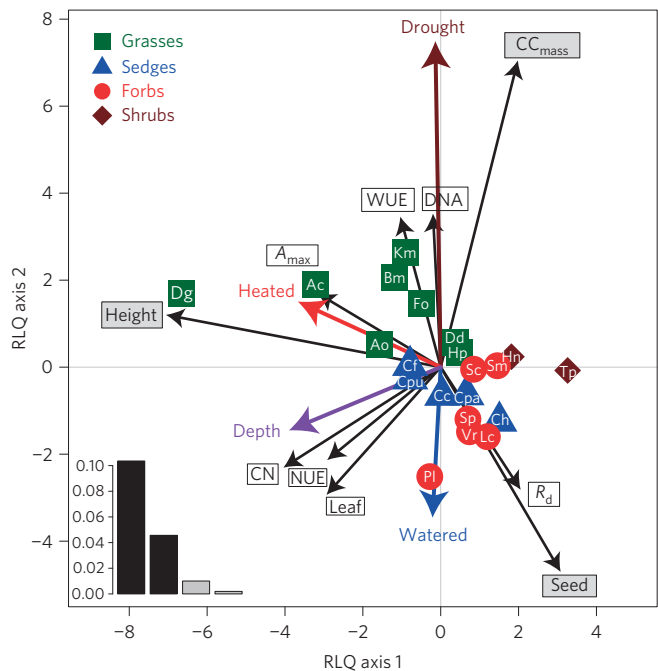


# Longer growing seasons shift grassland vegetation towards more-productive species

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Despite advances in plant functional ecology that provide a framework for predicting the responses of vegetation to environmental change<sup>1–3</sup>, links between plant functional strategies and elevated temperatures are poorly understood<sup>3–5</sup>. Here, we analyse the response of a species-rich grassland in northern England to two decades of temperature and rainfall manipulations in the context of the functional attributes of 21 coexisting species that represent a large array of resource-use strategies. Three principal traits, including body size (canopy height), tissue investment (leaf construction cost), and seed size, varied independently across species and reflect tradeoffs associated with competitiveness, stress tolerance, and colonization ability. Unlike past studies<sup>5–7</sup>, our results reveal a strong association between functional traits and temperature regime; species favoured by extended growing seasons have taller canopies and faster assimilation rates, which has come at the expense of those species of high tissue investment. This trait-warming association was three times higher in deep soils, suggesting species shifts have been strongly mediated by competition<sup>8</sup>. In contrast, vegetation shifts from rainfall manipulations have been associated only with tissue investment. Functional shifts towards faster growing species in response to warming may be responsible for a marginal increase in productivity in a system that was assumed to be nutrient-limited<sup>9</sup>.

