Contents lists available at SciVerse ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Long-term spatial pattern change in a semi-arid plant community: The role of climate and composition

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ABSTRACT

The spatial pattern of plant communities can be an indicator of the processes that regulate community structure and their interplay with environmental drivers such as climate. However, to exploit such indicators we need a fuller understanding of the links between spatial pattern and climate. We examined variation in spatial pattern of annuals/biennials and perennials in a range margin steppic plant community in Germany over 26 years. We assessed change in spatial pattern through time, and how this change was related to local variation in climate and community composition. We found increasing dissociation between annuals/biennials and perennials through time, and a response of spatial pattern to summer temperature and precipitation. These responses are associated with the occurrence of *Centaurea stoebe*, a species which establishes in the community mid-way through the recording period.

Our results indicate that in some circumstances spatial patterning of vegetation may not be directly linked to environmental severity, and that species turnover rather than changes in the interactions or abundance of species already in the community can influence the observed dynamics of vegetation spatial pattern. Thus, they support calls for a better understanding of the context-specificity of plant−plant interactions, their translation to spatial pattern, and their regulation by climate and other drivers such as species turnover.

1. Introduction

Spatial pattern within vegetation can range from the small- or local-scale, for example the relative position of neighbouring individuals within a plant community (Miriti, 2007) to the overall distribution of species or the arrangement of habitats at the landscape scale (Gustafson, 1998). Understanding the regulation of spatial pattern can give us insight into structuring forces at these different scales (Dale, 1999), including the changing role of plant interactions in relation to environmental severity. It may help us, for example, to assess whether or not competition is less influential or is replaced by net facilitative interactions in severe conditions (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Grime, 2001). However, in order to use spatial pattern in this way, we need to understand better the links between spatial pattern, plant interactions, and environmental drivers such as climate.

In this study we used long-term (26-year) monitoring data to examine the responses of small-scale vegetation spatial patterning in a water-limited range margin steppic plant community to changes in climatic conditions. We explored whether detected responses matched predictions from key models linking environmental conditions to plant interactions, a source of considerable debate in plant community ecology. One argument is that competition becomes relatively less important with increasing environmental severity (Grime, 2001; Brooker et al., 2005; Kikvidze et al., 2011), and that competition's decline may be in part responsible for facilitative plant−plant interactions becoming more common (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). The other argument is that competition is equally influential in resource-limited systems, but that it is competition for soil resources rather than light that is the key interaction process (Tilman, 1982, 1988).

In some instances spatial pattern is a good indicator of underlying plant−plant interactions. For example, positive associations of annuals and perennials are common in water-limited systems

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(Vetaas, 1992; Tielbörger and Kadmon, 1995; Pugnaire et al., 1996; Moro et al., 1997; Butterfield et al., 2010), whereas in productive systems competition can lead to an over-dispersed spatial pattern (Kikvidze et al., 2005). However, a detectable relationship between interactions, spatial pattern and climate may be dependent on those elements of the plant community that are more rapidly mobile (e.g. annuals/short-lived perennials) also being those that are responsive to climate variability and consequent changes in interactions. This is particularly true for inter-annual or short-term variation in interactions. We therefore focussed our investigation on changes in the relative spatial patterning of short-lived annuals/biennials and longer-lived perennial species in relation to variation in climatic conditions.

Changes in spatial pattern in response to varying environmental conditions may also be driven through species turnover, as well as through changing relationships between the *in situ* species. Changes in species composition may have greater effects on community-level characteristics such as spatial pattern than changes in the interactions between *in situ* species in the absence of species turnover (Lauenroth and Sala, 1992). It is therefore also important to explore the extent to which changes in species turnover, rather than changes in existing interactions, might influence changes in spatial pattern in response to climatic conditions through time.

Our study system is particularly suited to this analysis. The recorded data (maps of the location and size of individual plants within plots throughout the study period) enable us to examine changes in spatial pattern and community composition through time. In addition we have considerable *a priori* understanding of the key climatic drivers of the chosen species groups. Long-term increases in temperature (see Appendix Fig. A.1) are associated with an overall decline in vegetation cover in our system, but this is entirely driven by a decline in the perennials (Matesanz et al., 2009). Annuals/biennials are instead regulated by spring precipitation. Although inter-annual variation in spring precipitation strongly influenced their species richness and cover, annuals/biennials have not experienced increasingly harsh conditions *through time* (see Appendix Fig. A.1). Hence there is no *directional* temporal trend in the richness and cover of annual species, despite both the overall community and the perennial species showing over time a gradual decline in both cover and species richness. The analysis by Matesanz et al. (2009) considered a wide range of potential climatic variables, from which April temperature and May precipitation were selected as the most important (with R coefficient values typically of 40–50%) for the success of perennials and annuals, respectively.

In terms of changes in community composition, we can examine the impacts on spatial pattern of changes in the cover of the dominant species groups. In addition we can explore the impact of changes in the particular species present in the community. In our system the biennial/short-lived perennial *Centaurea stoebe* establishes in our plots in 1992, being present in all plots by 1994. It is the only colonising species that permanently establishes and attains abundance levels on a par with the existing vegetation (Fig. 1).

