

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

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1 **Abstract**

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

7 **Location:** A range-margin steppic grassland community in Central Germany.

8 **Methods:** Cover, number and size of all individuals of all plant species present in three
9 permanent 1-m² plots were recorded during spring for 26 years (1980 to 2005). Climatic
10 data for the study area was used to determine the best climatic predictor for each plant
11 community, functional group or species variable (annual data and interannual variation)
12 was determined with best-subsets regression.

13 **Results:** April and autumn temperature showed the highest correlations with both total
14 cover and species richness and interannual variation of cover and richness. However,
15 key climate drivers differed between the five most abundant species. Likewise, total
16 cover and number and cover of perennials significantly decreased over time, while no
17 trend was found for the cover and number of annuals. However, within functional
18 groups there were again contrasting species-specific responses. Long-term temperature
19 increases and high interannual variability in both temperature and precipitation were
20 strongly related to long-term trends and interannual variation in plant community data.

21 **Conclusions:** Temporal trends in vegetation were strongly associated with temporal
22 trends in climate at the study site, with key roles for autumn and spring temperature and
23 precipitation. Dynamics of functional groups and species within groups and their
24 relationships to changes in temperature and precipitation reveal complex long-term and
25 interannual patterns that cannot be inferred from short-term studies with only one or a

1 few individual species. Our results also highlight that responses detected at the
2 functional-group level may mask quite contrasting responses within functional groups.
3 We discuss the implications of these findings for attempts to predict the future response
4 of biodiversity to climate change.

5 **Keywords:** range-margin plant communities, climate change, perennial and annual
6 plants, cover, species richness

7 **Nomenclature:** Jäger & Werner (2005).

8

9 **Introduction**

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

21 Here we examine patterns of vegetation dynamics (long-term trends and
22 interannual variation) over a 26-year period in a range-margin steppic community in
23 Central Germany. This community is at the western distributional limit for this
24 community type, being under the warmest and most humid (i.e. most oceanic)
25 conditions within its range. These steppic communities are xeric in nature, and long-

1 term data from xeric systems is particularly scant despite their potentially high
2 sensitivity to environmental change (WallisDeVries et al. 2002; Stadler et al. 2007).

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

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

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

15

16 **Methods**

17 *Study Site*

18 The study area is a relatively arid region near Halle, Central Germany (51° 35' N, 11°
19 50' E) at 120 m a.s.l. on porphyritic outcrops with shallow soils characterized by a
20 mosaic of natural and seminatural dry and semidry grasslands within an agricultural
21 landscape (Winkler & Klotz 1997a,b). Mean annual temperature for the 1979-2005
22 period was 9.4 °C (range 7.1-11.5°C), and mean annual rainfall was 478 mm for the
23 same period (range from 260 to 654 mm; Meteorological Station Bad Lauchstädt of the
24 Helmholtz Centre for Environmental Research – UFZ; 15 km away from the plots at the
25 same altitude and similar topography).

1 The community studied has an average cover of 15-50% on extremely shallow
2 (5-15 cm), dry, nutrient-poor and acidic soils (Schubert et al. 2001). It is a remnant of
3 the postglacial natural vegetation of the area (more than 10⁴ years old) and covers small
4 areas of 10- 1000 m² within a mosaic of different communities. The underlying substrate
5 creates harsh conditions for plant growth and water appears to be the most limiting
6 growth factor. The community is not managed, except for occasional grazing by sheep
7 (less than once per year). During periods of grazing off-take levels are extremely low:
8 grazers appear to concentrate on the more attractive and productive neighbouring
9 vegetation types that are found outside the porphyritic outcrops. The community is
10 relatively species-poor, with an average of 10 species per m² found regularly over the
11 26 years studied. The main constituent of the community is *Festuca glaucina* Vill.
12 (Poaceae), a long-lived, tuft-forming grass. Other species present include perennial
13 grasses and herbs such as *Thymus serpyllum* L. (Labiatae), *Koeleria macrantha*
14 (Ledeb.) J.A. Schultes (Poaceae), *Hieracium pilosella* L. (Compositae) or *Silene otites*
15 (L) Wib (Caryophyllaceae), and a number of spring ephemerals such as *Spergula*
16 *morisonii* Boreau (Caryophyllaceae) or biennials like *Centaurea stoebe* L (Compositae).
17 For a full species list see Appendix 1. For the rest of this manuscript “annuals” refers to
18 both true annuals and the biannual *C. stoebe*.

19

20 *Data collection*

21 In 1980, three permanent plots of 1m x 1m were established within the porphyritic
22 outcrop community and marked with metal sticks. Vegetation composition was then
23 recorded every year until 2005 (2001 and 2004 data are missing). All three plots were
24 located within a 10 m diameter circle. The total size of the outcrop was more than 500
25 m². The plots were recorded once every year in spring or early summer by the same

1 observer (Stefan Klotz). Each plot was sampled using a square grid of 100 cells 1 dm²
2 in size, placed above the vegetation so disturbance due to sampling was minimal. The
3 number and size of all individuals was mapped each year.

4

5 *Correlations with climatic variables and statistical analyses*

6 Relationships between plant community variables and climatic data were assessed by
7 best-subset regression, a model-building technique which finds subsets of predictor(s)
8 variable(s) that best predict responses on a dependent variable by linear regression (Zar
9 1999), which is commonly used in detection of climate impact (e.g. Menzel 2003).
10 Temperature and precipitation data (monthly, 2- and 3-monthly means) of the recording
11 year (from January to measurement date) and the preceding year were used to build the
12 best single-predictor models. Plant community variables analysed were cover and
13 species richness of the community as a whole, and the same for individuals of
14 perennials (23 species) and annuals (11 species), as well as cover of the dominant
15 species, three perennial and two annual species (see below) that together represented
16 more than 80% of the plant cover.

