Journal of Vegetation Science 20: 299–310, 2009

Temporal dynamics of marginal steppic vegetation over a 26-year period of substantial environmental change

Matesanz, Silvia[1]*; Brooker, Rob W.[2]; Valladares, Fernando[1,3] & Klotz, Stefan[4]

[1]*Instituto de Recursos Naturales, CCMA, CSIC, Serrano 115, E-28006 Madrid, Spain;*
[2]*Macaulay Institute, Macaulay Drive, Craigiebuckler, Aberdeen AB15 8QH, Scotland, UK; E-mail r.brooker@macaulay.ac.uk;*
[3]*Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/Tulipán s/n, 28933 Móstoles, Spain; E-mail valladares@ccma.csic.es;*
[4]*Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Strasse 4, 06120 Halle, Germany; E-mail stefan.klotz@ufz.de;*
**Corresponding author; Fax +34 91 5640800; E-mail silvia@ccma.csic.es*

Abstract

Questions: (1) Is climate a strong driver of vegetation dynamics, including interannual variation, in a range margin steppic community? (2) Are there long-term trends in cover and species richness in this community, and are these consistent across species groups and species within groups? (3) Can long-term trends in plant community data be related to variation in local climate over the last three decades?

Location: A range margin steppic grassland community in central Germany.

Methods: Cover, number and size of all individuals of all plant species present in three permanent 1-m^2 plots were recorded in spring for 26 years (1980–2005). Climatic data for the study area were used to determine the best climatic predictor for each plant community, functional group and species variable (annual data and interannual variation) using best subsets regression.

Results: April and autumn temperature showed the highest correlation with total cover and species richness and with interannual variations of cover and richness. However, key climate drivers differed between the five most abundant species. Similarly, total cover and number and cover of perennials significantly decreased over time, while no trend was found for the cover and number of annuals. However, within functional groups there were also contrasting species-specific responses. Long-term temperature increases and high interannual variability in both temperature and precipitation were strongly related to long-term trends and interannual variations in plant community data.

Conclusions: Temporal trends in vegetation were strongly associated with temporal trends in climate at the study site, with key roles for autumn and spring temperature and precipitation. Dynamics of functional groups and species within groups and their relationships to changes in temperature and precipitation reveal complex long-term and interannual patterns that cannot be inferred from short-term studies with only one or a few individual species. Our results also highlight that responses detected at the functional group level may mask contrasting responses within functional groups. We discuss the implications of these findings for attempts to predict the future response of biodiversity to climate change.

Keywords: Climate change; Cover; Perennial and annual plants; Range margin plant communities; Species richness.

Nomenclature: Jäger & Werner (2005).

Introduction

Long-term vegetation data provide a unique opportunity to understand vegetation dynamics, including interannual variability in vegetation composition and long-term changes, and can be used to infer future responses of vegetation to predicted environmental change (Parmesan & Yohe 2003; Root et al. 2003; Peñuelas et al. 2007). Vegetation dynamics in range margin communities are of particular interest. Species at their distributional limit experience serious stress and are therefore highly responsive to abiotic environmental conditions (Lennon et al. 2002; Travis 2004), making range margin communities particularly sensitive to environmental change (Hoffmann & Blows 1994; Case et al. 2005). Furthermore, changes at range margins are likely to be the first step in range shifting, and are therefore of interest in determining to what extent communities might respond as units during environmental change.

Here, we examine patterns of vegetation dynamics (long-term trends and interannual variation) over a 26-year period in a range margin steppic community in central Germany. This community is at the western distributional limit for the community type, having the warmest and most humid (i.e. most oceanic) conditions within its range. Such steppic communities are xeric in nature, and long-term data from xeric systems is particularly scarce despite their potentially high sensitivity to environmental change (Wallis De Vries et al. 2002; Stadler et al. 2007).

Climate change has affected, and is currently affecting, ecosystems in many parts of the world (Sala et al. 2000; Root et al. 2003; Menzel et al. 2006). However, while most studies have focused on the impacts of global warming, other aspects of climate such as rainfall patterns and the intensity and amount of solar radiation reaching the Earth's surface have received far less attention (Meehl et al. 2005; Wild et al. 2005). Furthermore, to understand long-term and interannual changes in vegetation and their relationship to climate, it is essential to study responses at the community level, since climate affects whole communities as well as individual species, and may have both direct and indirect effects, the latter being mediated, for example, through interactions between species (Dunnett & Grime 1999; Brooker 2006).

Certain species or functional groups have disproportionately large effects on particular community characteristics, and climate responses of vegetation can be specific to particular species (Peñuelas et al. 2002; Walther 2003) or functional groups (Sternberg et al. 1999; Brooker & van der Wal 2003; Rodríguez et al. 2003; Morecroft et al. 2004; Ingerpuu & Kupper 2007). Thus, if different species or functional groups respond differently to climate drivers, key characteristics of plant communities, such as cover, species richness and species composition, might not respond to climate change in a simple, easily predictable manner. Furthermore, although functional groups provide an approach to simplifying vegetation responses, enabling easier extrapolation of predictions when species-level information is not available (Arft et al. 1999), if species responses within functional groups are not consistent, then functional groups become a potentially misleading tool.

Within our system, we consider that annuals and perennials belong to different functional groups. Previous studies in semiarid systems have shown consistency of response to climate, and consistent impacts of these groups both with respect to plant interactions and to community properties and processes (O'Connor & Roux 1995; Holzapfel & Mahall 1999; Anderson & Inouye 2001). Thus, it is reasonable to use them as the focus of our analysis at the functional group level. We investigated the long-term and interannual dynamics of our range margin steppic grassland community at the community, functional group and species levels to identify the causes of long-term temporal trends in community composition. Our study addressed the following questions: 1. Is climate a strong driver of vegetation dynamics, including interannual variation, in a range margin steppic community? 2. Are there long-term trends in cover and species richness in this community, and are these consistent across functional groups and species within groups? 3. Can the long-term trends in plant community data be related to variation in local climate over the last three decades?

