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Soil heterogeneity buffers community response to climate change in species-rich grassland

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Abstract

Climate change impacts on vegetation are mediated by soil processes that regulate rhizosphere water balance, nutrient dynamics, and ground-level temperatures. For ecosystems characterized by high fine-scale substrate heterogeneity such as grasslands on poorly developed soils, effects of climate change on plant communities may depend on substrate properties that vary at the scale of individuals ($<m^2$), leading to fine-scale shifts in community structure that may go undetected at larger scales. Here, we show in a long-running climate experiment in species-rich limestone grassland in Buxton, England (UK), that the resistance of the community to 15-year manipulations of temperature and rainfall at the plot scale ($9\,m^2$) belies considerable community reorganization at the microsite ($100\,cm^2$) scale. In individual models of the abundance of the 25 most common species with respect to climate treatment and microsite soil depth, 13 species exhibited significant soil depth affinities, and nine of these have shifted their position along the depth gradient in response to one or more climate treatments. Estimates of species turnover across the depth gradient reviewed in relation to measurements of water potential, nitrogen supply, pH, and community biomass suggest that communities of shallow microsites are responding directly to microenvironmental changes induced by climate manipulation, while those of the deepest microsites are shifting in response to changes in competitive interference from more nutrient-demanding species. Moreover, for several species in summer drought and winter heated treatments, climate response in deep microsites was opposite that of shallow microsites, suggesting microsite variation is contributing to community stability at the whole-plot level. Our study thus demonstrates a strong link between community dynamics and substrate properties, and suggests ecosystems typified by fine-scale substrate heterogeneity may possess a natural buffering capacity in the face of climate change.

Keywords: Buxton, calcareous grassland, multivariate analysis, plant competition, species coexistence

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Introduction

The interaction of vegetation with climate is mediated by substrate properties (Woodward, 1987; Prentice *et al*., 1992), which play an important role in ground-level thermal budgets (Rorison *et al*., 1986; Geiger *et al*., 2003) and moisture regimes (Porporato *et al*., 2004). In grasslands characterized by poorly developed soils, substrate properties such as soil depth often vary considerably at fine spatial scales due to irregularities in the structure of the underlying bedrock (Balme, 1953; Pigott, 1962). To the extent that substrate variation influences a plant's microclimate, effects of climate change in such systems may depend on environmental processes that vary at the scale of individuals, particularly in communities where plants are small and confined to particular microsites. Although there is general recognition that fine-scale heterogeneity may play a significant role in grassland community organization (Fitter, 1982; Reynolds *et al*., 1997; Baer *et al*., 2005), the potential for local substrate variation to mediate ecosystem response to climate change remains largely unexplored (Harte & Shaw, 1995).

Substrate heterogeneity can decouple species responses from climate forcing in two ways. First, the environmental properties of some microsites may be less sensitive to changes in ambient temperature and precipitation than others, thus providing 'microrefugia' that facilitate the persistence of species that experience little to no change in their immediate microenvironment. This mechanism could apply to a range of scale contrasts. At regional and landscape scales, the persistence of plant and animal taxa in 'thermal

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hotspots' in periglacial environments during the Pleistocene is supported by both fossil and genetic data (McLachlan & Clark, 2004; McLachlan *et al*., 2005; Soltis *et al*., 2006), and the heterogeneous response of Arctic ecosystems to contemporary climate change is attributed at least in part to landscape diversity (Post *et al*., 2009). An analogous process could occur within a single landscape, in that soil heterogeneity may have a buffering effect on changes in the local abundance of species in ecosystems typified by high local substrate variation (Bennie *et al*., 2006). However, few if any studies have examined how microsite variation can contribute to local community stability in the face of modern climate shifts. Second, varying substrate conditions may alter the direction of species responses to changes in ambient climate, particularly if local abundances are determined by species interactions that vary in intensity according to microsite conditions. For example, a species may be limited by moisture availability in shallow microsites and competitive interference in deep microsites; with increased precipitation the species may expand to shallower locations as soil water potential increases but decrease in response to increased competition in deeper soils (Grime & Curtis, 1976). Such compositional shifts may not be detected when abundance is measured at a scale that includes both shallow and deep microsites, but this would belie significant community-level change at finer spatial scales.

Since 1993, we have manipulated winter temperature and summer precipitation in unproductive grassland in Buxton, northern England (UK), to identify potential shifts in species composition and ecosystem processes that will accompany expected anthropogenic climate change ca. 2100. Over the first 5 years, species composition and productivity in experimental communities of 3×3 m remained largely insensitive to climate manipulations, although large changes in these properties were found in an identical set of climate manipulations in more productive grassland in Wytham, England (Grime *et al*., 2000). Experiments at the Wytham site were discontinued, but species composition and productivity were re-examined at Buxton after 13 years of continuous climate manipulation, to identify whether slow but progressive shifts in species composition were apparent that could eventually drive changes in ecosystem properties. Although annually droughted plots experienced small reductions in annual productivity, species composition had not further diverged by year 13 and no species had gone locally extinct in any climate treatment (Grime *et al*., 2008). The apparent resistance of this community to long-term climate manipulation prompted a more detailed study of whether species were responding at a scale undetected by our measurements covering the full 9 m^2 experimental units.