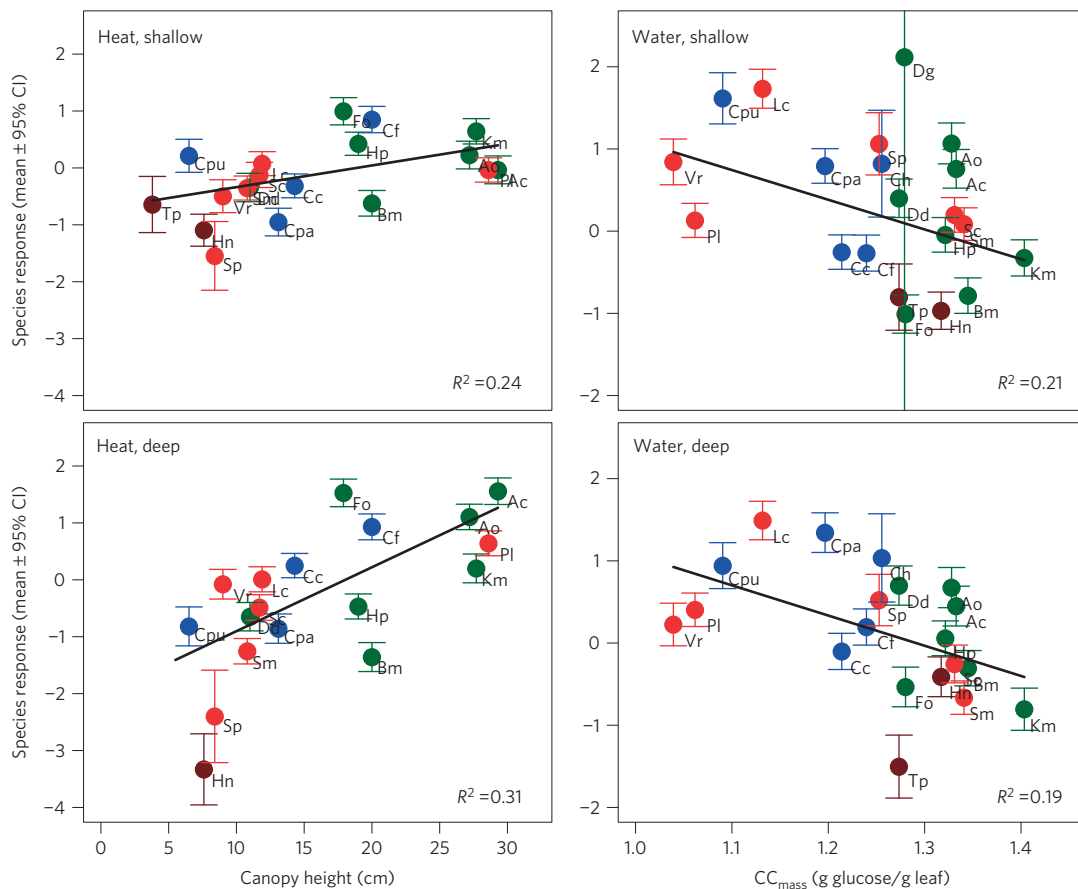
One of the main challenges to predicting the fate of temperate grasslands in the twenty-first century is to understand how temperature regimes shape their species composition and, in turn, how this composition influences ecosystem functioning<sup>3</sup>. On the one hand, developments in plant functional ecology have identified a small suite of traits related to carbon and nutrient economy that are strongly associated with both environmental gradients and the effects of plants on ecosystems<sup>10–13</sup>; such linkages have been shown to be powerful tools for predicting ecosystem responses to global change factors<sup>2,4,14</sup>. On the other hand, links between the environment, plant traits, and ecosystem functioning have been far more apparent for water and nutrient resources, and difficult to identify for temperature<sup>3–5</sup>. For example, soil-drying effects associated with temperature manipulations in arctic and alpine systems have been a primary driver of community shifts in single-site studies<sup>5,15,16</sup>; similarly, global correlations of plant functional traits with climate variables have revealed only weak correlations with site temperature, which have been interpreted as artefacts related to temperature's influence on water and nutrient supply<sup>7</sup>. Moreover, the large variation of plant functional traits within single communities has been difficult to explain as a consequence of environmental filtering<sup>7,14–18</sup>, and complicates the use of traits to predict impacts of climate change on ecosystems<sup>4</sup>.



**Figure 1 | Association of species' traits (black arrows) and environmental treatments (coloured arrows) as mediated by species abundances (symbols) in a co-inertia (RLQ) analysis of environment (R), community (L), and trait (Q) matrices.** Ordination shows species scores along orthogonal axes 1 and 2; eigenvalues are shown in the lower left inset. Species codes refer to Supplementary Table 1. Lengths of trait and treatment vectors are relative and were rescaled for visualization. Of 18 traits included in the analysis, only those of the top ten loadings are shown (see Supplementary Table 3), including (from highest to lowest loading) leaf construction cost (CC<sub>mass</sub>; 0.61), canopy height (Height, 0.60), seed mass (Seed, 0.47), leaf C:N ratio (CN, 0.39), leaf area (Leaf, 0.35), nitrogen use efficiency (NUE, 0.30), water use efficiency at a photosynthetic photon flux density of 50 (WUE, 0.30), max assimilation rate on an area basis (A<sub>max</sub>, 0.30), nuclear DNA content (DNA, 0.29), and leaf respiration rate on a mass basis (R<sub>d</sub>, 0.29).