Methods

Study site

The study area is a relatively arid region near Halle, central Germany (51°35′N, 11°50′E) at 120 m a.s.l., on porphyritic outcrops with shallow soils characterised by a mosaic of natural and seminatural dry and semidry grasslands within an agricultural landscape (Winkler & Klotz 1997a, b). Mean annual temperature for the 1979–2005 period was 9.4°C (range 7.1–11.5°C), and mean annual rainfall was 478 mm for the same period (range 260–654 mm; Meteorological Station Bad Lauchstädt, Helmholtz Centre for Environmental Research – UFZ; 15 km from the plots and at the same altitude and with similar topography).

The community studied has an average cover of 15–50% on extremely shallow (5–15 cm), dry, nutrient-poor and acidic soils (Schubert et al. 2001). It is a remnant of the post-glacial natural vegetation of the area (more than 10^4 years old) and covers small areas of 10–1000 m^2 within a mosaic of different communities. The underlying substrate creates harsh conditions for plant growth, and water appears to be the most limiting growth factor. The community is not managed, except for occasional grazing by sheep (less than once per year). During periods of grazing, off-take levels are extremely low: grazers appear to concentrate on the more attractive and productive neighbouring vegetation types that are found outside the porphyritic outcrops. The community is relatively species-poor, with an average of ten species per m^2 found regularly over the 26 years studied. The main constituent of the community is *Festuca glaucina* Vill. (Poaceae), a long-lived tuft-forming grass. Other species present include perennial grasses and herbs such as *Thymus serpyllum* L. (Labiatae), *Koeleria macrantha* (Ledeb.) J.A. Schultes (Poaceae), *Hieracium pilosella* L. (Compositae) and *Silene otites* (L) Wib (Caryophyllaceae), and a number of spring ephemerals such as *Spergula morisonii* Boreau (Caryophyllaceae) and biennials such as *Centaurea stoebe* L (Compositae). For a full species list see supporting information Appendix S1. For the rest of this manuscript, "annuals" refers to both true annuals and the biannual *C. stoebe*.

Data collection

In 1980, three permanent plots of 1 m × 1 m were established within the porphyritic outcrop community and marked with metal sticks. Vegetation composition was then recorded every year until 2005 (2001 and 2004 data are missing). All three plots were located within a 10-m diameter circle. The total size of the outcrop was more than 500 m^2. The plots were recorded once every year in spring or early summer by the same observer (Stefan Klotz). Each plot was sampled using a square grid of 100 cells of 1 dm^2, placed above the vegetation so that disturbance due to sampling was minimal. The number and size of all individuals was mapped each year.

Correlations with climatic variables and statistical analyses

Relationships between plant community variables and climatic data were assessed by best subset regression, a model-building technique that finds subsets of predictor(s) variable(s) that best predict responses on a dependent variable using linear regression (Zar 1999), which is commonly used in detection of climate impact (e.g. Menzel 2003). Temperature and precipitation data (1-, 2- and 3-monthly means) of the recording year (from January to measurement date) and the preceding year were used to build the best single predictor models. Plant community variables analysed were cover and species richness of the community as a whole, the same for individuals of perennials (23 species) and annuals (11 species), and cover of the dominant species (three perennial and two annual species, see below) that together represented more than 80% of plant cover.

To explore relationships between interannual variability of the plant community and climate, vegetation and climate data were detrended to remove temporal trends and autocorrelation, and interannual variation was then calculated from the residuals of each variable (Legendre & Legendre 1998). Interannual variation of vegetation data was then regressed against that of the climate data.

The existence of temporal trends in the composition and cover of the plant community was tested using a General Linear Model (GLM) for each dependent variable: cover and species richness for the full community and functional groups, with plot as a categorical predictor and year as a continuous predictor, together with separate analyses for the dominant species. When the assumptions of the model (constant variance, normality and independence of the residuals) were not satisfied, the dependent variable was log-transformed to meet the assumption of constant variance of the residuals, and a lagged version of the dependent variable was used as a covariate to meet the assumption of independence of the residuals (i.e. to account for the autocorrelation of the residuals). We further explored species-level variation in cover through PCA analyses and linear regression of the cover of each species against time. Finally, the relationships among the dependent variables were tested with simple linear Pearson correlation.

Temporal trends in climatic variables were tested by fitting linear regressions of the climate data against time. Although the specific key climate variable may vary among species and may not be represented precisely by those used in our analysis, as climatic parameters are commonly strongly correlated, the climatic parameters used here are likely to give a reasonable representation of changes in the parameters for plant species. All statistical tests were considered significant at $P < 0.05$. All the analyses were performed with Statistica 6.0 (2004, StatSoft Inc., Tulsa, OK, USA).