In this study, we examine the contribution of substrate heterogeneity to the long-term vegetation dynamics of the Buxton climate change experiment. Our overall objective was to determine whether species shifts in response to 15 years of continuous climate manipulation (winter warming, summer rainfall surfeit and deficit) have been occurring at the microsite scale (quadrats of 10×10 cm), despite limited evidence of such shifts at the scale of the climate treatments (3×3 m). Specifically, our objectives were to (1) characterize fine-scale variation in environmental properties in relation to soil depth and climate treatment (soil moisture dynamics, nitrogen supply rates, and soil pH); (2) examine the response to climate treatments of the 25 most abundant vascular plant species in the context of deep and shallow microsites; and (3) determine whether community-level (composition and richness) responses to climate treatment were dependent on substrate properties. Our analysis focuses on identifying properties of the Buxton ecosystem that confer apparent ($>m^2$) resistance of community-level shifts in response to climate change.

Materials and methods

Climate manipulation and vegetation surveys

The Buxton Climate Impacts Study was established in 1993 in calcareous grassland at the Health and Safety Laboratory, Harpur Hill, Derbyshire, UK. Annually maintained climate treatments in 30 3×3 m experimental units include (1) elevated temperature 3 °C above ambient by thermocouples on the soil surface Nov–April each year since 1993 (*heated* treatment); (2) interception of all rainfall throughout July and August since 1994 by automated transparent shelters (*drought* treatment); and (3) water supplementation of 20% above the long-term Buxton average from June to Sept since 1994 (*watered* treatment). Interaction treatments of (1 + 2: *heated-drought*) and (1 + 3: *heated-watered*) have also been maintained in addition to no-manipulation control plots. All six treatments are fully randomized within five blocks. Vegetation is cut in October each year to a height of ca. 50 mm to simulate sheep grazing. An annual temperature rise of 3–4 °C (1991–2080) is the average prediction of UK climate change scenarios, and a 20% decrease in summer rainfall for northern England remains consistent with latest projections (central estimates of 10–30%), although 20–30% wetter winters may result in little change in annual rainfall total (Murphy *et al*., 2009). Further details of climate manipulations and their influence on vegetation in the context of natural climate variation at Buxton are described in Grime *et al*. (2008).

In 2006, 120 10×10 cm microsite quadrats were established, including four in each 3×3 m experimental unit of the overall climate change study. In 2008, an additional 120 quadrats were established, adding four to each plot, for a total of eight microsite quadrats per plot (240 overall). Within each 3×3 m

plot, microsite locations were stratified based on soil depth, where two samples were placed in each of four depth strata of 0–7, 8–12, 13–20, and 21 + cm, with bins calculated from quantiles of an initial depth survey of ca. 1000 samples. For the 120 quadrats established in 2006, soil depths were sampled at nine points within each microsite, including the center and corners of the 100 cm^2 quadrat and four additional samples at the corners of a concentric 20 × 20 cm square. In 2006, surface pH was also sampled at the nine locations per microsite used for depth measurements by taking small soil samples (top 3 cm) analyzed by a pH meter in the laboratory. Soil depths for the remaining 120 microsites were surveyed in the same manner in 2008, but not pH due to concerns over destruction to the vegetation. In June 2008, we surveyed all vascular plants in each microsite with aerial shoots inhabiting the central 10 × 10 cm quadrat, scored by abundance according to five cover classes (0–4%, 5–24%, 25–49%, 50–74%, 75% +).

Characterization of microsite properties

In 2008 and 2009 we characterized the relationship between mean soil depth and ecosystem properties at the 100 cm^2 scale, including aboveground biomass, soil moisture dynamics, and soil nitrogen supply rates. A set of 30 water potential sensors (Decagon MPS-1 dielectric, Decagon Devices, Pullman, WA, USA) were deployed in 30 of the 240 microsites (top 5 cm) in control, watered, and heated-drought plots within each block and in deep (> 20 cm) and shallow (< 8 cm) microsites in 2009. Because biomass and soil nitrogen (N) measurements involved soil and vegetation disturbance and were associated with an ancillary study that did not involve the watered treatment, they were conducted in an additional set of microsite locations within existing climate treatments. Aboveground biomass was harvested in 100 cm^2 quadrats in fall 2009 across 332 (ancillary) microsites of varying soil depth in control, drought, and heated plots located in all five blocks. Volumetric water content of the top 5 cm was measured in these microsites on August 17, 2009 (during the drought treatment) using a Decagon ECH_2O Check moisture monitor. For a subset of 50 microsites, soil water potential was measured concomitantly with the above water potential sensors for constructing a water retention curve to translate all water volumetric measurements into water potential.

Nitrogen availability was assessed across 40 microsite locations in control, heated, drought, and heated-drought plots using PRS™ plant root simulator probes (Western Ag Innovations, Saskatoon, Canada). The 40 probes were placed in one deep and one shallow microsite within each of the above four treatments across all five blocks. The probes are ion exchange membranes encapsulated in a plastic casing. Four cation and four anion probes were inserted into the soil at each microsite to a depth of approximately 10 cm. Probes were buried in the field by cutting through the root mat with a knife, hammering the probes into the soil and using a knife to push the soil against the probe to ensure good soil contact. Probes were left in place for 4 weeks on four separate occasions (September 2008, November 2008, May 2009, August 2009). Upon removal they were cleaned in dionized water and returned to Western Ag Innovations for analysis. To remove ions from the exchange membranes probes are eluted with HCl and analysed for nitrate-N and ammonium-N by colorimetry using an autoanalyzer. The probes give a measure of N in the soil that is available to plants (nutrient surplus rather than net mineralization due to competition from plant roots) integrated over 10 cm^2 for the duration of the burial (Western Ag Innovations, 2008).