We have subjected a species-rich grassland community in Buxton, UK, to elevated winter temperatures, chronic summer drought, and supplemental summer rainfall since 1993<sup>19,20</sup>. Because our warming treatment has been limited to cool season months (November–April), its principal environmental effect has been the extension of the growing season by about 40 frost-free days ( $\pm 12$  s.d. over 20 yr; Supplementary Fig. 1A) along with an 83% increase

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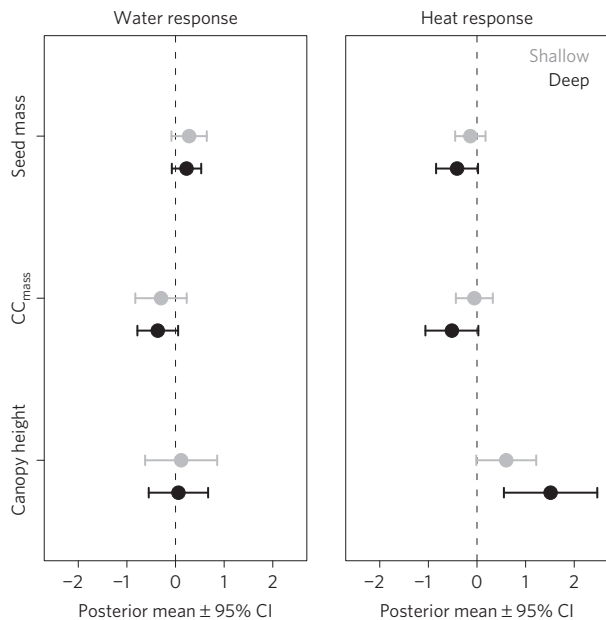
**Figure 2 | Maximum canopy height (left panels) and leaf construction cost (right panels) predict species' responses to heat and water manipulations, respectively, for both shallow (top panels) and deep (bottom panels) microsites.** Species' responses were modelled as changes in abundance (cover class) with respect to control plots in a hierarchical ordinal regression model including random effects for the experimental block and survey year (2008, 2012); means and 95% credible intervals are shown. Negative responses to water indicate increases in abundance in droughted plots compared to controls, and/or decreases in response to irrigation. Regression line is from ordinary least squares weighted by posterior precision. Note that, in six instances, species' sample size in a treatment was sufficiently low as to generate outlier posterior means of very low precision; these are not shown here, but are included in all statistical analyses. Symbol colours follow Fig. 1.

in growing degree-days (GDD) between January and April (from 42 to 77 GDD, base 10 °C; Supplementary Fig. 1A). Independent manipulation of soil water potential in summer from rainout shelters and irrigation (Supplementary Fig. 1B) allows an investigation of whether plant traits associated with primary functional strategies<sup>1,4,14</sup> are predictive of how communities shift in response to direct effects of elevated temperatures, such as extended growing seasons, versus indirect effects associated with summer water or nutrient limitation that have been a focus of other similar experiments<sup>15,16,21</sup>. Growing season duration is of particular importance in temperate ecosystems, where growth via cell division is typically not possible below 10 °C (ref. 22). Although growing season duration is among the best correlates of plant latitudinal and altitudinal limits<sup>23</sup> and annual carbon gain in temperate species<sup>24</sup>, there is at present no predictive framework for linking growing season length to plant functional traits<sup>3,4</sup>, despite this being among the most apparent impacts of global warming in temperate ecosystems<sup>25</sup>. We hypothesized that growing season length is of particular importance for those species at our site that exhibit high growth investment as a means of competitive superiority in patches of high nutrient and water availability, which at Buxton are highly variable at micro-scales (<1 m<sup>2</sup>) as a result of soil depth heterogeneity<sup>8</sup>.

Plant attributes related to carbon and nutrient economy are best described as syndromes that reflect coordinated variation in leaf, stem and root structure, chemistry, and morphology, as well as