Results

Mean total cover for the target community over the study period was 24.65 ± 1.02% (mean ± standard error; ranging from 10 to 51%; $n = 72$). Perennial species accounted for up to 90% of the total cover. A total of 34 plant species belonging to 15 families were recorded throughout the study. The most abundant perennial species in terms of cover were *Festuca glaucina, Hieracium pilosella* and *Koeleria macrantha*. The most abundant annual species were *Spergula morisonii* and *Centaurea stoebe*. The most abundant families were Compositae and Caryophyllaceae (both with 23%), followed by Poaceae

Table 1. Relationships between plant data and climatic variables, determined according to best subsets regression (see text for details). Top: relationships between total plant cover and species number, cover and number of perennial and annual species and cover of the five most dominant species with climatic variables. Bottom: relationship between the interannual variation of each dependent variable and the interannual variation in climate. *R* coefficient, sign and significance are shown for each relationship; $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

Variable	Best climatic predictor	*R*
Raw data		
Total cover (TC)	Mean April temperature	-0.56^{***}
Species richness (SR)	Mean April temperature	-0.39^{***}
Cover of perennial species (CP)	Mean April temperature	-0.54^{***}
Number of perennial species (NP)	Mean April–May temperature	-0.46^{***}
Cover of annual species (CA)	May precipitation	0.50^{***}
Number of annual species (NA)	May precipitation	0.43^{***}
Festuca glaucina (F. g.)	Mean April temperature	-0.31^{***}
Hieracium pilosella (H. p.)	Mean April temperature	-0.56^{***}
Koeleria macrantha (K. m.)	December–January precipitation	0.60^{***}
Spergula morisonii (S. m.)	April–May precipitation	0.50^{***}
Centaurea stoebe (C. s.)	September precipitation	0.41^{***}
Interannual variation data		
TC interannual variation	Autumn (September–November) temperature interannual variation	-0.54^{***}
SR interannual variation	April temperature interannual variation	-0.44^{***}
CP interannual variation	Autumn temperature interannual variation	-0.56^{***}
NP interannual variation	April–May temperature interannual variation	-0.51^{***}
CA interannual variation	April–May precipitation interannual variation	0.47^{***}
NA interannual variation	Spring precipitation interannual variation	0.40^{***}
F. g. cover interannual variation	Autumn temperature interannual variation	-0.70^{***}
H. p. cover interannual variation	April temperature interannual variation	-0.32^{*}
K. m. cover interannual variation	October–November temperature interannual variation	-0.47^{***}
S. m. cover interannual variation	April–May precipitation interannual variation	0.50^{***}
C. s. cover interannual variation	October–November Temp. Interannual variation	0.30^{**}

(17%). The average number of species found per year was ten (ranging from five to 14), with 20% being annual species (see Appendix S1 for cover and frequency values for each species).

Relationships between climate and plant community data

The best-fit single variable models of the relationships between climate and plant community data were in all cases highly significant (Table 1) and generally accounted for more than 50% of the total variation.

The best climatic predictor for total cover and species richness was mean April temperature (Table 1), with higher April temperatures associated with lower total cover and species richness. The same was true for the cover of perennial species, while the number of perennials was most closely correlated with mean April–May temperature and also showed a negative relationship. In contrast, the best climatic predictor for the cover and number of annual species was May precipitation, which correlated positively with these two variables. However, when the responses of the five dominant species were examined, species-specific patterns were found that did not match functional group patterns. For the perennials, while the cover of *F. glaucina* and *H. pillosela* responded negatively to increasing April temperatures, *K. macrantha* responded positively to

December–January precipitation. April–May and September precipitation were, respectively, the best predictors for the cover of the two most abundant annual species, *S. morisonii* and *C. stoebe* (Table 1).

The relationships between interannual variation in the plant community and climatic data were also dependent on functional groups and individual species. Interannual variability in autumn (September–November) temperature was the best predictor for the interannual variability in both total cover and cover of perennial species (Table 1). Interannual variation in species richness and the number of perennial species was best correlated with interannual variability in April and April–May temperature, respectively, concurring with the relationships found using the raw annual data. Similarly, interannual variation in cover and number of annual species correlated with the interannual variation in April–May and spring (March–May) precipitation (Table 1). At the species level, the best predictors for the interannual variation in the cover of *F. glaucina* and *K. macrantha* were autumn and October-November temperature, respectively. The interannual variation in cover of *H. pilosella* was again correlated with interannual variation in April temperature. Finally, the interannual variation in the two dominant annual species, *C. stoebe* and *S. morisonii*, was best correlated with interannual variation in October–November temperature and April–May precipitation.

Temporal trends in plant community data

Correlation of the response variables among plots was high over the study period (e.g. ranging from 0.72 to 0.82), and we can therefore conclude that characteristics of the three plots varied in a broadly similar manner. Furthermore, analysis of vegetation temporal trends indicated no significant plot×year interactions (Tables 2 and 3); hence, all plots showed similar temporal patterns.

Total cover showed a significant (50%) decline during the study period (Table 2). The same trend was found for the cover of perennial species, but cover of annual species showed no significant trend (Table 2). However, contrasting responses were again found for different species within functional groups (Table 3). Cover of the perennials *F. glaucina* – the species that accounted for most of the community cover – and *H. pilosella* declined significantly over time ($R = -0.44$, $P < 0.01$ and $R = -0.64$, $P < 0.001$, respectively). In contrast, cover of the perennial *K. macrantha* did not significantly change over time. While cover of the annual *S. morisonii* decreased over time ($R = -0.42$, $P < 0.01$), cover of the annual *C. stoebe* increased significantly ($R = 0.62$, $P < 0.001$; Table 3).

PCA analyses and linear regression of the cover of each species against time highlighted three main groupings within those species occurring with suffi-

Table 2. Results of the General Linear Model (degrees of freedom, *F* and *P* values) for temporal trends in total cover, cover of perennial and annual species, total species richness and number of perennial and annual species. Bold *P* values are significant. Variables with an asterisk were log-transformed and a lagged version of the variable was added to satisfy the assumptions of the model. Temporal trends over the study period – negative (−), non-significant (n.s.), and positive (+) – are also shown.