Analysis

We analyzed the response of vegetation in 240 100-cm^2 quadrats to climate treatment across the soil depth gradient in three ways. First, we used a community-level response variable (Sørensen distance) in a multivariate analysis of community composition in response to climate treatment, 'microsite', and their interaction, using the permutational MANOVA approach of Legendre & Anderson (1999), implemented in the R *vegan* library with the 'adonis' function (Oksanen *et al*., 2007). We illustrate multivariate relationships with a nonmetric multidimensional scaling (NMS) ordination calculated with the 'metaMDS' function in *vegan*, using double-relativized cover values of the most abundant 25 species; metaMDS attempts to find a stable NMS solution using 20 separate randomizations (Oksanen *et al*., 2007). The 'microsite' variable refers to the first principal component of a principal components analysis (PCA) of soil depth and pH measurements used to characterize the main axis of variation between microsites. For each microsite, we summarized depth and pH values using the mean, maximum, minimum, and coefficient of variation of all nine (400 cm^2) or the inner five (100 cm^2) measurements, plus the center depth and pH sample. pH values for the 120 microsites established in 2008 that lacked pH surveys were estimated before PCA analysis using a Bayesian PCA missing value estimator in the R *pcaMethods* package (Stacklies *et al*., 2007). PCA axis 1 was strongly related to mean soil depth of all nine samples (Pearson's $r = 0.95$), which we describe in more detail below.

Second, we assessed long-term changes in species richness with respect to climate treatment and microsite by creating four soil depth classes (corresponding to soil depths of 0–7, 8–12, 13–20, and 21 + cm) within each treatment and comparing the net effect of species gains and losses across the depth gradient. Species gains for each microsite class were calculated as those present in the treatment but not in the control of that particular microsite class within each experimental block; losses were those present only in the controls; and the net change in richness was the difference of gains and losses. The species gain and loss statistics were used to calculate the extent of species turnover in response to climate treatment along the microsite gradient. For this we chose the β_{sim} metric of species turnover that is insensitive to overall richness differences between microsites (Koleff *et al*., 2003):

$$\beta_{sim} = \min(\text{losses}, \text{gains})/[\min(\text{losses}, \text{gains}) + (\text{species in common})].$$

Species turnover, richness, and species/gain loss data were nonnormally distributed with respect to depth classes and were tested against depth within each treatment with the nonparametric Kruskal–Wallis rank sum test.

Third, individual responses of the 25 most abundant species to microsite (PCA Axis 1, including testing for a quadratic term), climate treatment, and their interaction were fitted with species-specific generalized linear models (GLMs) of species abundance (cover class) without transformation. We tested whether the Gaussian or Poisson (log link) error models were more appropriate with model AICc values (Burnham & Anderson, 2002). The Gaussian error resulted in better model fit for the majority of species; because the significance of terms based on residual deviance is evaluated differently for the Gaussian and Poisson GLMs (F vs. χ^2 tests), for consistency among species we present results of the Gaussian GLMs. Treatment contrasts were performed with Student's t tests (Table 1).

To examine how plant-relevant environmental factors relate to the microsite gradient, we tested whether microsite biomass, soil water potential, and N supply rates varied with respect to soil depth. Microsite biomass was separated into drought ($N = 149$) and nondrought ($N = 140$) subsets and each was regressed against soil depth in simple linear, quadratic, and asymptotic (Michaelis–Menten) models using general linear and nonlinear least-squares models in R, with best-fit models determined by AICc tests. Microsite water potential was calculated from sampled volumetric moisture content (VMC) using a 3-parameter water retention curve:

$$\text{kPa} = 7.71 \times (1 - \exp(-\exp(-2.17) \times (\text{VMC} - 0.62)))$$

fitted with a nonlinear least-squares model in R using 50 water potential and content observations (see inset of Fig. S1, provided in Supporting Information). Log-transformed water potential was then regressed against soil depth for drought and nondrought plots as above for biomass (with linear, quadratic, and asymptotic models compared via AICc). Total soil nitrogen supply was analyzed via ANOVAs performed separately by month, including climate treatment, soil depth as a binary variable (above or below 12 cm), and their interaction.

Results

Within-plot variation of soil depth

PCA of statistical summaries of soil depth and pH values for each microsite revealed a primary axis of substrate variation accounting for 80% of the variance in measured microsite properties, strongly associated with mean soil depth (Pearson's $r = 0.95$) and inversely related to mean pH ($r = -0.55$). Consistent with our expectations of high fine-scale substrate variance in this grassland, 80% of the variance of this primary axis was distributed within existing 3×3 m plots (ANOVA of 240 microsites in 30 plots, $F = 1.916$ on 29, 210 df; $P < 0.01$).