In order to test whether it is the impact of climatic conditions on annuals/biennials or perennials that regulates annual/biennial–perennial spatial pattern in this community, we propose two alternative hypotheses:

1. The impact of the environment on *perennials* is critical for regulating annual/biennial–perennial spatial pattern. Perennials respond to April temperature, which is increasing through time. Annual/biennial–perennial spatial pattern will therefore show both a change in relation to changes in April temperature, and a directional trend through time.
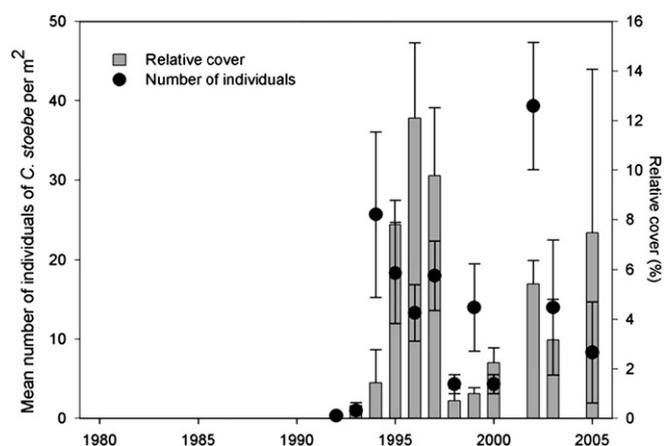

Fig. 1. Average number of individuals (dots) and relative cover (%, bars) of *Centaurea stoebe* in the study plots through time. No *C. stoebe* occurred in any plots prior to 1992. Error bars show the standard errors for the means; $n = 3$.

2. The impact of the environment on *annuals/biennials* is critical for regulating annual/biennial–perennial spatial pattern. Annuals/biennials respond to inter-annual variation in May precipitation, which does not show a directional change through time. Annual/biennial–perennial spatial pattern will therefore *not* show a long-term temporal trend, but will vary between years in line with May precipitation.

We tested which of these statements was true for our system by examining changes in annual/biennial–perennial spatial pattern through time, and against our key climate parameters. In addition we also assessed the response of spatial pattern to a number of additional climate variables to ensure that we were not excluding climatic factors that, although not driving changes in annual or perennial richness or cover (as indicated by the analysis of Matesanz et al., 2009), nevertheless influenced spatial pattern.

To explore the response of spatial pattern to change in community composition, we examined first whether changes in spatial pattern were associated with changes in overall vegetation cover. We then examined the consequences of the influx of *C. stoebe* for spatial pattern within our target community.

2. Materials and methods

2.1. Study site and data collection

The study site is located near to Halle, Germany (51° 35′ N, 11° 50′ E) at 120 m above sea level. The target community occurs on porphyritic outcrops, within a mosaic of natural and seminatural dry and semidry grasslands in an agricultural landscape (Winkler and Klotz, 1997a,b). Mean annual temperature 1979–2005 was 9.4 °C (range 7.1–11.5 °C), and mean annual rainfall 478 mm (range 260–654 mm), with peaks in precipitation in July and temperature in July–August (Fig. A.2). Despite these apparently relatively mesic conditions, the extremely shallow (5–15 cm), nutrient-poor, acidic porphyritic soils (Schubert et al., 2001), provide harsh growing conditions for plants (as indicated by a low average total cover of the community of between 15 and 50%; Matesanz et al., 2009), and water appears to be the main factor limiting plant growth. These harsh growing conditions allow steppic species to survive despite a climate which would otherwise favour more competitive species (as found in the surrounding landscape, away from the porphyritic soils). Animal disturbances are rare, except for occasional sheep grazing (less than once per year). The community is unmanaged

and species-poor, with approximately 10 species found regularly over the 26 years studied (Matesanz et al., 2009).

We split the species in our community into the two groupings of annuals/biennials and perennials as we expect the location of the annuals/biennials to be more variable between years, with the perennials being relatively long-lived and immobile "islands" within the community. The main constituent of the perennial group is the tussock-forming grass *Festuca glaucina* Vill. (Poaceae) which contributes over 60% of the total vegetation cover and is the main component of the perennials. Other species include *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) (for a full species list, see Matesanz et al., 2009). We included *C. stoebe* in the annuals/biennials group because of its relatively fast lifecycle compared to species such as *F. glaucina* within the perennials group.

To monitor the porphyritic outcrop community, three permanent 1×1 m plots were established in 1980. All three plots were located within a 10 m diameter circle, roughly equidistant but otherwise randomly located on the steppic vegetation. They were chosen so as to be typical of the porphyritic outcrop vegetation within the area. Vegetation in each plot was recorded using a square grid of 100, 10×10 cm quadrats. The number and size of all individuals of all species were mapped in each plot annually by the same observer (S.K) in spring—early summer until 2005 (excluding 2001 and 2004). Although detection of spatial pattern in relation to the environment is sensitive to both the scale of observation and the measure of environmental severity (Wiens, 1989), a 10×10 cm grain size has been found to be appropriate for detecting small-scale spatial associations in alpine plant communities (Dullinger et al., 2007) where target plants are of a similar size. For example, the mean diameter of the dominant *Festuca* plants is 2.3 cm (0.34 cm s.d), allowing space for other species to occur in quadrats with the *Festuca*, and hence it does not seem unreasonable to apply this grain size here.