Variable	Source of variation	Degree of freedom	*F*	*P*	Temporal trend
Total cover	Plot	2	12.0212	**<0.0001**	
	Year	1	33.5183	**<0.0001**	−
	Plot×year	2	2.5184	0.0883	
	Residuals	66			
Cover of perennial species	Plot	2	8.6345	**<0.0001**	
	Year	1	29.3666	**<0.0001**	−
	Plot×year	2	2.7845	0.0690	
	Residuals	66			
Cover of annual species*	Plot	2	0.4586	0.6341	
	Year	1	0.8247	0.3670	n.s.
	Plot×year	2	2.4263	0.0962	
	Residuals	66			
Total species richness	Plot	2	0.441	0.6450	
	Year	1	0.348	0.5571	n.s.
	Plot×year	2	1.555	0.2188	
	Residuals	66			
Number of perennial species	Plot	2	0.064	0.9382	
	Year	1	6.829	0.0110	−
	Plot×year	2	1.275	0.2862	
	Residuals	66			
Number of annual species	Plot	2	1.0356	0.3607	
	Year	1	10.3938	0.0019	+
	Plot×year	2	0.8296	0.4407	
	Residuals	66			

Table 3. Results of the General Linear Model (degree of freedom, F and P values) for temporal trends in the cover of the dominant species. Bold P values are significant. Variables with an asterisk were log-transformed and a lagged version of the variable was added to satisfy the assumptions of the model. P = Perennial, A = Annual. Selected species accounted for 80% of total cover in the plant community. Temporal trends over the study period – negative (–), non-significant (n.s.), and positive (+) – are also shown.

Variable	Source of variation	Degree of freedom	F	P	Temporal trend
Festuca glaucina (P)	Plot	2	1.22436	0.3005	
	Year	1	9.97116	**0.0023**	–
	Plot×year	2	1.22132	0.3014	
	Residuals	66			
Hieracium pilosella (P)	Plot	2	12.52774	**<0.0001**	
	Year	1	7.72193	0.0071	–
	Plot×year	2	6.25013	0.1331	
	Residuals	66			
Koeleria macrantha (P)	Plot	2	20.1945	**<0.0001**	
	Year	1	0.0154	0.9015	n.s.
	Plot×year	2	9.3088	0.275	
	Residuals	66			
Spergula morisonii (A)	Plot	2	0.999551	0.3735	
	Year	1	7.727734	**0.0070**	–
	Plot×year	2	0.989174	0.3773	
	Residuals	66			
*Centaurea stoebe** (A)	Plot	2	2.51165	0.0888	
	Year	1	31.03772	**<0.0001**	+
	Plot×year	2	2.52746	0.0875	
	Residuals	66			

cient frequency to be included in the analysis: decreasing, constant and increasing species (Fig. 1). These grouping did not entirely concur with our functional groups. Annual and perennial species were present in both the constant and decreasing groupings. However, only annual species were present within the increasing group, and of these only *C. stoebe* had substantial (but still limited) cover (Fig. 1 and Appendix S1).

There was no significant change in overall species richness through time (Table 2). While there was a significant decrease in the number of perennial species, there was a significant increase in the number of annual species (Table 2). Total cover was positively and significantly correlated with both the cover ($R = 0.98$, $P < 0.0001$) and number ($R = 0.38$, $P = 0.001$) of perennial species. However, cover and number of annual species showed negative correlations with total cover ($R = -0.23$, $P = 0.053$ for cover and $R = -0.24$, $P = 0.034$ for number of annual species).

Temporal changes in climatic conditions

During the period 1980–2005, mean annual temperature in our study area increased by 1.4°C (based on predicted values from linear regression of temperature against time, from 1980 to 2005, $R = 0.38$, $P < 0.05$). April temperatures increased by 2.3°C (Fig. 2). There was no significant change in autumn temperature. However, both mean annual temperature and April and autumn temperatures were positively correlated ($R = 0.36$, $P < 0.05$; $R = 0.58$, $P < 0.001$, respectively). Likewise, there were no significant changes in annual precipitation ($R = 0.09$, $P = 0.65$) or in May precipitation ($R = -0.08$, $P = 0.94$; Fig. 2) during the study period. May precipitation and annual precipitation were highly correlated ($R = 0.63$, $P < 0.001$).

Discussion

As in the analysis of many long-term data series (Parmesan & Yohe 2003), this study is inevitably correlative. However, there is strong evidence that interannual variability and long-term changes in local climate play a significant role in plant community dynamics. The relationships detected between climate drivers and vegetation can be explained by the ecology of the key species. In general, annuals in these systems germinate and grow in response to favourable water balances in autumn and spring (Winkler & Klotz 1997a, b), which concurs with our observed response of annuals to rainfall. Perennials integrate the precipitation-temperature balance over the course of a full year and may thus be more responsive to temperature, as observed here. Despite these common patterns, the five most abundant species showed species-specific variation in climate responses regardless of their functional group. The highly significant relationships detected