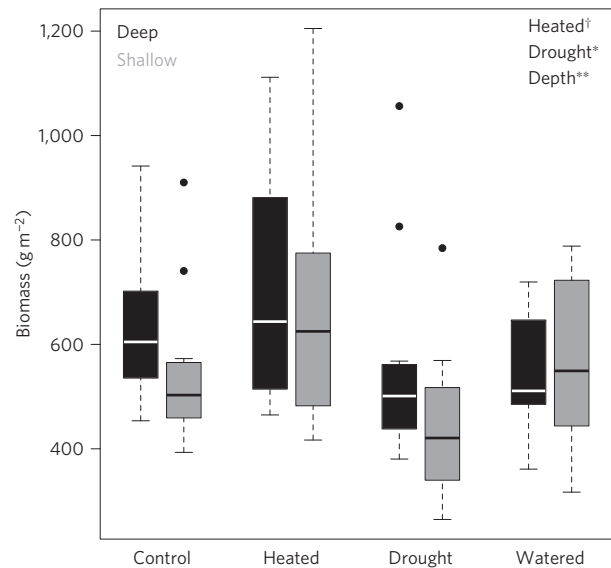
whole-plant tissue allocation and growth rate<sup>1,4,13,14</sup>. To characterize the distribution of these syndromes across the most common 21 plant species (Supplementary Table 1) at our site in relation to climate treatments, we measured 35 traits in a greenhouse study (Supplementary Table 2) and subjected a subset of 18 weakly or uncorrelated traits to multivariate analysis (Fig. 1). Among the several available methods for linking species' responses to the environment through their traits, RLQ analysis has the advantage of constraining axes of variation to those most associated with experimental treatments (ref. 26; see Supplementary Methods). This analysis revealed two major axes of treatment-associated trait variation: a primary axis describing short- to taller-statured species (Height), with the larger species exhibiting higher maximum carbon assimilation rate ( $A_{max}$ ) and larger (Leaf) and tougher (CN) leaves; and a secondary axis separating species of differential leaf-tissue investment (leaf construction cost,  $CC_{mass}$ ) and seed mass (Fig. 1). Specific leaf area and leaf dry matter content, although commonly viewed as key plant functional indicators across sites, were among the least informative traits in our study (Supplementary Table 3), consistent with other single-site studies<sup>27</sup>. However, our three primary traits of canopy height, leaf-tissue investment, and seed mass are strikingly concordant with the main axes of plant functional variation proposed in two well-established plant strategy theories<sup>1,28</sup>.

Multivariate analysis also indicated associations between functional traits and species' responses to climate treatments



**Figure 3 | Associations of species traits with climate responses, as estimated in a Bayesian phylogenetic regression accounting for the random effects of species and the joint effects of the three primary traits from multivariate analysis.** Mean and 95% credible intervals are shown for relative effect sizes after traits were standardized by zero mean and unit variance, and separate models were fitted for species' responses in deep (black) and shallow (grey) microsites. Greater abundances of species with high trait values in heated plots compared to the controls are estimated as positive effects and vice versa; negative water response values indicate higher trait values that are associated with droughted plots. Estimates of phylogenetic signal of species' responses to water and heat treatments were moderate (Pagel's  $\lambda$  0.41–0.54 across models).  $CC_{mass}$ , leaf construction cost.

and soil depth, with the primary axis associated with those species responding positively to warming and deeper soils, and the secondary axis separating differential responses of species to variation in summer rainfall (Fig. 1). To test for statistical associations between species traits and climate responses across the soil depth gradient, we used a hierarchical Bayesian (HB) model that modelled each species' climate response as a function of their values of the three primary traits identified by RLQ analysis, fitted separately for deep and shallow microsites. The HB framework allowed us to correct for the phylogenetic signal in traits (Fig. 1) to obtain a taxonomically independent link between traits and climate responses, while also accounting for uncertainty in our estimate of species' climate responses and avoiding issues of multiple testing with RLQ and related approaches (ref. 26; phylogenetic tree shown in Supplementary Fig. 2, see Supplementary Methods for phylogenetic analysis). Canopy height was a strong predictor of species' responses to warming, and this effect was nearly three times higher in deep soils (Figs 2 and 3; mean effect sizes of 1.27 and 0.43;  $P(\beta > 0) = 0.99$  and 0.97 in deep and shallow soils, respectively). The increasing abundance of larger species as a consequence of warming came at the expense of those species of high  $CC_{mass}$ , and again to a greater extent in deep soils (Figs 2 and 3; effect sizes of  $-0.65$  and  $-0.08$ ;  $P(\beta < 0) = 0.99$  and 0.67 in deep versus shallow soils). Conversely, the response of species to summer rainfall manipulation was predicted by  $CC_{mass}$ , with species of more expensive tissues favoured by drought (Fig. 2). Surprisingly, this effect was more pronounced in deep soils (mean deep soil effect size  $-0.40$ ,  $P(\beta < 0) = 0.97$ ; shallow  $-0.28$ ,  $P(\beta < 0) = 0.87$ ), suggesting two months without rainfall resulted in severe water