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

22 The existence of temporal trends in the composition and cover of the plant
23 community were tested by means of a General Linear Model (GLM) for each dependent
24 variable: cover and species richness for the full community and functional groups, with
25 plot as a categorical predictor and year as a continuous predictor, as well as separate

1 analyses for the dominant species. When the assumptions of the model (constant
2 variance, normality and independence of the residuals) were not satisfied, the dependent
3 variable was log-transformed to meet the assumption of constant variance of the
4 residuals, and a lagged version of the dependent variable was used as a covariate to
5 meet the assumption of independence of the residuals (i.e. to account for the
6 autocorrelation of the residuals). We further explored species-level variation in cover
7 through PCA analyses and linear regression of the cover of each species against time.
8 Finally, the relationships among the dependent variables were tested with simple linear
9 Pearson correlation.

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

17

18 **Results**

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

1 Poaceae (17%). The average number of species found per year was 10 (ranging from 5
2 to 14), with 20% of them being annual species (see Appendix 1 for cover and frequency
3 values for each species).

4

5 *Relationships between climate and plant community data*

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

9 The best climatic predictor for total cover and species richness was mean April
10 temperature (Table 1), with higher April temperatures associated with lower total cover
11 and species richness. The same was true for the cover of the perennial species, whilst
12 the number of perennials was most closely correlated with mean April-May temperature
13 and also showed a negative relationship. By contrast, the best climatic predictor for the
14 cover and number of annual species was May precipitation, which correlated positively
15 with these two variables. However, when the responses of the five dominant species
16 were examined, species-specific patterns were found that did not match functional-
17 group level patterns. For the perennials, while the cover of *F. glaucina* and *H. pillosela*
18 responded negatively to increasing April temperatures, *K. macrantha* responded
19 positively to December-January precipitation. April-May and September precipitation
20 were, respectively, the best predictors for the cover of the two most abundant annual
21 species, *S. morisonii* and *C. stoebe* (Table 1).

22 The relationships between interannual variation in plant community and climatic
23 data were also dependent on functional groups and individual species. Interannual
24 variability in autumn (September-November) temperature was the best predictor for the
25 interannual variability in both total cover and cover of the perennial species (Table 1).

1 Interannual variation in species richness and the number of perennial species was best
2 correlated with the interannual variability in April and April-May temperature,
3 respectively, concurring with the relationships found using the raw annual data.
4 Similarly, interannual variation in the cover and number of annual species correlated
5 with the interannual variation in April-May and spring (March-May) precipitation
6 (Table 1). At the species level, the best predictors for the interannual variation in the
7 cover of *F. glaucina* and *K. macrantha* were autumn and October-November
8 temperature, respectively. The interannual variation in the cover of *Hieracium pilosella*
9 was again correlated with interannual variation in April temperature. Finally, the
10 interannual variation in the two dominant annual species, *C. stoebe* and *S. morisonii*,
11 was best correlated with interannual variation in October-November temperature and
12 April-May precipitation.

13

14 *Temporal trends in plant community data*

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

20 Total cover showed a significant (50%) decline during the study period (Table
21 2). The same trend was found for the cover of the perennial species, but cover of annual
22 species showed no significant trend (Table 2). However, contrasting responses were
23 again found for different species within functional groups (Table 3). Cover of the
24 perennials *F. glaucina* - the species that accounted for most of the community cover -
25 and *H. pilosella* declined significantly over time ($R = -0.44$, $P < 0.01$ and $R = -0.64$, $P <$

1 0.001, respectively). In contrast, cover of the perennial *K. macrantha* did not
2 significantly change over time. While cover of the annual *S. morisonii* decreased over
3 time ($R = -0.42$, $P < 0.01$), cover of the annual *C. stoebe* increased significantly ($R =$
4 0.62 , $P < 0.001$; Table 3).

5 PCA analyses and linear regression of the cover of each species against time
6 highlighted three main groupings within those species occurring with sufficient
7 frequency to be included in the analysis: decreasing, constant and increasing species
8 (Fig. 1). These grouping did not entirely concur with our functional groups. Annual and
9 perennial species were present in both the constant and decreasing groupings. However,
10 only annual species were present within the increasing group and of these only *C.*
11 *stoebe* had substantial (but still limited) cover (Fig. 1 and Appendix 1).

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

19

20 *Temporal changes in climatic conditions*

21 During the period 1980-2005, mean annual temperature in our study area increased by
22 1.4°C (based on predicted values from linear regression of temperature against time,
23 from 1980 to 2005, $R = 0.38$, $P < 0.05$). April temperature increased by 2.3°C (Fig. 2).
24 There was no significant change in autumn temperature. However, both mean annual
25 temperature and April and autumn temperature were positively correlated ($R = 0.36$, $P <$

1 0.05; $R = 0.58$, $P < 0.001$ respectively). Likewise, there were no significant changes in
2 annual precipitation ($R = 0.09$, $P = 0.65$), or in May precipitation ($R = -0.08$, $P = 0.94$;
3 Fig. 2) during the study period. May precipitation and annual precipitation were highly
4 correlated ($R = 0.63$, $P < 0.001$).