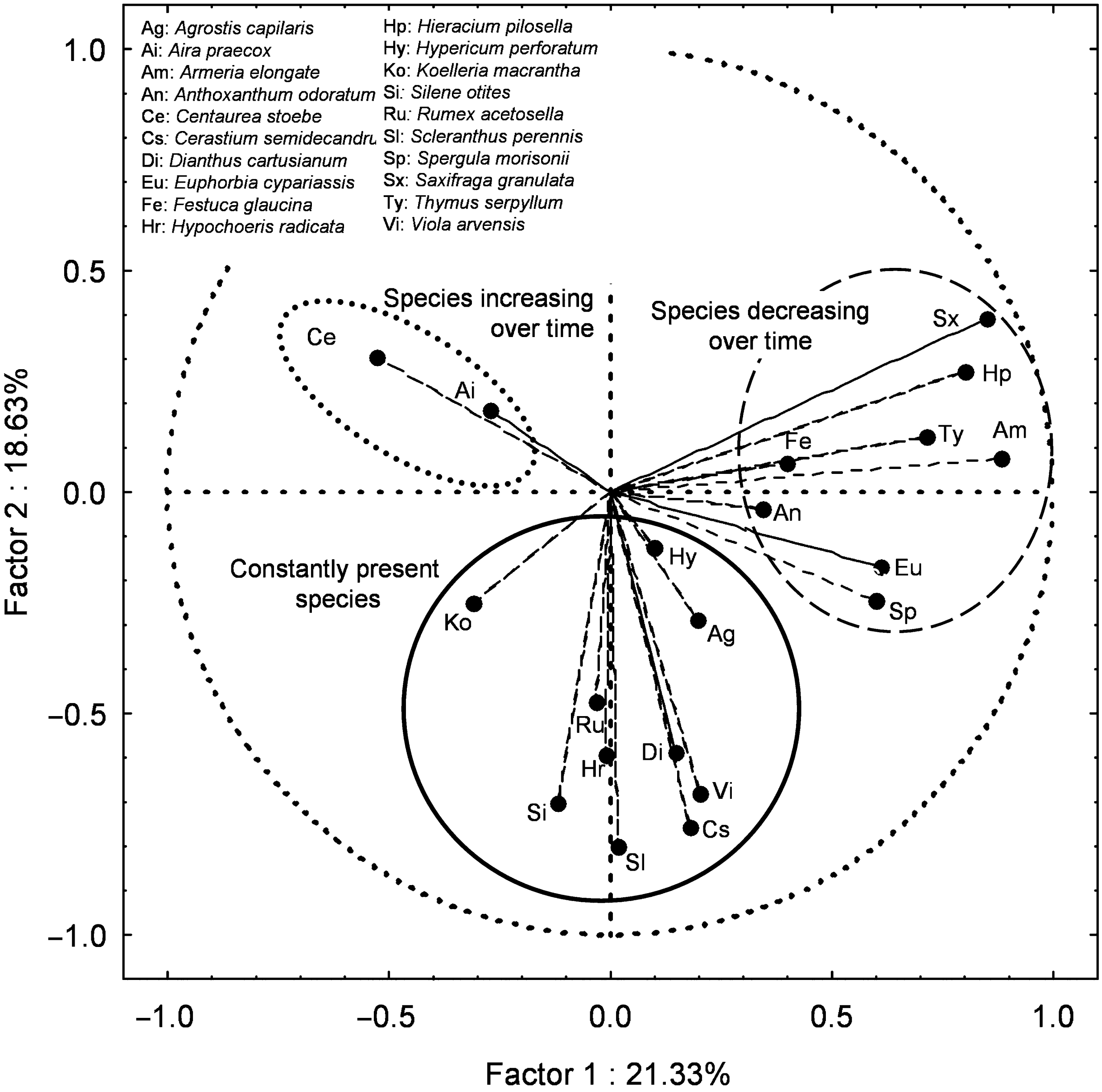

Fig. 1. Principal component analysis (PCA) of species cover over the study period. The average cover of the species in the three plots in each year was used in the analysis. Extremely infrequent species, i.e. those appearing in <3 years in the 26-year study, were excluded. Different patterns indicate different temporal trends of the species according to linear regression against time (empty circle, species increasing over time; light grey, species decreasing over time; dark grey, constantly present species). The combined results of the PCA and linear regressions were used to group the species (see Appendix S1) according to their temporal trend.

between climate (particularly spring conditions) and plant performance support the hypothesis that species within xeric range margin communities are highly responsive to changes in climate. Furthermore, these results highlight that responses detected at the functional group level may mask quite contrasting responses within functional groups.

Analyses of interannual variation support the proposed influence of climate on vegetation in this system, particularly the role of spring conditions: interannual variation in spring temperature (April or April–May) or precipitation (April–May or March–May) was strongly related to interannual variability in many of the plant community variables (e.g. species richness, number of perennial and annual species, cover of annual species and cover of *Hieracium pilosella* and *Spergula morisonii*). However, autumn temperatures had an important

