognize that the primary threat to the survival of unproductive ecosystems relates to the disruptive impacts of eutrophication and habitat modification rather than the tightening constraints of climate change.

Methods

Climate Manipulation. Three climate treatments have been applied to 3 × 3 m plots.

1. Temperature has been elevated from November to April each year, beginning in November 1993. Each heated plot contains two 1000 W, 240-V AC heating cables secured to the soil surface in parallel runs spaced 50 mm apart. Soil surface temperature of heated plots is maintained at 3°C above ambient by thermocouples in heated and control plots linked to a PC-based control system.
2. Rainfall has been intercepted above the vegetation throughout July and August since the summer of 1994 by means of automatically operating, semitransparent shelters that slide across the plots at the onset of rain and retreat to an off-plot position when rain ceases. Plots of intercepted summer rainfall have significantly reduced summer soil moisture levels compared with control plots, particularly within the interior 2 × 2 m subject to vegetation monitoring (48) [supporting information (SI) Fig. S1]. In 2004, a decision was made to shift the drought treatment to alternate years (thus suspending simulated droughts in 2004 and 2006).
3. Since 1994, additional water has been added on a monthly basis to the plots during the months of June to September (inclusive), to maintain an input at least 20% above the long-term (1972–1982) Buxton average for each month. Because poorly developed soils like those at Buxton do not have a high capacity for water storage, changing rainfall patterns in the form of greater consistency, rather than simply total amount, are hypothesized to play a larger role in vegetation response than a treatment of proportional rainfall supplementation, and guided our experimental design of a watering treatment of greater total amount and consistency.

In addition to treatments 1, 2, and 3, two combinations, (1 + 2) and (1 + 3), have been maintained. All five treatments, together with untreated controls, are included in a fully randomized block, replicated 5 times. An average annual temperature rise of 3°C remains near the midrange of what is expected across the U.K. by 2080, although greater warming in summer and autumn is now expected (49). Drier summers, by up to 50% by 2080, are also predicted, although wetter winters may result in little change in the annual rainfall total. Table S1 lists the annual rainfall and temperature regimes for each climate treatment in relation to control plots.

Maintenance and Data Collection. In October each year the vegetation has been cut to a height of 40–50 mm, and the cuttings have been removed to simulate annual sheep grazing. Over the course of the experiment estimates of annual species abundance in each plot have been made by point-quadrat analysis. Each year we record the number of contacts with living shoots of each vascular plant species when 25 steel pins of diameter 2.5 mm are lowered vertically into the vegetation occupying the central (2.5 × 2.5 m) area of each plot. In 2003, surveys were changed from June/July to early October. Species data were not collected in

2005. Total living aboveground biomass was sampled in each plot from a central 0.25 m² area in 2004. In 2006, four 10- × 10-cm permanent survey quadrats were established in each plot and the total cover of each vascular plant species was recorded in five cover classes. Species nomenclature follows ref. 50.

Statistical Analysis. Responses of species groups based on simple life-form and taxonomic guilds (forbs, grasses, sedges, prostrate shrubs) were established by summing the annual abundance of species in each category over each treatment, and modeling group abundance in MANOVA. Responses of aboveground biomass in 2004, and species richness in 4 100 cm² quadrats per plot in 2006, were analyzed via ANOVA. Differences in species composition between treatments were established with a pairwise distance matrix of Sørensen (Bray-Curtis) dissimilarity, using the total annual abundance of each species summed across replicates and relativized by total annual contacts. Ordination of the distance matrix using a non-metric multidimensional scaling (NMS) 2-axis solution was performed in R (51) using the MASS library. To test the hypothesis that treatment communities exhibit progressive change through time compared with control communities, we conducted a time series analysis of compositional dissimilarities using an autoregressive mixed-effect model of Sørensen distances through time for each treatment. We used linear mixed-effect models from the NLME library in R (52) to describe Sørensen distances between control and treatment communities for each block ($n = 5$) nested within year ($n = 12$), and included the “corAR1” autocorrelation structure to account for lag-1 temporal correlation (53). Likelihood ratio tests

were used to test for the significant contribution of a fixed year effect against a model including only random year effects. Community response to treatments was tested with multivariate analysis of variance of distance matrices, following the approach of ref. 54 and implemented in R with the VEGAN library (55). We modeled the Sørensen distance matrix of species abundances summed over replicates for each year in response to treatment, year, and their interaction. Effects were tested for significance via nonparametric permutation (54). The qualitative robustness of these results was verified with two additional multivariate procedures: 1) Mantel tests using a Euclidean distance matrix of treatment water and temperature regimes (+/- heating, +0/- water), and 2) nonparametric tests of within-group compositional structure (multiresponse permutation procedure, MRPP) using either climate treatments ($n = 6$) or years ($n = 12$) to define groups (56). Mantel tests were also used to test for correlations between annual compositional changes and climate fluctuations, including seasonal mean temperature and precipitation totals measured from the nearby Buxton meteorological station (High Peak Borough Council, Derbyshire, U.K.).

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