5

6 **Discussion**

7 As for the analysis of many long-term data series (Parmesan & Yohe 2003) this study is
8 inevitably correlative. However, there is strong evidence that interannual variability and
9 long-term changes in local climate played a significant role in plant community
10 dynamics. The relationships detected between climate drivers and vegetation can be
11 explained by the ecology of the key species. In general, annuals in these systems
12 germinate and grow in response to the favourable water balance in autumn and spring
13 (Winkler & Klotz 1997a,b), which concurs with our observed response of annuals to
14 rainfall. Perennials integrate the precipitation-temperature balance over the course of the
15 full year and may thus be more responsive to temperature, as observed. Despite these
16 common patterns, the five most abundant species showed species-specific variation in
17 climate responses regardless of their functional group. The highly significant
18 relationships detected between climate (particularly spring conditions) and plant
19 performance support the hypothesis that species within xeric range-margin communities
20 are highly responsive to changes in climate. Furthermore, these results highlight that
21 responses detected at the functional-group level may mask quite contrasting responses
22 within functional groups.

23 Analyses of interannual variation supported the proposed influence of climate on
24 vegetation in this system, particularly the role of spring conditions: interannual variation
25 in spring temperature (April or April-May) or precipitation (April-May or March-May)

1 was strongly related to interannual variability in many of the plant community variables
2 (e.g. species richness, number of perennial and annual species, cover of annual species
3 and cover of *Hieracium pilosella* and *Spergula morisonii*). However, autumn
4 temperatures had an important influence on total cover, cover of the perennials, and
5 cover of *Festuca glaucina*, *Koeleria macrantha* and *Centaurea stoebe*, concurring with
6 previous studies highlighting the importance of autumn conditions for the germination
7 of these species (Bruun et al. 2007; Winkler & Stöcklin 2002). Other studies have also
8 found that short-term or interannual climatic variability has a strong influence on plant
9 community dynamics and physiology (Peñuelas et al. 2007; Martínez-Alonso et al.
10 2007; MacDougall et al. 2008) and so it is reasonable to conclude that interannual
11 variation in climate is partly driving interannual variation in vegetation.

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

22 Factors like land use and pollution probably play a proportionately small role in
23 our study area. Land management activities and grazing are relatively unimportant
24 drivers because the community is not managed and livestock are rarely present on the
25 site. Neighbouring vegetation is more attractive to grazers and grazing is rare.

1 Furthermore, grazing - unless at very high levels - would lead to increased community
2 productivity and invasion of more competitive species (Milchunas & Lauenroth 1993):
3 in contrast we see a general long-term decline in cover in this system. On the other
4 hand, nitrogen deposition can directly influence the productivity and dynamics of
5 ecosystems (Bobbink 1998; Bobbink et al. 1998; van der Wal et al. 2003). However,
6 while local output of some pollutants decreased considerably after German reunification
7 (e.g. 86% decrease in particulates emissions from 1990 to 1999), increased transport
8 emissions and agricultural activity have largely maintained N deposition levels (e.g.
9 18% decrease in NH₄ deposition in the same period; Environmental data Germany,
10 <http://www.umweltdaten.de>). Reduced N deposition would favour slow-growing stress
11 tolerant species typical of the environment examined in our study (van der Wal et al.
12 2003), and is unlikely to have lead to the detected declines in species cover and
13 richness.

14 There is a considerable body of evidence indicating a primary role for water
15 availability in determining plant performance in xeric communities (Churkina et al.
16 1999; Sternberg et al. 1999; Zavaleta et al. 2003; Lloret et al. 2004). Increased
17 temperature could lead to reduced plant water availability even if it is not associated
18 with long-term decreases in precipitation (as in our case). Furthermore, solar radiation
19 may also influence water availability. This region experienced a significant increase in
20 solar radiation during the study period ($R = 0.85$, $P < 0.0001$; Fig. 2). Although contrary
21 to the well-known ‘solar dimming’ (Stanhill & Cohen 2001), this trend is consistent
22 with recent reports of a reversal from dimming to brightening during the 1990s in many
23 regions (Wild et al. 2005; Pinker et al. 2005) and substantial (86%) recent reductions in
24 particulate emissions in our region. To test for the combined impact of climate trends on
25 water availability, we calculated potential evapotranspiration (PET) values for typical

1 dry and wet days in the first and last two years of the study period using the Penman
2 calculator (<http://www.tfrec.wsu.edu/Orchard/pET/pETCalc.html>, Penman 1948). These
3 calculations show a possible 40-90% increase in PET (wet and dry April days
4 respectively, 0.5-2.0 mm in 1980-81 to 0.7-3.8 mm in 2004-2005) during this time.
5 Increased water stress is therefore likely to have contributed to the significant decrease
6 in total plant cover and cover of two of the dominant perennial species over the study
7 period. Similar findings were observed by Anderson & Inouye (2001) in sagebrush
8 steppe and by Morecroft et al. (2004) in temperate grassland systems. Although the
9 cover of the other three dominant species did not change significantly over the study
10 period, this is also consistent with climatic trends at this site: their success correlates
11 strongly with precipitation or autumn temperature, which showed no long-term
12 temporal trend.

13 We did not find a significant temporal trend in total species richness, but there
14 was a negative correlation of total species richness and its interannual variation with
15 April temperature. Previous studies have reported responses of community species
16 richness to changes in climate (Chapin et al. 1995; Dunnet et al. 1998; Zavaleta et al.
17 2003). Chapin et al. (1995) found that elevated temperature led to the loss of 30-50% of
18 species after 9 years in an arctic tundra community, and Stenberg et al. (1999) found a
19 significant decrease in species richness after winter warming in calcareous grassland.
20 However, these species losses were driven by expansion of dominant perennial species.
21 In our study perennial species and total cover declined over time. As adult perennial
22 species in xeric systems may produce favourable microclimatic conditions for
23 germination (Gomez-Aparicio et al. 2004; Maestre et al. 2005), both reduced adult
24 perennial plant cover and the direct negative effects of increased environmental severity
25 may limit seedling germination and establishment, increasing the chances of species

1 loss. However, the number of annual species showed a significant increase through
2 time, and 2 annual species were grouped together in our PCA analysis because of a
3 common trend toward increased cover through time. Annual species may be less
4 dependent on facilitation from perennials for germination – they germinate at times of
5 increased water availability. Additionally, decreasing cover of two perennials may be
6 enabling the establishment of annual species through reduced competition. This is
7 concluded by the negative correlations between total cover and either the cover or the
8 number of annuals species, providing evidence for the role of interactions between
9 species in mediating climate change impacts on plant communities (McCarthy 2001;
10 Fitter & Fitter 2002; Brooker 2006).