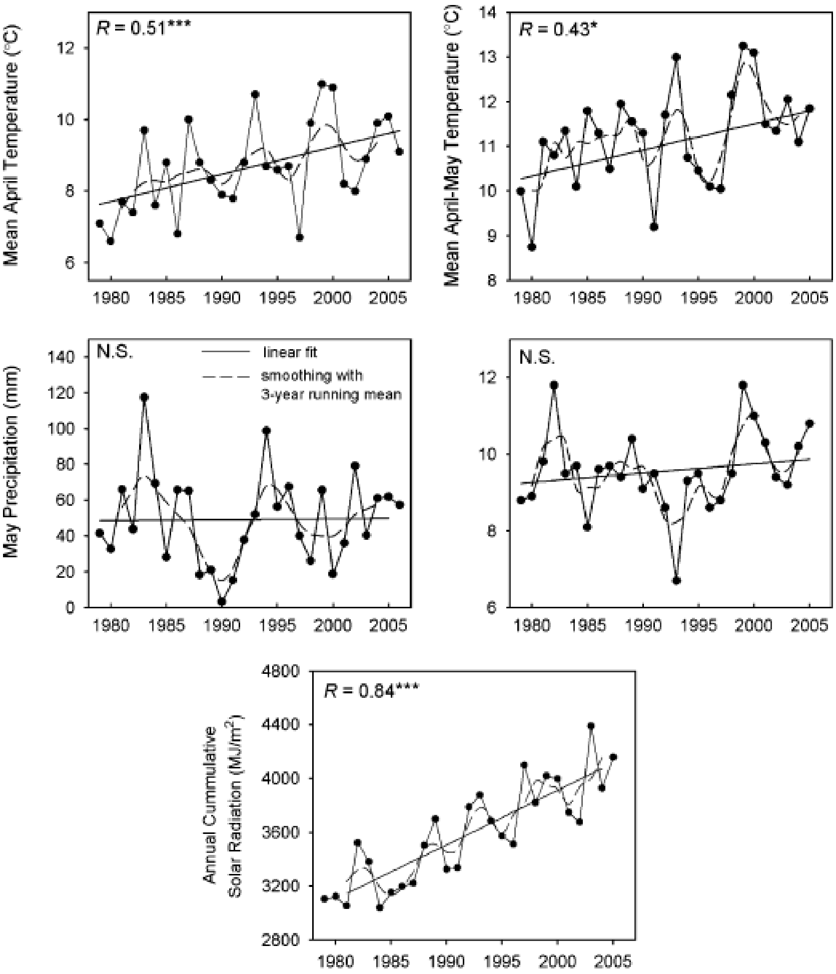

Fig. 2. Trends for climatic variables in the study area (measured at the Meteorological Station Bad Lauchstädt, UFZ Centre for Environmental Research Leipzig-Halle) during the study period. Mean April temperature (upper left), Mean April–May temperature (upper right), May precipitation (middle left), Autumn temperature (middle right), and annual cumulative solar radiation (bottom left). $^{*}P<0.05$, $^{**}P<0.01$ $^{***}P<0.001$, n.s. = not significant.

influence on total cover, cover of perennials, and cover of *Festuca glaucina*, *Koeleria macrantha* and *Centaurea stoebe*, concurring with previous studies highlighting the importance of autumn conditions for the germination of these species (Winkler & Stöcklin 2002; Bruun et al. 2007). Other studies have also found that short-term or interannual climatic variability has a strong influence on plant community dynamics and physiology (Martínez-Alonso et al. 2007; Peñuelas et al. 2007; MacDougall et al. 2008), and therefore it is reasonable to conclude that interannual variation in climate is partly driving interannual variation in vegetation.

We also found long-term temporal trends in plant community variables, but again functional group level responses appear to be masking species-specific effects. The negative temporal trend in total cover of the community was driven in particular by reductions in the cover of two dominant perennials – *F. glaucina* and *H. pilosella* – but there was no significant long-term trend in cover of the third dominant perennial, *K. macrantha*. Contrasting responses of the most abundant annual species (*S. morisonii* and *C. stoebe*) led to no overall temporal cover trend for the annuals as a group. Thus, long-term temporal changes in species richness were apparent only when the data were analysed at the community or functional group level: perennial species number declined significantly over time, while number of annual species showed a positive trend.

Factors such as land use and pollution probably play a proportionately small role in our study area. Land management activities and grazing are relatively unimportant drivers because the community is not managed and livestock are rarely present on the site. Neighbouring vegetation is more attractive to grazers and grazing is rare. Furthermore, grazing – unless at very high levels – would lead to increased community productivity and invasion of more competitive species (Milchunas & Lauenroth 1993); in contrast, we see a general long-term decline in cover in this system. On the other hand, nitrogen deposition can directly influence the productivity and dynamics of ecosystems (Bobbink 1998; Bobbink et al. 1998; van der Wal et al. 2003). However, while local output of some pollutants decreased considerably after German reunification (e.g. 86% decrease in particulate emissions from 1990 to 1999), increased transport emissions and agricultural activity have largely maintained N deposition levels (e.g. 18% decrease in NH_4 deposition in the same period; environmental data for Germany, http://www.umweltdaten.de). Reduced N deposition would favour slow-growing stress-tolerant species typical of the environment examined in our study (van der Wal et al. 2003), and is unlikely to have led to the detected declines in species cover and richness.

There is a considerable body of evidence indicating a primary role for water availability in determining plant performance in xeric communities (Churkina et al. 1999; Sternberg et al. 1999; Zavaleta et al. 2003; Lloret et al. 2004). Increased temperature could lead to reduced plant water availability, even if it is not associated with long-term decreases in precipitation (as in our case). Furthermore, solar radiation may also influence water availability. This region experienced a significant increase in solar radiation during the study period ($R = 0.85$, $P < 0.0001$; Fig. 2). Although contrary to the well-known "solar dimming" (Stanhill & Cohen 2001), this trend is consistent with recent reports of a reversal from dimming to brightening during the 1990s in many regions (Pinker et al. 2005; Wild et al. 2005), and substantial (86%) recent reductions in particulate emissions in our region. To test for the combined impact of climate trends on water availability, we calculated potential evapotranspiration (PET) values for typical dry and wet days in the first and last 2 years of the study period using the Penman calculator (http://www.tfrec.wsu.edu/Orchard/pET/pETCalc.html, Penman 1948). These calculations show a possible 40–90% increase in PET (wet and dry April days, respectively, 0.5–2.0 mm in 1980–1981 to 0.7–3.8 mm in 2004–2005) during this time. Increased water stress is therefore likely to have contributed to the significant decrease in total plant cover and cover of two of the dominant perennial species over the study period. Similar findings were observed by Anderson & Inouye (2001) in sagebrush steppe and by Morecroft et al. (2004) in temperate grassland systems. Although the cover of the other three dominant species did not change significantly over the study period, the results are also consistent with climatic trends at this site: their success correlates strongly with precipitation or autumn temperature, which showed no long-term temporal trend.