2.2. Small-scale spatial analyses

Spatial pattern analyses were conducted using spatial analysis by distance indices, SADIE (Perry, 1998; Perry et al., 1999). SADIE uses spatially referenced counts and is based on the distance to regularity, the distance in space that the variable under study must move to achieve an arrangement such that all sampling points in a quadrat have the same value for that variable. SADIE provides the local index of clustering (v). This quantifies the degree to which data cluster into patches (areas with above-average counts of the study variable) and gaps (areas with below-average counts), and the degree to which each quadrat contributes to the overall data clustering.

It is also possible to analyse spatial associations between variables (Winder et al., 2001; Perry and Dixon, 2002). Local spatial association can be measured using an index (χ_i) based on the similarity between the clustering indices (v) of the two variables (e.g. the number of individuals of two species or groups) measured locally at the ith sample unit. If the values of v (local cluster index) for the first species are denoted v_1, with mean q_1 and those of the second are denoted v_2, with mean q_2, a measure of local spatial association for a sampling unit i (χ_i) is given by:

$$\chi_i = \frac{n(v_{i1} - q_1)(v_{i2} - q_2)}{\sqrt{\sum_i (v_{i1} - q_1)^2 (v_{i2} - q_2)^2}}$$

where n is the number of quadrats (100 in our study). The overall spatial association, X is the mean of these local values, $X = \Sigma i \chi_i / n$.

Also, X is the correlation coefficient between the clustering indices of each variable. We quantified the overall spatial association between perennial and annual/biennial species in each year and plot using 5967 randomizations in the permutation tests, the maximum allowed by the program.

2.3. Statistical analyses

We undertook a number of analyses to explore drivers of variation in the annual/biennial-perennial spatial pattern in our plant community.

2.3.1. Variation in spatial pattern through time

Before looking at the impact of climate or community composition, and to analyse temporal variation in spatial patterning of perennials and annual/biennials, we used association indices (X) for each year and plot as the dependent variable, and fitted regression models using the generalized least squares approach, with plot, year and their interaction as predictors. This technique allows for errors to be autocorrelated, accounting for the autocorrelation potentially present in time series data. Regression models were fitted using the "gls" function in the package "nlme" (Pinheiro et al., 2010) in R 2.12 (R Development Core Team, 2010) using corAR1 as the correlation function, with year as the time covariate and plot as the grouping factor.

We also used chronological clustering (Legendre et al., 1985; Legendre and Legendre, 1998) to identify abrupt changes in temporal trends of spatial association indices. With this method, a set of sequential clusters differing in spatial association can be identified within time series data. Chronological clustering requires two parameters: the connectedness, and α (a clustering sensitivity parameter), which quantifies the clustering resolution. We used a connectedness value of 0.2 and a small value of α (0.05), which are suitable for detecting major discontinuities in the data, and hence our analysis is relatively conservative (Zuur et al., 2007; see Almaraz and Oro, 2011 for a similar example). Chronological clustering was performed with Brodgar 2.5.1 (Highland Statistics Ltd., Newburgh, UK; http://www.highstat.com/brodgar.htm) interfaced with R 2.12 (R Development Core Team, 2010).

2.3.2. Impact of climate on spatial pattern

To explore whether variation in spatial pattern is related to local variation in climate, we again used generalized least squares models, with plot and key climatic variables, April temperature or May precipitation, as predictors. In addition, and to check that responses at the species-group level were not masking different responses at the species level, we tested the response of the relative spatial pattern of the 3 most common perennials (*F. glaucina*, *H. pilosella*, and *K. macrantha*) and the two most common members of the annuals/biennial group (*S. morisonii* and *C. stoebe*) to both of our original climate variables and to time.

To assess whether climate variables other than the two highlighted by our previous analyses might be driving changes in spatial pattern, we repeated the above analyses using additional climate parameters, specifically annual mean spring (March—May), summer (June—August), autumn (September—November) and winter (December—February) temperature (calculated as the average of the three contributing monthly mean values), and the sum precipitation values for each of these periods.

2.3.3. Impact of community cover and composition

To assess whether the impact of climate on spatial pattern might be indirect, and mediated instead through the impact of climate on overall vegetation cover or community composition, we first assessed the impact on spatial association of total, annual and

perennial cover using the same analytical approach as that used for assessing the impact of climate parameters. Second, to assess whether changes in species composition − specifically the influx of *C. stoebe* to the site − also play a role in driving changes in annual/biennial-perennial spatial pattern, we excluded this species from the dataset used to calculate the association indices, and repeated the chronological clustering analysis and analysis of the impacts of climate.

3. Results

3.1. Variation in spatial pattern through time

We found that spatial association of annual/biennials and perennials decreased significantly through time ($F_{1,60} = 7.149$, $P = 0.010$; Fig. 2a), from a random pattern toward significant dissociation. There was no effect of plot on annual/biennial−perennial spatial association ($F_{2,60} = 0.744$, $P = 0.479$), nor a significant plot × year interaction ($F_{2,60} = 0.712$, $P = 0.201$), indicating that declining spatial association through time was common across plots.

Notably, chronological clustering indicated distinct temporal groupings in the long-term trend in annual/biennial−perennial spatial association, with a major decrease in 1994 (taking clusters identified at $\alpha < 0.05$ as indicating significant changes in the time series).