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

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

12

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1 **Table 1.** Relationships between plant data and climatic variables, determined according
2 to best-subsets regression (see text for details). Top: Relationships between total plant
3 cover and species number, cover and number of perennial and annual species, and cover
4 of the five most dominant species with climatic variables. Bottom: Relationships
5 between the interannual variation of each dependent variable and the interannual
6 variation in climate. *R* coefficient, sign and significance are shown for each relationship;
7 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
8

Raw data		
Variable	Best climatic predictor	<i>R</i>
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***
<i>Festuca glaucina</i> (<i>F. g.</i>)	Mean April Temperature	-0.31***
<i>Hieracium pillosela</i> (<i>H. p.</i>)	Mean April Temperature	-0.56***
<i>Koeleria macrantha</i> (<i>K. m.</i>)	December-January Precipitation	0.60***
<i>Spergula morisonii</i> (<i>S. m.</i>)	April-May Precipitation	0.50***
<i>Centaurea stoebe</i> (<i>C. s.</i>)	September Precipitation	0.41***
Interannual variation data		
Variable	Best climatic predictor	<i>R</i>
TC Interannual variation	Autumn (Sept.-Nov.) Temp. Interannual variation	-0.54***
SR Interannual variation	April Temp. Interannual variation	-0.44***
CP Interannual variation	Autumn Temp. Interannual variation	-0.56***
NP Interannual variation	April-May Temp. Interannual variation	-0.51***
CA Interannual variation	April-May precipitation Interannual variation	0.47***
NA Interannual variation	Spring precipitation Interannual variation	0.40***
<i>F. g.</i> cover Interannual variation	Autumn Temp. Interannual variation	-0.70***
<i>H. p.</i> cover Interannual variation	April Temp. Interannual variation	-0.32*
<i>K. m.</i> cover Interannual variation	Oct.-Nov. Temp. Interannual variation	-0.47***
<i>S. m.</i> cover Interannual variation	April-May precipitation Interannual variation	0.50***
<i>C. s.</i> cover Interannual variation	Oct.-Nov. Temp. Interannual variation	0.30**

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

7

Variable	Source of Variation	Degrees of freedom	F	P	Temporal trend
Total Cover	Plot	2	12.0212	< 0.0001	-
	Year	1	33.5183	< 0.0001	
	Plot x 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 x Year	2	2.7845	0.0690	
	Residuals	66			
Cover of Annual Species *	Plot	2	0.4586	0.6341	N.S.
	Year	1	0.8247	0.3670	
	Plot x Year	2	2.4263	0.0962	
	Residuals	66			
Total Species Richness	Plot	2	0.441	0.6450	N.S.
	Year	1	0.348	0.5571	
	Plot x 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 x 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 x Year	2	0.8296	0.4407	
	Residuals	66			

8

9

10

1 **Table 3.** Results of the General Linear Model (degrees of freedom, F and *p*-values) for
 2 temporal trends in the cover of the dominant species. Variables with an asterisk were
 3 log-transformed and a lagged version of the variable was added to satisfy the
 4 assumptions of the model. P = Perennial, A = Annual. Selected species accounted for
 5 80% of total cover in the plant community. Temporal trends over the study period -
 6 negative (-), non-significant (N.S.), and positive (+) – are also shown.

7

Variable	Source of Variation	Degrees of freedom	F	P	Temporal trend
<i>Festuca glaucina</i> (P)	Plot	2	1.22436	0.3005	
	Year	1	9.97116	0.0023	-
	Plot x Year	2	1.22132	0.3014	
	Residuals	66			
<i>Hieracium pilosella</i> (P)	Plot	2	12.52774	< 0.0001	
	Year	1	7.72193	0.0071	-
	Plot x Year	2	6.25013	0.1331	
	Residuals	66			
<i>Koeleria macrantha</i> (P)	Plot	2	20.1945	< 0.0001	
	Year	1	0.0154	0.9015	N.S.
	Plot x Year	2	9.3088	0.275	
	Residuals	66			
<i>Spergula morisonii</i> (A)	Plot	2	0.999551	0.3735	
	Year	1	7.727734	0.0070	-
	Plot x Year	2	0.989174	0.3773	
	Residuals	66			
<i>Centaurea stoebe</i> * (A)	Plot	2	2.51165	0.0888	
	Year	1	31.03772	< 0.0001	+
	Plot x Year	2	2.52746	0.0875	
	Residuals	66			

8

Figure 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 less than 3 years in the 26-years 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 1) according to their temporal trend.