Community-level responses to climate treatment and microsite

Fifteen years of annual manipulations of winter temperature and summer precipitation led to significant but weak divergence in community composition at the microsite scale of 100 cm^2 (Fig. 1, left panel; climate treatment variable in permutational MANOVA, $F = 7.971$ on 5, 222 df, $P < 0.001$, partial $R^2 = 0.14$). The most significant compositional gradient to emerge separated control and watered treatments from the drought treatment, involving species characteristic of wetter grassland sites in the former (e.g., *Potentilla erecta*, *Succisa pratensis*, several *Carex* species), and the latter involving drought-resistant suffrutescent shrubs (*Thymus polytrichus*, *Helianthemum nummularium*) and the early season grass *Briza media* (Fig. 1, left panel). An orthogonal gradient differentiated heated microsites, typified by several potentially dominant grasses with dense leaf canopies in heated treatments (*Agrostis capillaris*, *Dactylis glomerata*, *Anthoxanthum odoratum*). However, the overall compositional effect size of climate treatment was similar to that of microsite variation within treatment [Fig. 1, right panel; microsite (PCA Axis 1) variable in permutational MANOVA, $F = 13.827$ and 1.785 on 1, 222 df; $P < 0.001$ and $P < 0.05$ for linear and quadratic terms, respectively, combined partial $R^2 = 0.05$]. From deep to shallow soils there was a general shift to a more xerophytic community regardless of climate treatment (Fig. 1, right panel). This shift was particularly dramatic in the drought treatment and relatively minor in the watered treatment; MANOVA confirmed a significant interaction between climate and microsite in the control of community composition ($F = 1.414$ on 5, 222 df, $P < 0.05$).

Species richness and compositional turnover

We detected several trends related to soil depth involving changes in microsite species richness and species turnover in response to climate treatment. Microsites of control plots contained on average 19.6 species (SE = 0.62), and drought microsites lost an average of 2.7 species during the 15-year course of the experiment. However, compared with the species composition of deep microsites in the control plots, the deepest microsites in droughted plots gained more species than shallower microsites (Kruskal–Wallis test, $P < 0.05$, $\chi^2 = 8.75$ on 3 df), and therefore experienced no net loss in species richness (Fig. 2). In contrast, there was no net shift in species richness in watered plots (Student's t, $P > 0.6$), and there was only marginal evidence that species gains or losses varied along the soil depth gradient (Fig. 2; Kruskal–Wallis test of species losses vs. soil depth, $P = 0.06$, $\chi^2 = 7.12$ on 3 df). Heated microsites experienced a net reduction of 2.4 species on average, with a trend toward larger net losses at intermediate microsites (Fig. 2), due in part to marginally fewer species gains in these locations ($P = 0.06$, $\chi^2 = 7.16$ on 3 df). The combination of heating and

Table 1 Coefficients of generalized linear models describing the influence of microsite (linear and quadratic terms), climate treatment ($N = 6$), and their interaction on the abundance of 25 of the most abundant species across 240 100-cm^2 quadrats in June 2008

Species	Growth form	Total cover	Frequency	Microsite effect	Climate effects	Microsite × treatment interaction
Festuca ovina	Grass	332	223	ns	Drought 0.697*** watered −0.353*	ns
Plantago lanceolata	Forb	301	166	0.016***	Heated/watered 0.539*	Heated/watered:depth^2 −0.001** Watered:depth^2 −0.001*
Lotus corniculatus	Forb	292	161	0.007*	Drought −1.245*** heated −0.512* heated/drought −0.569*	Drought:depth −0.026*
Sanguisorba minor	Forb	291	155	−0.002***	Drought 0.554*	Heated/watered:depth^2 0.001*
Carex flacca	Sedge	284	206	ns	Watered −0.381*	ns
Carex caryophyllea	Sedge	273	179	ns		ns
Potentilla erecta	Forb	265	146	0.023***	Drought −1.365*** heated −0.956*** heated/drought −1.245***	ns
Helictotrichon pratense	Grass	210	134	−0.008**		ns
Carex panicea	Sedge	195	139	ns	Drought −0.831*** heated −0.635*** heated/drought −1.176*** Heated/watered −0.484**	Heated/watered:depth 0.002*
Briza media	Grass	168	105	−0.018*	Heated/drought −0.539*	ns
Agrostis capillaris	Grass	167	118	0.018***	Heated/drought 0.435*	ns
Scabiosa columbaria	Forb	162	116	−0.007*	Heated/drought −0.419* watered −0.542**	Watered:depth^2 0.001**
Anthoxanthum odoratum	Grass	157	112	0.002*	Heated 0.742***	Heated:depth 0.022* Heated:depth^2 0.001*
Koeleria macrantha	Grass	156	104	ns	Drought 0.655** heated/watered 0.417*	ns
Danthonia decumbens	Grass	139	102	ns	Drought −0.435* heated/drought −0.460*	ns
Helianthemum nummularium	Suffrutescent shrub	128	70	−.008**	Heated/drought −0.523* heated/watered −0.596**	Heated:depth^2 0.001*
Campanula rotundifolia	Forb	110	108	ns	ns	ns
Linum catharticum	Forb	105	104	ns	Drought 0.332*	ns
Carex pulicaris	Sedge	91	65	ns	Drought −0.340***	ns
Hypericum pulchrum	Forb	80	72	ns	ns	ns
Viola riviniana	Forb	70	60	ns	Drought −0.330* heated −0.322*	ns
Succisa pratensis	Forb	52	26	−0.0001 (depth^2)	Heated/drought −0.044*	Watered:depth^2 0.001***
Thymus polytricus	Suffrutescent shrub	27	21	−0.003*	Drought 0.224*	ns
Dactylis glomerata	Grass	25	14	<0.001	Heated/watered 0.331**	Heated:depth^2 <0.001*
Carex hostiana	Sedge	17	10	ns	Drought 0.205* Watered 0.296**	ns