3.2. Impact of climate on spatial pattern

Despite the known strong links at this study site between the abundance and species richness of annual/biennials and perennials and May precipitation and April temperature, respectively, annual/biennial−perennial spatial association showed no relationship to either April temperature or May precipitation, with there being no effect of plot or any significant plot−climate interaction effects (Table 1). Our additional analyses at the species-pair level demonstrated firstly that the relative spatial pattern of individual annual/biennial-perennial species pairings also showed no response to either of these climate variables (Appendix Table A.1). Secondly, and in contrast to the response at the species-group level, their spatial pattern showed no response to time (Appendix Table A.2).

Of the additional climate variables tested, significant effects were found only for summer precipitation and temperature (Table 1). Both climate parameters showed a positive long-term temporal trend (Fig. 3). In order to assess further the nature of the link between summer temperature and precipitation and annual−perennial spatial pattern, spatial pattern and climate data were detrended to remove the temporal trends and autocorrelation, and inter-annual variation was then calculated from the residuals of each variable (Legendre and Legendre, 1998). Inter-annual variation in spatial pattern was then regressed against that of the climate variables. These additional analyses indicated that there was no significant effect of either climate parameter following the removal of long-term temporal trends (Table 1), although there was a significant interaction effect of plot and summer temperature on annual−perennial spatial pattern (indicating that spatial pattern appeared to respond on a plot-specific basis to variation in summer temperature).

3.3. Impact of community cover and composition

Analysis of the impact of vegetation (total, perennial species, and annual species) cover on annual/biennial-perennial spatial pattern indicated no impact of any cover parameters on spatial pattern, although there was a significant interactive effect of plot
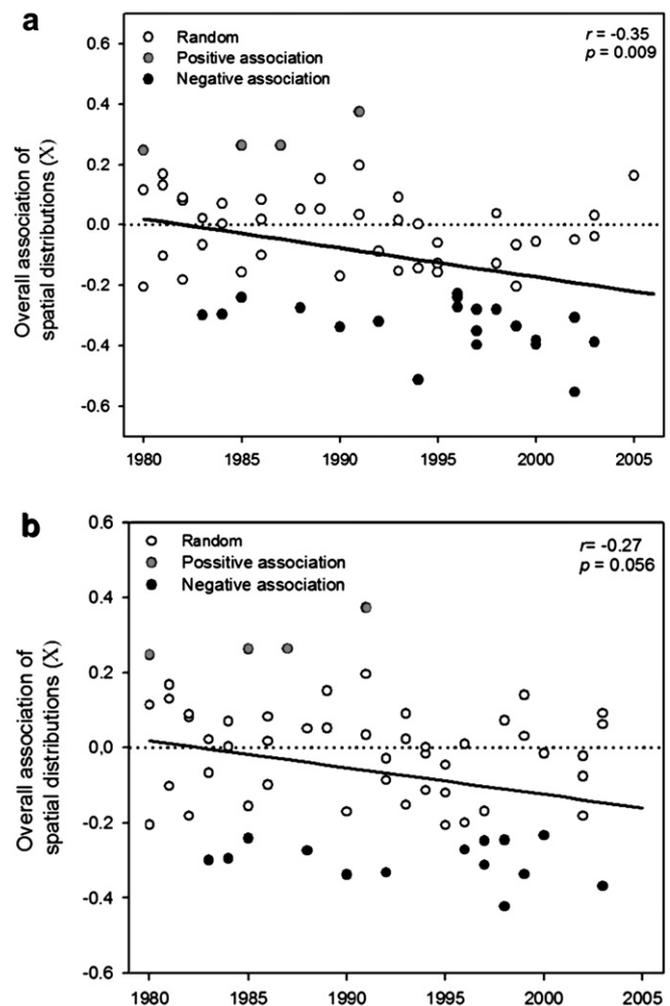

Fig. 2. Change in annual/biennial-perennial spatial pattern association index (X) through time (1980−2005) either (a) including *Centaurea stoebe* or (b) following exclusion of *C. stoebe* from the dataset. Points shown are plot-level values, with closed grey or black points showing significant positive or negative spatial associations, respectively. Regression results (*r* and *p* values) are derived from the simple linear regression between time and X, as the factor plot was not significant (see text for details).

and cover of perennial species, and a trend toward a similar interactive effect for plot and total vegetation cover (Table 2), again indicating between-plot idiosyncrasies in response.

Excluding *C. stoebe* from the data used to calculate spatial pattern affected the long-term temporal trend in annual/biennial−perennial spatial association: the negative temporal trend was now marginally non-significant (Table 3), trending less toward dissociation and with the regression line remaining in the zone of random association (Fig. 2b). Again there was no effect of plot or any plot × year interaction effect on spatial association (Table 3). Notably chronological clustering analysis in the absence of *C. stoebe* showed no temporal clustering of X at $\alpha = 0.05$ or below. Removal of *C. stoebe* from the dataset therefore removed the 1994 step-change in annual/biennial−perennial spatial association, and reduced the strength of the long-term temporal trend.