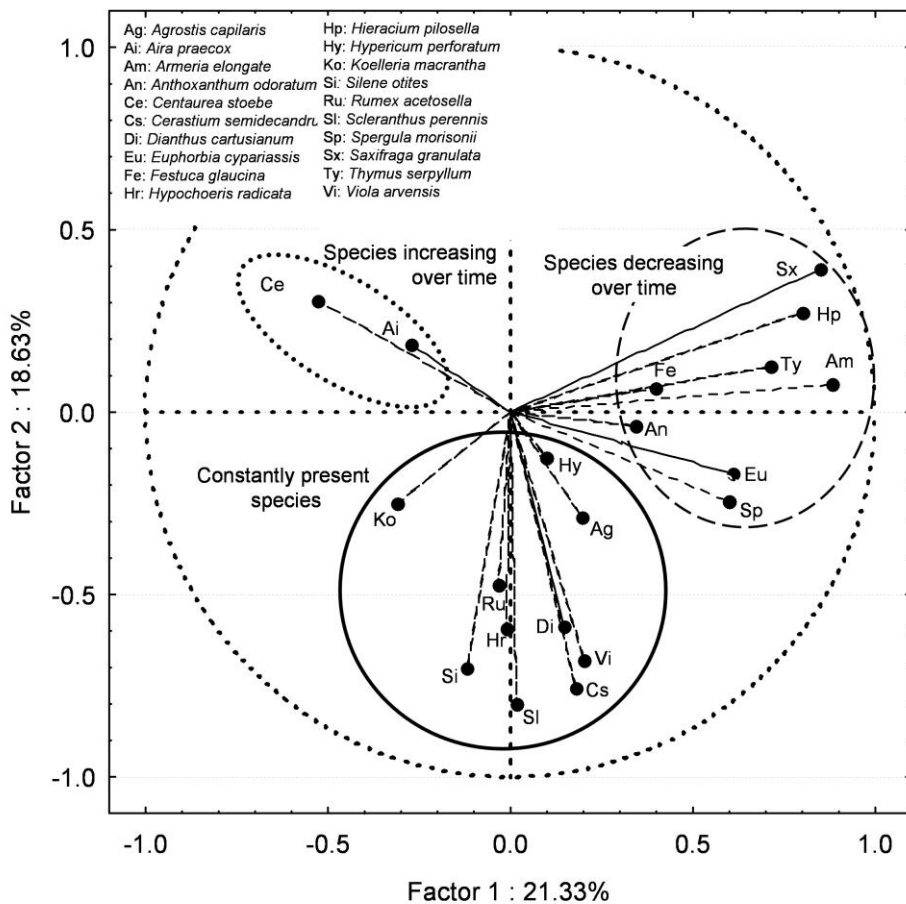
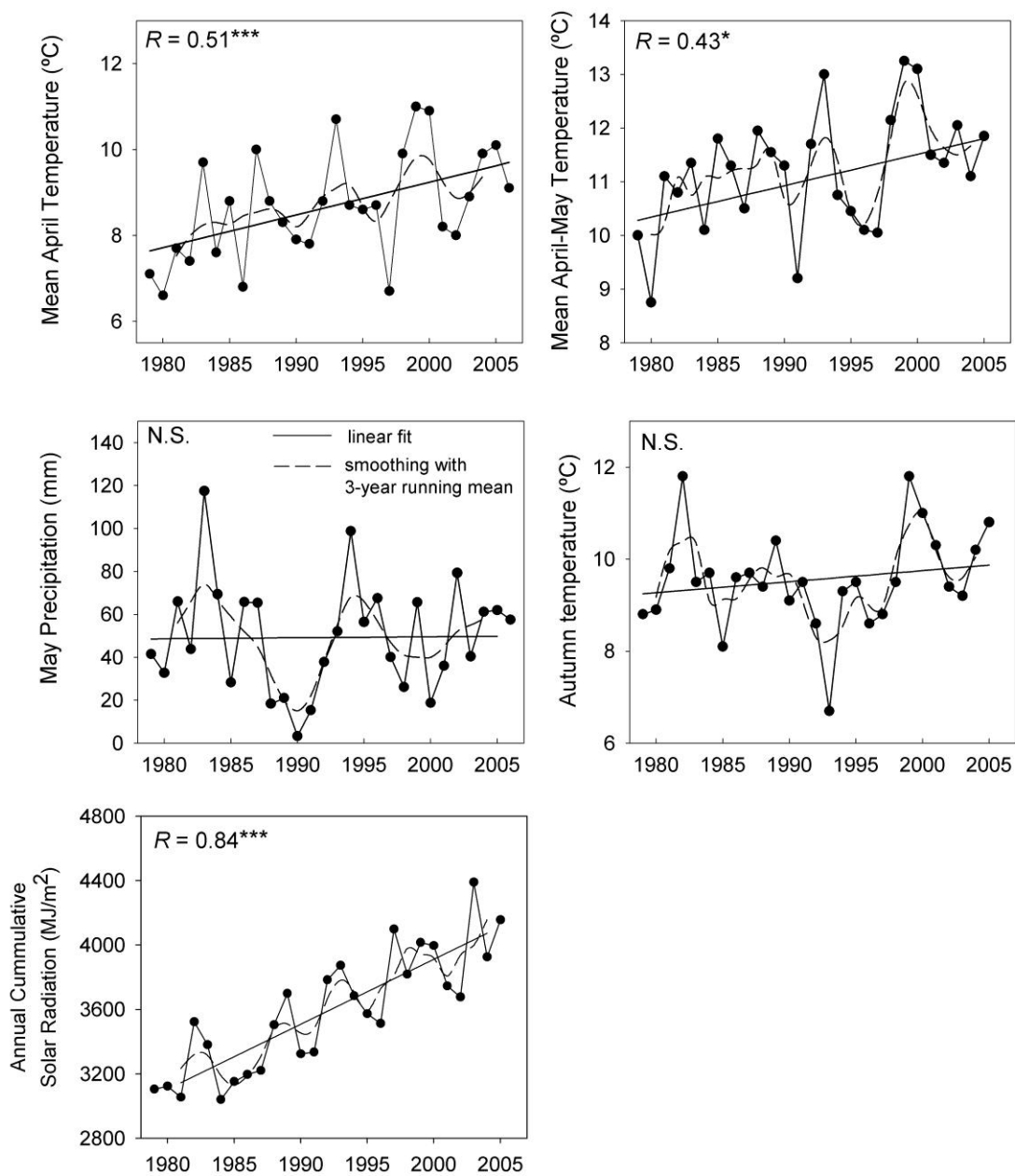