We did not find a significant temporal trend in total species richness, but there was a negative correlation of total species richness and its interannual variation with April temperature. Previous studies have reported responses of community species richness to changes in climate (Chapin et al. 1995; Dunnett et al. 1998; Zavaleta et al. 2003). Chapin et al. (1995) found that elevated temperature led to the loss of 30-50% of species after 9 years in an arctic tundra community, and Sternberg et al. (1999) found a significant decrease in species richness after winter warming in a calcareous grassland. However, these species losses were driven by expansion of dominant perennial species. In our study, perennial species and total cover declined over time. As adult perennial species in xeric systems may produce favourable microclimatic conditions for germination (Gomez-Aparicio et al. 2004; Maestre et al. 2005), both reduced adult perennial plant cover and the direct negative effects of increased environmental severity may limit seedling germination and establishment, increasing the chances of species loss. However, the number of annual species showed a significant increase through time, and two annual species were grouped together in our PCA analysis because of a common trend toward increased cover through time. Annual species may be less dependent on facilitation from perennials for germination – they germinate at times of increased water availability. Additionally, decreasing cover of two perennials may be enabling the establishment of annual species through reduced competition. This is concluded from the negative correlations between total cover and either the cover or the number of annuals species, providing evidence for the role of interactions between species in mediating climate change impacts on plant communities (McCarthy 2001; Fitter & Fitter 2002; Brooker 2006).

Interestingly, overall variation in climate during the study period can be attributed to both interannual variability and long-term climate trends. For example, both April and autumn temperatures were positively correlated to mean annual temperature. However, although April and annual temperatures showed a long-term positive trend, autumn temperatures did not. This would suggest that long-term trends in annual temperature are driven more strongly by changes in spring conditions, while interannual variation is driven to a larger extent by autumn temperature. Such patterns are mirrored in the responses of the vegetation. For example, autumn temperatures influenced interannual variation in the cover of perennials, but long-term negative trends in perennial cover were associated with increasing spring temperatures. Such results concur with previous studies showing that springtime climatic conditions have stronger long-term temporal effects as a result of climate change, and that plant processes in spring result in stronger long-term climate change responses (Fitter & Fitter 2002; Sparks & Menzel 2002).

In conclusion, despite the general decrease in cover and species richness with rising temperatures, the various long-term trends and responses to climate found in this study highlight the need for studies that adopt a hierarchical approach, i.e. that examine responses at the community, functional group or growth form, and species levels. Long-term responses are the result of both climatic and non-climatic factors (e.g. biotic interactions), and different characteristics of a community – for example, plant cover and species richness – may respond to different climatic drivers in a complex, non-parallel manner. We found that there can be considerable variation in response within functional groups, and that communities such as this are unlikely to respond as a whole to climatic drivers. Future predictions of species responses to climate change must therefore account for such variations.

Acknowledgements. This manuscript is the result of a collaboration that originated within Alter-Net (A long-term biodiversity, ecosystem and awareness research network, FP6-505298. VI EU Framework Programme). The authors would like to thank Mark Brewer (Macaulay Institute) for his advice on the statistical analyses, Robin Pakeman (Macaulay Institute) for useful comments on the manuscript, and Uwe Franko and Petra Peterson (UFZ) for providing the meteorological data. We also thank Chechu Camarero and Adrian Escudero for advice on data analyses. S.M. was supported by a CSIC. doctoral fellowship (I3P-2003). F.V. and S.M. were also supported by two grants from the Spanish Ministry of Education of Science (RASINV CGL2004-04884-C02-02/BOS and PLASTOFOR AGL2004-00536). R.B. received funding from the Scottish Government Rural and Environment Research and Analysis Directorate (RERAD).

References

Anderson, J.E. & Inouye, R.S. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71: 531–556.

Arft, A.M., et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* 69: 419–511.

Bobbink, R. 1998. Impacts of tropospheric ozone and airborne nitrogenous pollutants on natural and semi-natural ecosystems: a commentary. *New Phytologist* 139: 161–168.

Bobbink, R., Hornung, M. & Roelofs, J.G.M. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86: 717–738.

Brooker, R.W. 2006. Plant-plant interactions and environmental change. *New Phytologist* 171: 271–284.

Brooker, R.W. & van del Wal, R. 2003. Can soil temperature direct the composition of high arctic plant communities? *Journal of Vegetation Science* 14: 535–542.

Bruun, H.H., Scheepens, J.F. & Tyler, T. 2007. An allozyme study of sexual and vegetative regeneration in *Hieracium pilosella*. *Canadian Journal of Botany* 85: 10–15.

Case, T.J., Holt, R.D., McPeek, M.A. & Keitt, T.H. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108: 28–46.

Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711.

Churkina, G., Running, S.W. & Schloss, A.L.The participants of the Postdam NPP model intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. *Global Change Biology* 5: 46–55.

Dunnett, N.P. & Grime, J.P. 1999. Competition as an amplifier of short-term vegetation responses to climate. *Functional Ecology* 13: 388–395.

Dunnett, N.P., Willis, A.J., Hunt, R. & Grime, J.P. 1998. A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology* 86: 610–623.

Fitter, A.H. & Fitter, R.S.R. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.

Gomez-Aparicio, L., Zamora, R., Gomez, J.M., Hodar, J.A., Castro, J. & Baraza, E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.

Hoffmann, A.A. & Blows, M.W. 1994. Species borders – ecological and evolutionary perspectives. *Trends in Ecology and Evolution* 9: 223–227.

Holzapfel, C. & Mahall, B.E. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80: 1747–1761.

Ingerpuu, N. & Kupper, T. 2007. Response of calcareous grassland vegetation to mowing and fluctuating weather conditions. *Journal of Vegetation Science* 18: 141–146.