Following the exclusion of *C. stoebe*, spatial association of annual/biennials and perennials still showed no relationship to April temperature or May precipitation, with there being again no effect of plot nor any significant plot−year interaction effects (Table 3). The lack of relationship in our initial analysis was not, therefore, a consequence of *C. stoebe* − perennial relationships hiding climate-driven changes in other annual/biennial−perennial

Table 1
Results of analysis of annual/biennial-perennial spatial pattern against climatic variables: P and associated F values from the generalized least squares models for the effect of plot, the selected climate parameter, and the plot–climate parameter interaction. Significant effects ($P < 0.05$) are shown in bold, and trends ($P < 0.10$) in italics. Also shown are results of analysis of inter-annual variation of spatial pattern vs. summer temperature and precipitation following removal of the temporal trend (for details see text). Degrees of freedom are Plot = 2, Climate parameter = 1, Plot × Climate parameter = 2, residual d.f. = 60 (except for the analyses of inter-annual variation, where residual d.f. = 51 because of missing data for 1991, 2001 and 2004).

	Plot		Climate parameter		Plot × Climate parameter	
	F	P	F	P	F	P
April temperature	0.406	0.667	0.054	0.816	0.088	0.915
May precipitation	0.389	0.679	0.767	0.384	0.652	0.524
Spring temperature	0.446	0.643	2.312	0.134	2.486	*0.092*
Spring precipitation	0.361	0.699	1.723	0.194	0.390	0.679
Summer temperature	0.452	0.638	4.439	**0.039**	1.774	0.178
Summer precipitation	0.540	0.585	5.497	**0.022**	0.652	0.525
Autumn temperature	0.411	0.665	0.150	0.700	0.009	0.991
Autumn precipitation	0.551	0.579	0.707	0.404	0.576	0.565
Winter temperature	0.422	0.657	2.343	0.131	0.069	0.933
Winter precipitation	0.450	0.640	0.941	0.336	0.331	0.720
Summer temperature (temporally detrended data)	0.356	0.702	0.223	0.639	5.506	**0.007**
Summer precipitation (temporally detrended data)	0.247	0.782	1.322	0.256	0.487	0.617

spatial patterns. Furthermore, the impacts on spatial pattern of Summer temperature and precipitation were no longer significant (Table 3), although there remained a trend ($P < 0.10$) toward an effect of summer precipitation.

4. Discussion

Our analysis of long-term (26-year) variation in annual/biennial–perennial spatial pattern in this range margin steppic plant community indicated a change in spatial pattern over time from random association toward significant dissociation of these species groups. However, this change was not significantly correlated with either of two key climate parameters, May precipitation and April temperature, known to affect species richness and cover. We therefore find no support for either of our two principal hypotheses.

Given both the relatively greater between-year mobility of the annual/biennials, and the fact that plant interactions in water-limited systems are commonly asymmetric, with larger (often) perennial plants having greater impacts on smaller (often) annual species (Cheplick, 2005; Lortie and Turkington, 2008) we might expect that climatic drivers of annual/biennial cover and richness would be more important for regulating spatial pattern. The lack of response of spatial pattern to changes in April temperature (a driver of perennial success) is therefore unsurprising, but the lack of response to variation in May precipitation (a driver of annual/biennial success) is more difficult to explain.

One possible explanation is that the species groups are not interacting. However, although this is a severe environment with low productivity and cover, it would be surprising if all plant–plant interactions in this environment − including facilitation − had ceased: this occurs in *extremely* severe environments (deserts, high alpine sites, and high-latitude arctic ecosystems; Michalet et al., 2006). Alternatively, if positive and negative interactions were perfectly balanced (giving the appearance of zero net interactions), we might still expect some response in spatial pattern to climate, as inter-annual variation drives very substantial changes in the cover of annuals/perennials (Matesanz et al., 2009).
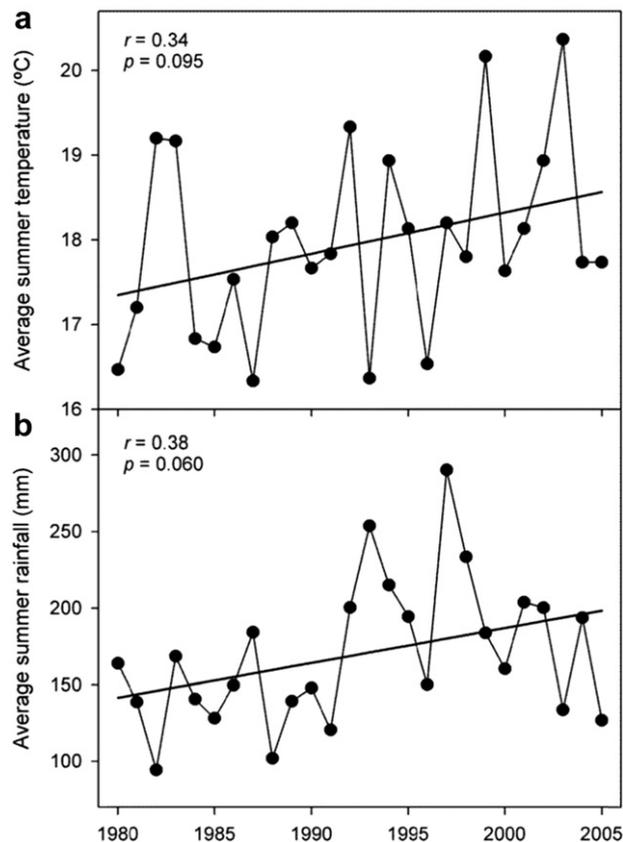

Fig. 3. Variation in (a) average summer temperature (June–August, °C) and (b) rainfall (mm) against time during the study period. Correlation results (r and p values) are shown.