Figure 2. Trends for climatic variables in the study area (measured in Meteorological Station Bad Lauchstädt of the UFZ-Centre for Environmental Research Leipzig-Halle) during the period of study. Mean April temperature (upper left), Mean April-May temperature (upper right), May precipitation (middle left), Autumn temperature (middle right) and annual cumulative solar radiation (bottom left). * $P < 0.05$, ** $P < 0.01$, P *** < 0.001 , N.S., non significant.



Appendix 1. Percentage of each species in each plot and year. Species are grouped in relation to temporal trends over the study period following linear regression and PCA analysis (Fig. 1). RG= PCA and regression response group, CD=Common species decreasing, RD=Rare species decreasing, CI=Common species increasing, RI=Rare species increasing, Con=Constant over time, EI=Extremely infrequent species (excluded from PCA analysis), FG=Functional group, A=Annual (including the biannual *C. stoebe*), P=Perennial. Total cover, percentage of bare soil, and number of species are also shown.

PLOT 1		RG	FG	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2002	2003	2005
Species																											
<i>Festuca glauca</i>	CD	P	16.2	14.59	22.71	14.89	19.49	19.84	20.56	14.23	20.74	17.46	12.3	15.65	14.56	17.36	14.71	8.32	9.05	8.66	9.94	14.78	13.49	13.14	14.64	6.51	
<i>Hieracium pilosella</i>	CD	P	13.01	0.39	0.18	0.15	0.18	1.02	1.05	0.06	0.18	0.12	0	0	0	0.09	0.39	0.24	0.27	0.69	0.87	0.57	0.09	0.75	1.23	0.27	
<i>Euphorbia cyparissias</i>	CD	P	0.9	1.82	6.31	1.8	1.99	1.55	1.98	1.23	2.63	3.11	2.28	2.69	0.1	0.15	0.1	0.1	0.3	0.35	0.3	0.3	0.07	0.602	0.23	0.73	
<i>Spergula morisonii</i>	RD	A	0	0	0.15	2.98	0.1	1.4	0.1	0	0	0	0.008	0.3	0.103	0.202	0.001	0.037	0.004	0.077	0.01	0.014	0.002	0.112	0.06	0	
<i>Anthoxanthum odoratum</i>	RD	P	0	0.23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armeria elongata</i>	RD	P	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	
<i>Saxifraga granulata</i>	RD	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thymus serpyllum</i>	RD	P	1.8	0	0	0	0	0	0.2	0	0.15	0	0	0.1	0	0	0	0.001	0	0	0	0	0	0.006	0.05	0	
<i>Centaurea stoebe</i>	CI	A	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.4	1.14	0.95	2.4	1.98	0.02	0.24	0.56	1.33	1.33	2.38	
<i>Aira praecox</i>	RI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	
<i>Cerastium semidecandrum</i>	Con	A	0	0.014	0	0.001	0.001	0	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Agrostis capillaris</i>	Con	P	0.25	0	0.5	0	0.65	2.15	2.55	1.16	2.55	1.55	0.75	2.67	1.35	1.4	6	0.52	0.1	0.17	0.35	0	0.15	0.45	0.3	0.37	
<i>Dianthus cartusianum</i>	Con	P	0.2	0	0	0.95	1.05	0.65	1	1.4	1.6	1.66	1.33	0.53	0.001	0.2	0.001	0	0	0	0	0	0	0	0	0.02	
<i>Hypericum perforatum</i>	Con	P	0	0	0	0	0.25	0.1	0.151	0	0.4	0.15	0.1	0.05	0	0	0.102	0.2	0.22	0	0	0.001	0.3	0.15	0		
<i>Hypochoeris radicata</i>	Con	P	0	0	0	0.15	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Koeleria macrantha</i>	Con	P	1.7	1.6	2.05	1.65	4.93	4.83	6.27	5.85	7.64	7.16	4.33	4.61	3.853	4.33	4.7	1.398	1.1	0.83	1.55	1.33	1.62	1.733	2.03	1	
<i>Silene otites</i>	Con	P	0	0	0	0	0.8	0.95	1.15	1.13	1.08	1.3	1.66	1.97	1.2	0.98	0.5	1.38	0.43	0.05	0.4	0.001	0	0	0	0	
<i>Rumex acetosela</i>	Con	P	0	0	0	0	1.1	1.58	0.1	0	0	0	0	0.6	0.002	0.002	0.2	0.017	0	0	0	0	0.9	0	0		
<i>Viola arvensis</i>	Con	A	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0.001	0	0	0	
<i>Scleranthus perennis</i>	Con	P	0	0	0	0	1.3	0	0	0	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0.2	0.15	0	
<i>Erophila verna</i>	EI	A	0.009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Campanula rotundifolia</i>	EI	P	0.88	0	0	1.58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Gallium sp.</i>	EI	P	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Lactuca serriola</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	
<i>Myosotis stricta</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	
<i>Scleranthus annuus</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	
<i>Senecio vernalis</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Achillea millifolia</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Festuca ovina</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0.05	0	0	0	0	
<i>Luzula campestris</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Plantago lanceolata</i>	EI	P	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Poa sp.</i>	EI	P	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Taraxacum officinalis</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0	0	0	0	0	0	0	0	
<i>Arenaria serpyllifolia</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0.15	0	0	0	0	0	0	0	0	0.272	0.18	0	
Bare soil (%)			64.75	81.35	68.1	75.85	68.01	65.93	64.79	74.94	63.03	67.39	77.24	70.72	78.58	74.69	72.26	86.74	86.14	86.98	86.56	82.71	84.02	80.1	79.45	88.72	
Total Cover (%)			35.25	18.65	31.9	24.15	31.99	34.07	35.21	25.06	36.97	32.61	22.76	29.28	21.42	25.32	27.74	13.26	13.86	13.02	13.44	17.29	15.98	19.9	20.55	11.28	
N. of species			11	7	6	9	13	10	13	7	9	9	8	11	10	11	10	15	9	9	8	8	9	14	12	7	