Species are listed in order of total cover summed across quadrats; frequency describes species occurrence within 240 quadrats. Positive microsite coefficients indicate higher abundances on deeper soils, and positive climate coefficients indicate higher abundance in climate treatment compared to controls. P values of overall microsite effects were produced via F tests based on residual deviance, while those of particular climate treatments and climate-microsite interactions were produced via Student's t tests.
*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$. ns indicates $P > 0.05$.

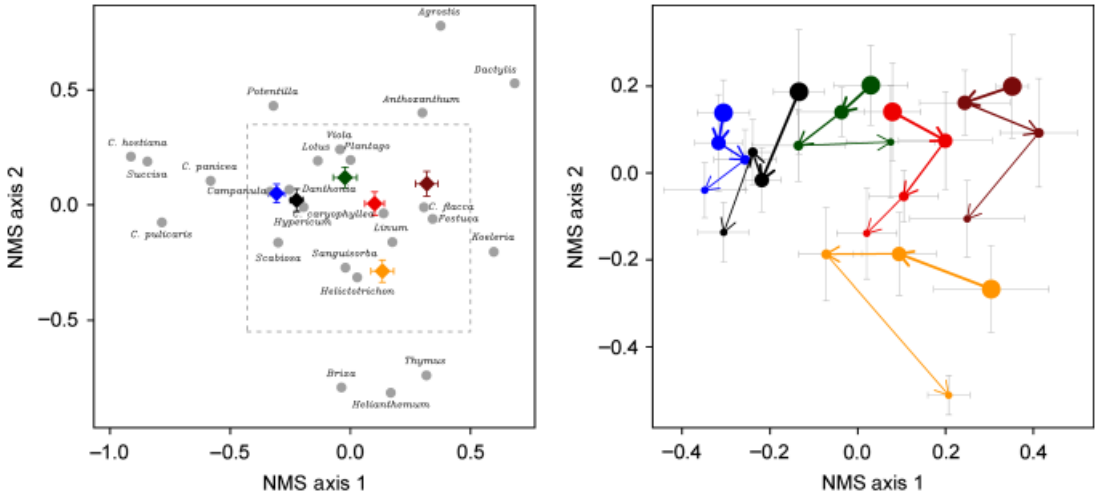

Fig. 1 Compositional relationships of climate treatments after 15 years, as shown by a two-axis nonmetric multidimensional scaling (NMS) ordination of 240 100-cm^2 vegetation plots in control (black), watered (blue), drought (orange), heated (red), heated-watered (green), and heated-drought (brown) treatments. Left-hand panel shows the mean (± SE) NMS score of 40 plots in each treatment in relation to variation in the abundance of the most abundant 25 species listed by genus (see Table 1), as produced by a species ordination of the same plot-species matrix. Dashed lines delimit the ordination region displayed in the right-hand panel, where climate treatments are further separated into mean (± SE, $N = 10$) NMS scores by soil depth, with symbol size proportional to soil depth class, and arrows showing compositional change along a deep-to-shallow gradient.

drought significantly reduced richness by an average of 4.9 species across depths (Student's t, $P < 0.001$, Fig. 2), with marginal evidence of greater reduction at intermediate depths ($P = 0.08$, $\chi^2 = 6.88$ on 3 df). There was no significant evidence of species gain, loss, or richness change in heated-watered plots, despite a trend of richness reductions at intermediate depths (Fig. 2).

Species turnover, measured as β_{sim} using differences in species composition in treatments and controls, showed a trend toward higher turnover at the ends of the depth gradient in all climate treatments except the watered treatment (Fig. 3). The effect of soil depth was only marginally significant in heated and drought treatments (Kruskal–Wallis test, drought $P = 0.06$, heated $P = 0.09$) and was not significant in heated-drought and heated-watered treatments (both $P > 0.2$). Species turnover was relatively constant along the depth gradient for the watered treatment ($P > 0.7$; Fig. 3).