An alternative explanation for the lack of response of spatial pattern to climate is that spatial pattern is driven by climate parameters other than April temperature and May precipitation. Our assessment of additional climate parameters indicated that summer temperature and precipitation were related to annual/biennial–perennial spatial pattern. Summer temperature and precipitation showed increases through time, suggesting that changes in these climate parameters drive the long-term change (increasing dissociation) in annual/biennial–perennial spatial pattern.

Increasing dissociation is generally interpreted as the consequence of increasing competition, for example during drought (e.g. Maestre and Cortina, 2004; Maestre et al., 2005, 2006; Miriti, 2007). However, for a number of reasons increased resource competition is unlikely between annuals and perennials in our plots: summer precipitation is actually increasing through time (although it is of course possible that this does not off-set the negative impact of increased temperatures on soil water availability); rooting depths differ between perennials and annuals (with drought-tolerant perennials having deeper rooting depths than annuals); stressful periods are avoided by the annuals; it is the perennials that are in long-term decline. Furthermore, inter-annual variation in spatial pattern was not related to inter-annual variation in summer temperature and precipitation, which indicates that these climate parameters are not having an immediate (year-by-year) impact on spatial pattern. This suggests that the effect of these climate parameters is indirect, and possibly mediated through changes in community composition rather than by a direct impact on plant–plant interactions.

Previous analyses (Matesanz et al., 2009) demonstrated long-term declines in total cover and cover of perennial species in this

Table 2
Results of analysis of annual/biennial-perennial spatial pattern against total vegetation cover, and cover of perennial and annual species. Columns show the degrees of freedom (d.f.), *F* values and *P* values for the analyses. Significant effects ($P < 0.05$) are shown in bold, with trends ($P < 0.10$) in italics.

Cover variable	Model parameter	d.f.	F	P
Total cover	Plot	2	0.424	0.657
	Cover	1	0.995	0.323
	Plot × Cover	2	3.140	*0.051*
	Residual	60		
Cover of perennials	Plot	2	0.411	0.665
	Cover	1	0.872	0.354
	Plot × Cover	2	4.055	**0.022**
	Residual	60		
Cover of annuals	Plot	2	0.391	0.678
	Cover	1	0.074	0.786
	Plot × Cover	2	2.165	0.127
	Residual	60		

system. However, there were no significant impacts of any metric of plant cover on spatial pattern. We also examined the possible impact on spatial pattern of the appearance in the plots of *C. stoebe*. Although native to Germany, with a range incorporating our study sites (Ochsmann, 2001; Jäger and Werner, 2005), prior to 1992 *C. stoebe* was not present in our plots, even as an occasional transient species (Fig. 1). The step-change in annual/biennial−perennial spatial association in 1994 coincides with the first occurrence of *C. stoebe* in all three plots. This step-change is lost, and the temporal trend reduced, when we exclude *C. stoebe* from the dataset.

The analysis of association of individual species pairs (Table A.2) supports the argument that the spatial relationships between *Centaurea* and the perennials are overall more negative than between the annuals (such as *Spergula*) and the perennials, and that the temporal response − particularly the step-change in spatial pattern − detected at the species-group level results in part from the arrival of *C. stoebe* rather than a gradual change in existing annual−perennial spatial pattern with time. In addition, when we exclude *C. stoebe* from the data, the impact of summer temperature and precipitation on annual/biennial−perennial spatial pattern is lost (Table 3).

Because of its relatively transient biennial nature we have included *C. stoebe* with the annuals in our spatial pattern analysis. *Centaurea*'s growth form differs from that of the other species within this grouping, being commonly a taller, more robust species. Although

Table 3
Results of analysis of annual−perennial spatial pattern against year and climate parameters following exclusion of *Centaurea stoebe* from the data used to assess spatial pattern. Columns show the degrees of freedom (d.f.), *F* values and *P* values for the analyses. Trends ($P < 0.10$) are shown in italics.

Explanatory variable	Model parameters	d.f.	F	P
Year	Plot	2	0.839	0.437
	Year	1	3.819	*0.056*
	Plot × Year	2	1.312	0.277
	Residual	57		
April temperature	Plot	2	0.738	0.482
	Climate	1	0.203	0.654
	Plot × Climate	2	0.472	0.626
	Residual	57		
May precipitation	Plot	2	0.563	0.603
	Climate	1	0.130	0.719
	Plot × Climate	2	2.637	*0.080*
	Residual	57		
Summer temperature	Plot	2	0.840	0.437
	Climate	1	1.100	0.298
	Plot × Climate	2	1.817	0.171
	Residual	57		
Summer precipitation	Plot	2	0.752	0.475
	Climate	1	3.168	*0.080*
	Plot × Climate	2	0.782	0.462
	Residual	57		

in our study plots *Centaurea* does not get particularly big (1.9 cm mean diam., 0.8 cm s.d.), *Centaurea* is present during the spring and early summer periods when resource limitation might drive competitive interactions between itself and perennial species such as *F. glaucina*. Intriguingly a form of *C. stoebe*, *C. stoebe* subsp. *micranthos*, also known as *Centaurea maculosa* (Ochsmann, 2001), is a significant invasive in North American grasslands. Even in European grasslands *Festuca* species can be strongly impacted by *Centaurea* species (Grime et al., 1987; Carey et al., 2004), and *F. glaucina* is our dominant perennial (Winkler and Klotz, 1997a; Matesanz et al., 2009).