**Figure 4 | Standing biomass across main climate treatments in 2013, by soil depth class.** Box plots show middle quartiles of the data ( $N=12$  per box) on either side of the median (data range within whiskers) and outliers as filled circles. Symbols indicate the statistical significance ( $^\dagger P < 0.1$ ;  $*P < 0.05$ ;  $**P < 0.01$ ) of factors in analysis of the variance of log-transformed biomass against the main effects of heating, drought, watering, heat-water treatment interactions, and a main effect of soil depth class (ANOVA multiple  $R^2 = 0.21$ ).

stress throughout the rooting zone. As in the RLQ analysis, smaller seed mass was associated with positive responses to warming and drought, even after accounting for the smaller seed mass of grasses through phylogenetic correction. However, the effect size was small, and limited to deep soils (Fig. 3).

Advantages of tall-statured species of high assimilation rate in heated treatments, and particularly in deeper microsites, beg the question as to whether compositional shifts from elevated spring temperatures have driven ecosystem-level changes in productivity despite past evidence of nutrient limitation, particularly phosphorus<sup>9,19</sup>. Although chronic summer drought in our study has decreased annual production, there was no heating effect on annual net primary productivity (ANPP) after ten years in 2004<sup>20</sup>. In 2013, however, a July/August biomass harvest revealed a 16% marginal increase in NPP in heated plots compared to controls, with the highest increases in deep microsites (heated-control comparison in analysis of variance (ANOVA)  $t = 1.75$  on 1 degree of freedom,  $P = 0.08$ ; Fig. 4). That this increase was marginal might suggest early-season increases in net primary productivity (NPP) from heating decay later in the season as a result of nutrient limitation; if so, the warming-induced shift to species of higher assimilation rate is not necessarily tied to an overall shift in ANPP. Continuing experiments are attempting to identify the potential contributions of nutrient leaching and microbial stimulation of P mineralization that may interact with or facilitate the shift to more-productive species in heated plots<sup>29</sup>. We further expect the heating effect to fluctuate annually depending on the duration of ambient cold conditions in spring; that of 2013 in particular was among the coldest since the experiment began (Supplementary Fig. 1A). Reductions in standing biomass of 15% from drought were significant ( $t = -2.56$  on 1 degree of freedom,  $P < 0.05$ ) but less than the 35% reduction in 2004, potentially as a result of local adaptation<sup>30</sup>, and nearly identical to biomass differences between deep and shallow microsites in control plots ( $t = -2.67$  on 1 degree of freedom,  $P < 0.01$ ).

Two decades of climate manipulation in the Buxton study have shifted our perspective of how a grazed ecosystem responds to

systematic changes in temperature and moisture regimes. Slow to negligible responses over the first decade, particularly in comparison with a companion study on more fertile soils<sup>19</sup>, pointed to the importance of grazing and low productivity as potentially strong buffers of climate impacts<sup>20</sup>. Subsequent monitoring at a finer spatial scale has revealed the dominant role of soil depth heterogeneity, and associated local variation in moisture and nutrient supply, in mediating the response of species to both the direct impacts of climate change on resources and indirect effects through altered competitive intensity<sup>8</sup>. In moving the focus from taxonomic and life-form composition<sup>20</sup> to functional composition, results of the present study further suggest that the impacts of climate change on vegetation are predictable within the broad confines of existing plant strategy theory, depending on local limits to NPP, the sensitivity of those limits to temperature and rainfall, and well-established links between site productivity and plant functional traits<sup>12</sup>. Although shifts to more stress tolerant vegetation are widely expected where climate change will depress NPP, by the same token we expect increases in potential NPP, particularly in temperate and boreal ecosystems where NPP is limited in part by growing season duration, to favour more competitive, resource-acquisitive species. Such shifts are concerning from the standpoint of local biodiversity, particularly where current productivity levels are at or above thresholds associated with competitive exclusion<sup>12</sup>.

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## Author contributions

J.D.F. and J.P.G. designed the study with input from A.P.A.; A.P.A. and J.P.G. maintained the climate experiment; J.D.F. and J.S.L. conducted the greenhouse trait assays; J.P.G. and J.D.F. performed plot surveys; A.P.A. and J.P.G. performed the biomass survey; and J.D.F. analysed the data and wrote the paper.

## Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to J.D.F.

## Competing financial interests

The authors declare no competing financial interests.