Species-level responses

When analyzed individually, 13 of the 25 most common species exhibited significant linear or second-order responses to the primary axis of microsite variation (Table 1). Several drought-sensitive or calcifuge (high pH intolerant) species were restricted in distribution to deeper microsites, including the forbs *P. erecta* and *Plantago lanceolata* and several relatively productive grass species. The suffrutescent shrubs *H. nummularium* and *T. polytrichus* were strongly limited to shallow sites of nearly bare substrate, and shallow soils were also favored by several other slow-growing forbs (e.g., *S. minor*) and grasses (e.g., *B. media*). After 15 years of altered water and temperature regimes, more than a third of these 25 species shifted their microsite affinities (Table 1; significant interactions of climate treatment and microsite at the $P < 0.05$ level occurred in 9/25 species GLMs). For example, chronic summer drought effectively removed the drought sensitive species *L. corniculatus* from shallow soils, but the presence of deep microsites prevented widespread extinction of this species in droughted plots. Other species varied in their response to winter heating depending on soil depth. For example, the shallow-rooted sedge *C. panicea* was particularly susceptible to heating effects in shallow soils, but scarcely affected elsewhere; conversely, *P. erecta* was significantly more sensitive to heating effects in the deepest soils. On a species-by-species basis, there was a wide range of responses to both soil depth and climate treatment, alone or in combination, as only three of the 25 commonest species exhibited no depth or climate response (Table 1).

Environmental properties associated with the microsite gradient

Aboveground biomass increased with soil depth up to 18 cm in microsites of both drought and nondrought

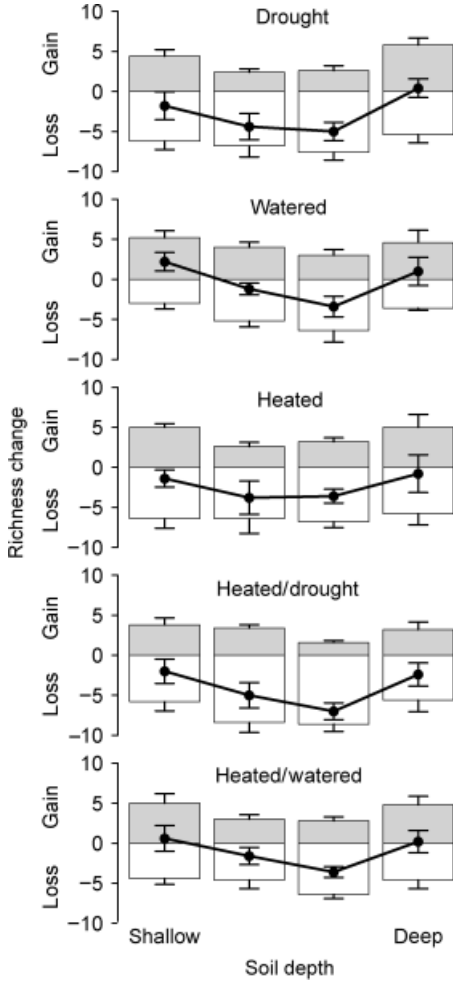

Fig. 2 Species gains (gray bars), losses (white bars), and net change in richness (lines) in each climate treatment with respect to soil depth class (from left to right: 0–7, 8–12, 13–20, and 21 + cm). Errors bars are ± SE ($N = 5$). Each value is a comparison of species composition in treatment and control plots.

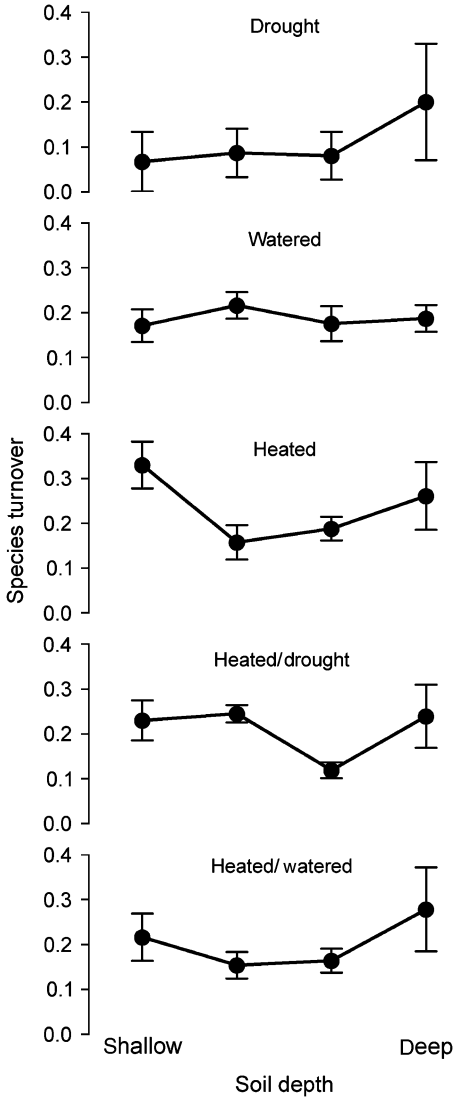

Fig. 3 Species turnover (β_{sim}) along the soil depth gradient in each climate treatment with respect to soil depth class. Depth classes are those from Fig. 2. Bars are means + SE of five blocks of treatment-control comparisons.