The precise mechanism clearly requires investigation, but the establishment of *Centaurea* in these plots appears to drive much of the detected dissociation of annuals/biennials and perennials in our system, and the relationship of spatial pattern to summer climate parameters. The influx of *Centaurea* illustrates the important point, demonstrated previously by Lauenroth and Sala (1992), that sudden changes in community-level properties can result from species turnover, and that changes in species composition may have greater effects on community-level characteristics such as spatial pattern than changes in the interactions between *in situ* species in the absence of species turnover. This strengthens recent arguments concerning the species- and growth form-specific nature of interactions, both facilitative and competitive (Callaway, 2007; Maestre et al., 2009; Leger and Espeland, 2010; Lortie and Turkington, 2008). However, it should be noted that even following removal of *C. stoebe* from the spatial pattern dataset, there is still a sizable trend toward an impact of time on spatial pattern (Table 3); the influx of *Centaurea* is clearly not the only process contributing to the long-term trend in spatial pattern.

In conclusion, in our study system there appear to be no responses of small-scale annual/biennial−perennial spatial pattern to variation in climatic drivers that are known to regulate the cover and richness of these species groups. However, spatial pattern does appear to respond to additional climatic parameters whose effects may in turn be mediated through changes in community composition. This demonstrates the difficulty of extrapolating biotic processes from spatial patterns (Escudero et al., 2005; Hegazy and Kabiel, 2007), and reinforces calls (Callaway, 2007; Maestre et al., 2009) for a better understanding of the mechanistic cause of environmental severity (stress) and how it translates into spatial pattern through the mediating effect of plant−plant interactions. By breaking severity into climatic subcomponents, understanding their impact on species groups, and understanding which interactions are likely to set spatial associations, we will gain further insight into the relationship between plant−plant interactions and their translation into community-level properties. Our results clearly demonstrate the important role that the influx of new species can play in determining temporal patterns of community characteristics such as vegetation spatial pattern.
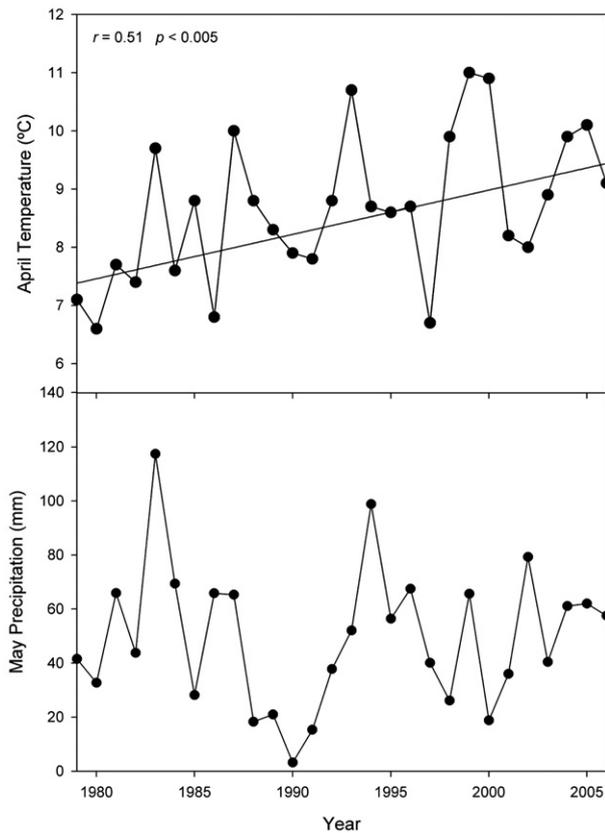
Acknowledgements

Appendix A

Figure A.1. Variation in mean April temperature (°C) and May precipitation (mm) against time (measured at the Meteorological Station Bad Lauchstädt, UFZ Centre for Environmental Research Leipzig-Halle) during the study period. There is a significant correlation between mean April temperature and time ($P < 0.005$) but not between May precipitation and time. This data has been reproduced from Matesanz et al. (2009) with permission of the Journal of Vegetation Science, the International Association of Vegetation Science, and Wiley Blackwell Publishing (Matesanz et al., 2009). Temporal dynamics of marginal steppic vegetation over a 26-year period of substantial environmental change. *J Veg Sci* 20: 299–310).
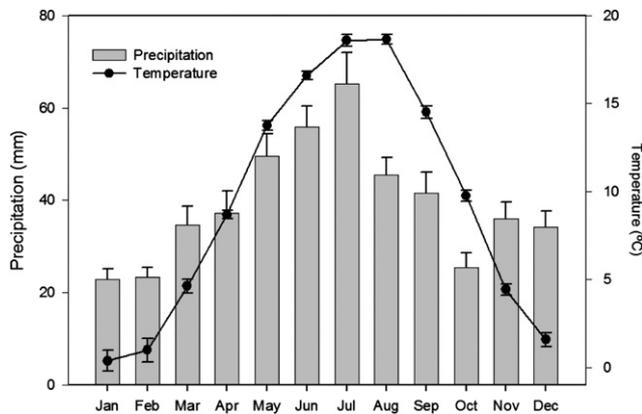

Figure A.2. Average monthly precipitation (mm) and temperature (°C) during the study period (1980–2005) recorded close to the study site (15 km distant, at the same altitude) at Meteorological Station Bad Lauchstädt, Helmholtz Centre for Environmental Research, UFZ. Error bars represent standard errors for the means.