PLOT 2

Species	RG	FG	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2002	2003	2005
<i>Festuca glauca</i>	CD	P	15.11	15.64	19.68	7.89	11.41	12.59	15.8	11.85	17.02	17.1	12.11	11.23	10.73	16.7	19.15	11.43	9.61	11.61	12.89	13.11	10.09	14.89	19.28	3.94
<i>Hieracium pilosella</i>	CD	P	5.3	0.21	0.66	0.12	1.23	1.89	2.85	1.08	2.16	0.99	0.48	0.42	0.15	0.6	2.52	0.96	0.66	1.68	3.09	3.3	2.31	3.72	6.04	0.69
<i>Euphorbia cyparissias</i>	CD	P	0.7	0.29	1.5	0	0.25	0.2	0.35	0.28	0.35	0.11	0.23	0.1	0	0	0	0.05	0	0.13	0.12	0.1	0.1	0	0.8	1.81
<i>Spergula morisonii</i>	RD	A	0	0	0.9	7.12	6.55	1.447	0.563	0.35	0.702	0.45	0.013	3.71	0.939	0.26	0.002	0.023	0.005	0.039	0.011	0.031	0	0.231	0.04	0
<i>Anthoxanthus odoratum</i>	RD	P	0	1.401	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armeria elongate</i>	RD	P	0.1	0.25	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Saxifraga granulata</i>	RD	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thymus serpyllum</i>	RD	P	4.1	0.23	0.15	0	0.03	0.1	0.25	0.8	1.15	0.83	1.43	1.45	0	0	0	0	0	0	0	0	0	0	0	0
<i>Centaurea stoebe</i>	CI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.25	1.1	0.89	1.49	0.06	0.24	0.2	0.86	0.73	0.21
<i>Aira praecox</i>	RI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.063	0	0
<i>Cerastium semidecandrum</i>	Con	A	0	0.009	0	0.003	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Agrostis capilaris</i>	Con	P	2.8	0	5.5	0	0.91	4.45	6.15	3.57	5.5	0.75	0.4	0.75	0.3	0.65	2.45	1.61	1.12	2.81	1.5	0.62	0.25	1.2	2.3	1
<i>Dianthus cartusianum</i>	Con	P	0.2	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0.1	0.001	0.1	0.15	0	0.3	0.2	0.15
<i>Hypericum perforatum</i>	Con	P	0	0	0	0	0	0.05	0.001	0.13	0	0	0	0	0	0	0	0	0.2	0.23	0.053	0.001	0.15	0.601	0.1	0.2
<i>Hypochoeris radicata</i>	Con	P	0	0	0	0.2	0.77	0.85	0	0	0.55	0	0	0	0	0	0	0.401	0.1	0.001	0	0.003	0	0	0	0
<i>Koelleria macrantha</i>	Con	P	0.7	0.752	0.7	0.2	0.001	0.65	1.55	1.15	1.75	0.63	1.05	0.86	0.55	1.45	1.85	0.547	0.25	0.4	0.85	0.4	0.4	1.45	1.1	0.65
<i>Silene otites</i>	Con	P	0	1.15	1.35	0.85	0.35	1.1	0.55	0.48	0.4	0.53	0.33	0.481	0.05	0.2	0	0.75	0.2	0.2	0.2	0.701	0.3	0.7	0	0
<i>Rumex acetosela</i>	Con	P	0	0	0	0	0	0	0	0	0	0	0.1	0.772	0	0	0	0.102	0	0	0	0	0	0	0	1.38
<i>Viola arvensis</i>	Con	A	0	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scleranthus perennis</i>	Con	P	0	0	0	0	0.4	0	0	0.65	0	0	0	0.53	0	0	0.15	0	0	0	0	0	0	0	0	0
<i>Erophila verna</i>	EI	A	0.055	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Campanula rotundifolia</i>	EI	P	2.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gallium sp.</i>	EI	P	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lactuca serriola</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myosotis stricta</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scleranthus annuus</i>	EI	A	0	0	0	0	0	0	0	0	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Senecio vernalis</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Achillea millifolia</i>	EI	P	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Festuca ovina</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Luzula campestris</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0
<i>Plantago lanceolata</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Poa sp.</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Taraxacum officinalis</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0
<i>Arenaria serpyllifolia</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.063	0	0
Bare soil (%)			68.39	80.07	69.16	83.62	78.1	76.67	71.94	79.66	70.41	78.61	83.86	79.7	87.28	80.14	73.63	83.03	86.87	81.41	81.13	81.34	86.2	75.94	69.41	89.97
Total Cover (%)			31.62	19.93	30.84	16.38	21.9	23.33	28.07	20.34	29.59	21.39	16.14	20.31	12.72	19.86	26.37	16.97	13.13	18.59	18.88	18.66	13.8	24.06	30.59	10.03
N. of species			11	10	10	7	10	10	10	10	10	8	9	10	7	6	7	11	10	11	10	11	8	11	10	9