plots, and declined slightly in the deepest soils (Fig. 4; linear and quadratic depth terms significant at $P < 0.01$ for both drought and nondrought datasets, F tests on 1, 137 df and 1, 146 df, respectively). Total nitrogen supply (mg per 10 cm^2 $month^{-1}$) did not vary with respect to the depth of soil in the microsite for any sample period, either as a main effect (F tests with 1, 27 df, all $P > 0.1$) or as an interaction with climate treatment (F tests with 2, 27 df, all $P > 0.25$). Main effects of climate treatment on N supply were only detected in September 2008 in the drought treatment and were marginal (Tukey HSD test comparing control and drought treatments, adjusted $P = 0.08$), although the mean N supply was nearly doubled immediately after the drought (14.7 vs. 6.8 mg N per 10 cm^2 $month^{-1}$ in drought and control treatments, respectively). Surface water potential was influenced by drought and watering treatments (Fig. S1, Supporting Information) but microsite responses were minor (Fig. 4). For drought plots, water potential measurements near the end of the annual drought period showed significant linear and quadratic trends along the soil depth gradient (F tests on 1, 146 df; $P < 0.001$ and 0.05, respectively), with wetness of the top 5 cm remaining slightly higher in deep microsites (Fig. 4). No effects of soil depth on surface water potential were detected for microsites in nondrought plots (F tests for linear and quadratic terms on 1, 137 df, $P > 0.7$). Surface pH declined significantly with depth (F test on 1,115 df; $P < 0.001$; Fig. 4).

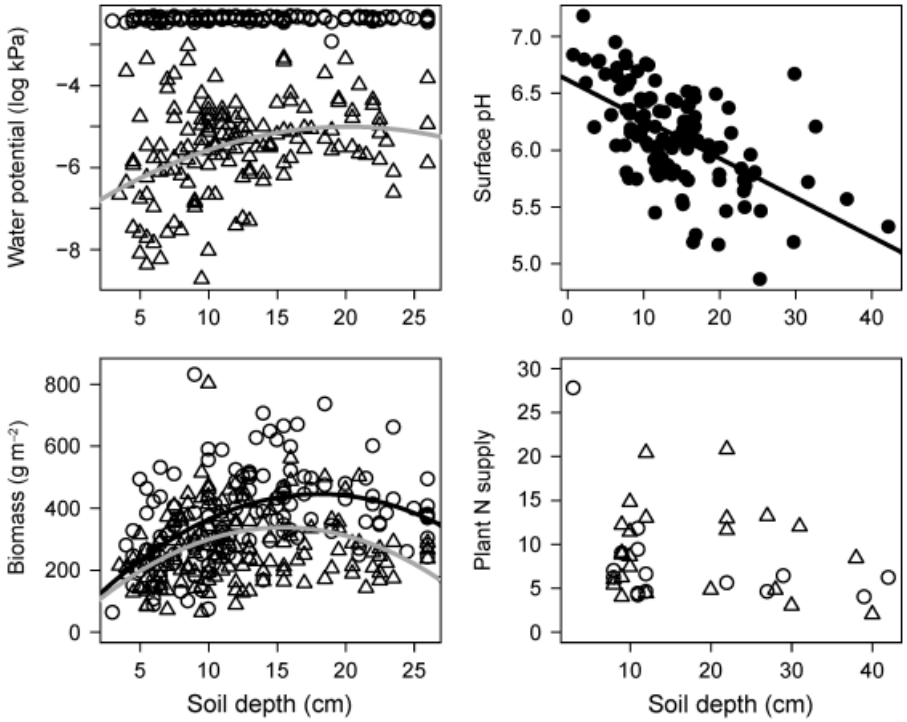

Fig. 4 Soil properties and plant biomass along the soil depth gradient. Soil water potential was derived from a survey of volumetric water content (top 5 cm) in August 2009 across 332 microsites, transformed to potential with the water retention curve shown in Fig. S1. Open circles describe microsites from nondroughted (heated and control) plots; open triangles describe microsites from drought (July–August) plots, with quadratic least-squares regression line. Biomass was measured in late fall 2009 from 100 cm^2 samples of the same 332 microsites [symbols as for the water potential panel; quadratic regression lines for drought (gray) and nondrought (black) plots]. Surface pH is the mean of nine measurements surveyed within a 20×20 cm area of each of 117 microsites across all climate treatments in 2006 (with least-squares linear regression line). Plant nitrogen supply (mg per 10 cm^2 $month^{-1}$) is the sum of plant-available nitrate and ammonium measured over 4 weeks in September 2008 in 24 drought (triangle) and 15 nondrought plots. Note water potential and biomass measurements do not include microsites of over 26 cm depth.

Discussion

Results of our microsite study indicate that the coarse-scale resistance of this community to experimental climate shifts is underlain by significant fine-scale community reorganization. Moreover, the nature of some species' responses, involving opposing climate responses in different microsites, suggests that fine-scale substrate heterogeneity has been an important contributor to the apparent lack of community response at the 9 m^2 scale.

Three key results point to the significance of microsite properties to community dynamics across climate treatments: (1) a multivariate response variable (Sørensen distance) revealed similar effect sizes for climate treatment and microsite (Fig. 1), and also confirmed a significant treatment-microsite interaction; (2) in independent species-level analyses, 13 of the 25 most abundant species exhibited significant microsite affinities, and nine of these shifted their microsite position in response to one or more climate treatments (Table 1); and (3) changes in species richness with temperature and precipitation shifts could be positive, negative, or neutral depending on whether a quadrat was located in deep or shallow soils (Fig. 2). That two of the most abundant forbs in the control plots showed opposing responses to summer drought in deep vs. shallow soils (*S. minor* and *L. corniculatus*), and similar patterns emerged for *L. corniculatus* and two other species in heated plots, is additional evidence that compositional stability in response to climate change in the Buxton ecosystem is strongly scale-dependent. Indeed, at the microsite (100 cm^2) scale, only three of the top 25 species showed no statistical response to climate, microsite, or their interaction (Table 1), including *Carex caryophyllea* and *Campanula rotundifolia*, both suspected to have high levels of morphological plasticity and local genetic differentiation (Fridley *et al.*, 2007; Whitlock *et al.*,

2007) and able to persist as subordinates under a wide range of ecological conditions (Grime, 1998).