Table A.1

Results of generalized linear model least squares regression analyses of the spatial association index (X) for each of the species pairings of the three perennial species *Festuca glaucina*, *Hieracium pilosella*, and *Koelleria macrantha*, with the annual species *Spergula morisonii* and the short-lived perennial *Centaurea stoebe*, against our two key climate parameters (April rainfall and May precipitation). Analyses were conducted as described in the Methods section for analysis of annual–perennial spatial pattern against climate parameters. Note that the residual degrees of freedom change between tests because not all species pairings are present in all years.

		Degrees of freedom	F	P
Festuca–Spergula	Plot	2	0.0541	0.9474
	April temperature	1	1.0836	0.3032
	Plot × April temperature	2	3.3174	**0.0449**
	Residuals	47		
	Plot	2	0.0351	0.9655
	May precipitation	1	1.5322	0.2219
	Plot × May precipitation	2	1.5133	0.2307
	Residuals	47		
Festuca–Centaurea	Plot	2	2.6758	0.0885
	April temperature	1	0.5008	0.4857
	Plot × April temperature	2	0.9163	0.4130
	Residuals	25		
	Plot	2	2.9650	0.0699
	May Precipitation	1	1.4725	0.2363
	Plot × May precipitation	2	0.8417	0.4428
	Residuals	25		
Hieracium–Spergula	Plot	2	0.7374	0.4841
	April temperature	1	0.6034	0.4414
	Plot × April temperature	2	0.8012	0.4551
	Residuals	45		
	Plot	2	0.7394	0.4831
	May Precipitation	1	0.5310	0.4699
	Plot × May precipitation	2	0.7712	0.4685
	Residuals	45		
Hieracium–Centaurea	Plot	2	1.3581	0.2755
	April temperature	1	0.5819	0.4527
	Plot × April temperature	2	0.6195	0.5463
	Residuals	25		
	Plot	2	1.3038	0.2893
	May precipitation	1	0.2409	0.6279
	Plot × May precipitation	2	0.9844	0.3877
	Residuals	25		
Koelleria–Spergula	Plot	2	0.1126	0.8938
	April temperature	1	1.2208	0.2754
	Plot × April temperature	2	0.4227	0.6580
	Residuals	43		
	Plot	2	0.0696	0.9329
	May precipitation	1	0.6556	0.4226
	Plot × May precipitation	2	0.2469	0.7823
	Residuals	43		
Koelleria–Centaurea	Plot	2	10.086	**0.0006**
	April temperature	1	0.0430	0.8374
	Plot × April temperature	2	0.8536	0.4379
	Residuals	25		
	Plot	2	10.1389	**0.0006**
	May precipitation	1	2.3800	0.1355
	Plot × May precipitation	2	1.0536	0.3636
	Residuals	25		

Significant effects ($P < 0.05$) are shown in bold.

Table A.2

Results of generalized linear model least squares regression analyses of the spatial association index (X) for each of the species pairings of the three perennial species *Festuca glaucina*, *Hieracium pilosella*, and *Koelleria macrantha*, with the annual species *Spergula morisonii* and the short-lived perennial *Centaurea stoebe* against time (Year). Analyses were conducted as described in the Methods section for analysis of annual–perennial spatial pattern against time. Note that the residual degrees of freedom change between tests because not all species pairings are present in all years.

Species pairing	Model factor	Degrees of freedom	F	P
Festuca–Spergula	Plot	2	0.045281	0.9558
	Year	1	0.514494	0.4767
	Plot × Year	2	3.563953	**0.0362**
	Residuals	47		
Festuca–Centaurea	Plot	2	2.257769	0.1255
	Year	1	0.548196	0.4660
	Plot × Year	2	0.701885	0.5052
	Residuals	25		
Hieracium–Spergula	Plot	2	1.32853	0.2715
	Year	1	0.05345	0.8178
	Plot × Year	2	0.29050	0.7488
	Residuals	45		
Hieracium–Centaurea	Plot	2	1.545464	0.2329
	Year	1	0.432086	0.5170
	Plot × Year	2	2.421210	0.1094
	Residuals	25		
Koelleria–Spergula	Plot	2	1.13781	0.3262
	Year	1	0.10299	0.7492
	Plot × Year	2	1.27873	0.2846
	Residuals	43		
Koelleria–Centaurea	Plot	2	6.922680	**0.0041**
	Year	1	1.423905	0.2440
	Plot × Year	2	2.280731	0.1231
	Residuals	25		

Significant effects ($P < 0.05$) are shown in bold.

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