PLOT 3

Species	RG	FG	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2002	2003	2005
<i>Festuca glaucina</i>	CD	P	16.75	18.89	28.35	5.84	9.39	10.92	14.91	12.36	22.06	18.38	17.92	19.28	17.35	20.4	23.55	12.3	9.23	13.47	13.54	16.51	13.3	14.25	18.04	5.07
<i>Hieracium pilosella</i>	CD	P	15.05	14.64	13.05	1.83	5.4	12.3	4.71	3.3	4.71	3.75	4.29	3.12	0.36	0.51	1.83	1.02	0.48	0.87	1.77	2.64	2.85	5.49	4.71	5.96
<i>Euphorbia cyparissias</i>	CD	P	0.73	0.3	1.15	0.4	0.82	1.15	0.402	0.45	1.4	0.42	0.15	0.15	0.1	0.18	0.07	0.04	0.65	1.34	0.81	0.35	0.07	0	0	0.79
<i>Spergula morisonii</i>	RD	A	0	0	0.302	7.776	0.1	0.11	0.006	0	0.95	0	0	0.1	0.09	0.016	0	0.014	0.008	0.003	0.008	0.012	0.003	0.007	0.005	0
<i>Anthoxanthus odoratum</i>	RD	P	0	0	0	0	0.25	1.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armeria elongate</i>	RD	P	1.7	1.751	1.7	1.5	0.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Saxifraga granulata</i>	RD	P	0.15	0.15	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thymus serpyllum</i>	RD	P	0.75	0.15	0.8	0	0.25	0.68	0.25	0	0	0	0	0.15	0	0	0	0.001	0	0	0	0	0	0	0.15	0
<i>Centaurea stoebe</i>	CI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.08	2	1.98	1.33	0.37	0.13	0.37	1.6	0.25	0.01
<i>Aira praecox</i>	RI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0	0
<i>Cerastium semidecandrum</i>	Con	A	0	0.071	0.015	0.037	1.7	0.01	0.019	0.001	0	0	0	0	0	0	0	0	0.004	0	0	0	0	0	0	0
<i>Agrostis capilaris</i>	Con	P	1.85	1.15	3.7	1.42	4.88	8.16	15.95	7.93	17.38	3.23	0.58	0.6	0.1	0.2	1.3	0.21	0.66	1.83	0.79	0	0.1	0.1	0.1	0.22
<i>Dianthus cartusianum</i>	Con	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypericum perforatum</i>	Con	P	0	0.5	0.78	0	0.35	0.451	0.252	0.15	0.801	0.2	0.18	0.1	0	0	0	0	0.15	0.3	0.2	0.15	0.1	0	0	0
<i>Hypochoeris radicata</i>	Con	P	0	0	0	0	0.4	0.15	0.001	0	0	0	0	0	0	0	0	1.551	0	0	0	0	0	0	0	0
<i>Koelleria macrantha</i>	Con	P	0	0.35	0.8	0	0.751	1.1	2.05	2.051	2.3	2.8	1.13	1.75	2.456	4.6	5.58	1.813	2.1	1.081	2.81	3.52	2.71	3.81	4.251	1.55
<i>Silene otites</i>	Con	P	0.75	0.2	0	2.04	2.67	0.93	1.38	1.1	1.06	2.11	1.3	3.153	1.85	2.35	1.1	0.65	0.84	0.55	0.35	0.45	0.45	1.2	1.5	1.65
<i>Rumex acetosela</i>	Con	P	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0.002	0.001	0	0	0	0	0	0	0
<i>Viola arvensis</i>	Con	A	0	0	0	0.801	0.85	0	0.011	0	0	0.005	0	0	0	0	0	0	0	0	0	0.101	0	0	0	0
<i>Scleranthus perennis</i>	Con	P	0	0	0	0	1.16	0	0	0.007	0	0	0	0.355	0	0	0.1	0.97	0.202	0.003	0	0	0	0	0	0
<i>Erophila verna</i>	EI	A	0.517	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0
<i>Campanula rotundifolia</i>	EI	P	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gallium sp.</i>	EI	P	1.55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lactuca serriola</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myosotis stricta</i>	EI	A	0	0	0	0	0	0	0	0	0	0.103	0	0	0	0	0	0.102	0	0	0	0	0	0	0	0
<i>Scleranthus annuus</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Senecio vernalis</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0
<i>Achillea millifolia</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Festuca ovina</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.22	0	0	0
<i>Luzula campestris</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0
<i>Plantago lanceolata</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Poa sp.</i>	EI	P	0	0	0	0	0	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Taraxacum officinalis</i>	EI	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0
<i>Arenaria serpyllifolia</i>	EI	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0
Bare soil (%)			59.8	61.85	49.22	78.35	70.13	62.29	60.06	72.65	49.34	69	74.45	71.14	77.69	71.74	66.39	79.32	83.7	79.23	79.36	75.82	80.05	73.49	71	84.75
Total Cover (%)			40.2	38.15	50.78	21.65	29.87	37.71	39.94	27.35	50.66	31	25.55	28.86	22.31	28.26	33.61	20.68	16.3	20.77	20.65	24.19	19.96	26.51	29	15.25
N. of species			11	11	11	9	15	13	12	9	8	9	7	11	7	7	8	14	12	10	10	11	9	10	8	7