With the exception of the watered treatment, compositional shifts in response to climate manipulation were strongest at the ends of the soil depth gradient (<7 and >21 cm, Fig. 3), a combination of high concomitant species gains and losses (Fig. 2). Our expectation was that shallow microsites would experience the greatest microenvironmental changes with climate manipulation, due to the role soil depth plays in buffering temporal variation in moisture and nutrient availability (Grime & Curtis, 1976; Porporato *et al*., 2004). Water potential and N supply measurements across soil depths only weakly support this hypothesis (Fig. 4), but we note that our measurements were restricted to surface soils (<5 cm) even in deep microsites, and thus our ability to fully characterize microenvironmental differences experienced by plants in shallow and deep soils is limited by a lack of data at depth. Nonetheless, the strong decline of productive species with extensive mesophytic leaf canopies in shallow microsites (*L. corniculatus*, *S. minor*, *A. odoratum*), and the shallow-site expansion of species typical of rock outcrops (*T. polytrichus*, *H. nummularium*) in both heated and drought treatments suggests compositional shifts in the shallowest soils were primarily caused by climate-driven changes in substrate conditions associated with soil moisture. That the watered treatment has driven a much smaller compositional shift overall is consistent with our measurements of water potential that show larger rhizosphere moisture changes in response to summer drought than summer watering.

More difficult to interpret is the pattern of greater compositional change in the deepest soils (>21 cm) relative to intermediate depths (8–20 cm) across all plots that experienced winter heating, summer drought, or both (Fig. 3). We suspect the deep microsite signal of compositional change is driven by how precipitation and especially winter heating influence competitive hierarchies in more productive, less alkaline sites, in that highly competitive species are generally absent from all but the deepest microsites due to moisture stress and severe nutrient shortage (and particularly low phosphorus availability in high calcium soils; Grime & Curtis, 1976). In this context it is notable that three grass species of strong competitive ability, *A. odoratum*, *D. glomerata*, and *Agrostis capillaris*, increased in heated plots only in the deepest soils (Table 1, although the *A. capillaris* interaction was not significant), and several species thought to be particularly sensitive to competitive displacement showed decreases in the same microsites, including *Briza media*, *Succisa pratensis*, *Danthonia decumbens*, and *Scabiosa columbaria* (Grime *et al*., 2007). We suggest that, by altering phenological patterns of spring leaf extension (as suggested by observational studies of leaf growth in these species; Grime *et al*., 1985 and J.P. Grime, unpublished results), winter heating has disrupted competitive hierarchies that are most prominent in deeper, more nutrient-rich soils (Dunnett & Grime, 1999). Communities of intermediate soil depths, although more prone to species losses from changes in soil moisture than those of the deepest microsites, may be more resistant to species gains from climate manipulation (Fig. 2) because there is insufficient nutrient supply to promote large expansions of nutrient-demanding species.

We have asserted previously (Grime *et al*., 2000, 2008) that the coarse-scale resistance of the Buxton grassland to climate forcing and its existing status as an important refuge for a wide diversity of native plants and animals stems from a combination of severe nutrient deficiency and regular grazing disturbance, which prevent rapid competitive displacement of slow-growing species under changing climate regimes. From the present study we conclude that of equal or greater importance is local substrate heterogeneity, which appears in part to drive species coexistence at spatial scales at and above ca. m^2. The close spatial proximity of species restricted to deep or shallow microsites under ambient conditions allows for considerable vegetative expansion and contraction of individuals in response to climate shifts, which may in part explain the apparent compositional stability of these grasslands over many centuries of climate fluctuations (Tansley, 1939; Buckland *et al*., 1997) and their capacity to retain similar species membership in contrasted topographic positions (Perring, 1960; Rodwell, 1990). To the extent that substrate heterogeneity drives fine-scale plant coexistence in other ecosystems, we expect that the presence of niches related to microsite temperature, nutrient, or water regimes (Silvertown *et al*., 1999) will modulate the effects of climate forcing. Although given enough time we would expect significant coarse-scale shifts in vegetation composition and structure with large climate changes, the unproductive nature of the ecosystem suggests such changes may take many decades and be reset by natural fluctuations that spur continual fine-scale reshuffling of species abundances across microsites. For these reasons, ecosystems on such heterogeneous and unproductive soils may represent particularly recalcitrant systems in the context of both past and future climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Water potential measurements (mean ± S.E.) in control (circle), watered (triangle), and drought (square) plots, summer and fall 2009. A total of 10 probes (2 per block, top 5 cm) were located in each treatment. Dashed lines delimit the summer drought period (July 1–Aug 31), and 'W' symbols indicated days where water was added to watered treatments. Inset shows the water retention curve relating site volumetric water content (%) to potential, measured in control, watered, and droughted plots in August and September 2009.

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