Jäger, H.E.J. & Werner, K. 2005. *Exkursionsflora von Deutschland, Band 4, Gefßpflanzen: Kritischer Band. 10., bearbeitete Auflage*. Elsevier Spektrum Akademischer Verlag, München, DE.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier, Amsterdam, NL.

Lennon, J.J., Kunin, W.E., Corne, S., Carver, S. & van Hees, W.W.S. 2002. Are Alaskan trees found in locally more favourable sites in marginal areas? *Global Ecology and Biogeography* 11: 103–114.

Lloret, F., Peñuelas, J. & Estiarte, M. 2004. Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. *Global Change Biology* 10: 248–258.

MacDougall, A.S., Wilson, S.D. & Bakker, J.D. 2008. Climatic variability alters the outcome of long-term community assembly. *Journal of Ecology* 96: 346–354.

Maestre, F.T., Valladares, F. & Reynolds, J.F. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93: 748–757.

Martínez-Alonso, C., Valladares, F., Camarero, J.J., López Arias, M., Serrano, M. & Rodríguez, J.A. 2007. The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a Mediterranean Scots pine forest. *Forest Ecology and Management* 253: 19–29.

McCarthy, J.P. 2001. Ecological consequences of recent climate change. *Conservation Biology* 15: 320–331.

Meehl, G.A., Arblaster, J.M. & Tebaldi, C. 2005. Understanding future patterns of increased precipitation intensity in climate model simulations. *Geophysical Research Letters* 32: L18719.

Menzel, A. 2003. Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Climatic Change* 57: 243–263.

Menzel, A., Sparks, T.H., Estrella, N.C., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissollik, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Gdahl, A., Fila, C.D., Donnelly, A., Filella, I., Jatczak, K., Mage, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Vliet, A.J.H.V., Wielgolaski, F-E., Zach, S. & Zust, A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1–8.

Milchunas, D.G. & Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327–366.

Morecroft, M.D., Masters, G.J., Brown, V.K., Clarke, I.P., Taylor, M.E. & Whitehouse, A.T. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Functional Ecology* 18: 648–655.

O'Connor, T.G. & Roux, P.W. 1995. Vegetation changes (1949-71) in a semiarid, grassy dwarf shrubland in the Karoo, South Africa - Influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* 32: 612–626.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Penman, H.L. 1948. Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London A – Mathematica et Physica* 193: 120–145.

Peñuelas, J., Filella, I. & Comas, P. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8: 531–544.

Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., de Angelis, P., de Dato, G., Emmett, B.A., Estiarte, M., Garadnai, J., Gorissen, A., Lang, E.K., Kroel-Dulay, G., Llorens, L., Pellizzaro, G., Riis-Nielsen, T., Schmidt, I.K., Sirca, C., Sowerby, A., Spano, D. & Tietema, A. 2007. 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. *Global Change Biology* 13: 2563–2581.

Pinker, R.T., Zhang, B. & Dutton, E.G. 2005. Do satellites detect trends in surface solar radiation? *Science* 308: 850–853.

Rodríguez, C., Leoni, E., Lezama, F. & Altesor, A. 2003. Temporal trends in species composition and plant traits in natural grasslands of Uruguay. *Journal of Vegetation Science* 14: 433–440.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.

Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Schubert, R., Hilbig, W. & Klotz, S. 2001. *Bestimmungsbuch der Pflanzengesellschaften Deutschlands*. Spektrum Akademischer Verlag, Heidelberg, DE.

Sparks, T.H. & Menzel, A. 2002. Observed changes in seasons: an overview. *International Journal of Climatology* 22: 1715–1725.

Stadler, J., Trefflich, A., Brandl, R. & Klotz, S. 2007. Spontaneous regeneration of dry grasslands on set-aside fields. *Biodiversity Conservation* 16: 621–630.

Stanhill, G. & Cohen, S. 2001. Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agriculture and Forest Meterorology* 107: 255–278.

Sternberg, M., Brown, V.K., Masters, G.J. & Clarke, I.P. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. *Plant Ecology* 143: 29–37.

Travis, J.M.J. 2004. A method for simulating patterns of habitat availability at static and dynamic range margins. *Oikos* 104: 410–416.

van der Wal, R., Pearce, I., Brooker, R.W., Scott, D., Welch, D. & Woodin, S. 2003. Interplay between nitrogen deposition and grazing causes habitat degradation. *Ecology Letters* 6: 141–146.

Wallis De Vries, M.F., Poschlod, P. & Willems, J.H. 2002. Challenges for the conservation of calcareous grasslands in Northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* 104: 265–273.

Walther, G-R. 2003. Plants in a warmer world. *Perspectives in Plant Ecology* 6: 169–185.

Wild, M., Gilgen, H., Roesch, A., Ohmura, A., Long, C.N., Dutton, E.G., Forgan, B., Kallis, A., Russak, V. & Tsvetkov, A. 2005. From dimming to brightening: decadal changes in solar radiation at Earth's surface. *Science* 308: 847–850.

Winkler, E. & Klotz, S. 1997a. Long-term control of species abundances in a dry grassland: a spatially explicit model. *Journal of Vegetation Science* 8: 189–198.

Winkler, E. & Klotz, S. 1997b. Clonal plant species in a dry-grassland community: a simulation study of long-term population dynamics. *Ecological Modelling* 96: 125–141.

Winkler, E. & Stöcklin, J. 2002. Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Annals of Botany* 89: 525–536.

Zar, J.H. 1999. *Biostatistical analysis*. 4th ed. Prentice-Hall, New Jersey, NJ, US.

Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B. & Mooney, H.A. 2003. Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecological Monographs* 73: 585–604.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Percentage of each species in each plot and in each year.

Received 26 September 2007;
Accepted 6 June 2008.
Co-ordinating Editor: O. Wildi.