

TROPHIC LEVELS ARE DIFFERENTIALLY SENSITIVE TO CLIMATE

WINFRIED VOIGT,^{1,4} JÖRG PERNER,¹ ANDREW J. DAVIS,² TILL EGGERS,^{3,5} JENS SCHUMACHER,¹
RUDOLF BÄHRMANN,¹ BÄRBEL FABIAN,¹ WOLFGANG HEINRICH,¹ GÜNTER KÖHLER,¹ DORIT LICHTER,¹
ROLF MARSTALLER,¹ AND FRIEDRICH W. SANDER¹

¹*Institute of Ecology, Friedrich Schiller University, 07743 Jena, Germany*

²*Institute of Low Temperature Science, Hokkaido University, Sapporo, Japan*

³*NERC Centre for Population Biology, Imperial College of Science, Technology and Medicine, Silwood Park, Ascot, Berkshire SL5 7PY United Kingdom*

Abstract. Predicting the response of communities to climate change is a major challenge for ecology. Communities may well not respond as entities but be disrupted, particularly if trophic levels respond differently, but as yet there is no evidence for differential responses from natural systems. We therefore analyzed unusually detailed plant and animal data collected over 20 years from two grassland communities to determine whether functional group climate sensitivity differed between trophic levels. We found that sensitivity increases significantly with increasing trophic level. This differential sensitivity would lead to community destabilization under climate change, not simple geographical shifts, and consequently must be incorporated in predictive ecological climate models.

Key words: arthropods; climate sensitivity; community; functional groups; grasslands; plants; trophic levels.

INTRODUCTION

Climate is a major driver of organism distributions and species life histories and, therefore, affects population dynamics, community composition, and the ecosystem services arising from them (Harrington and Stork 1995, Institute of Biology 1999, Lawton 2000, Parmesan et al. 2000). Consequently, predicting community responses to climate change and their impacts on human welfare is an important area of global change ecology and one of its major challenges. Nevertheless, the potential effects on complete communities are still unclear (May 1998, Harrington et al. 1999, Lawton 2000, IPCC 2001), although considerable progress has been made in understanding the responses of model systems (Ayres 1993, Jones et al. 1998, Petchey et al. 1999, Cramer et al. 2001). There is considerable evidence, however, that species respond individually to climate (Parmesan et al. 1999, Lawton 2000, Pimm 2001, Thomas et al. 2001, Bale et al. 2002, Watt and McFarlane 2002). Because of this, communities will be disrupted by climate change (Walther et al. 2002) since differential species responses will inevitably disrupt species interactions (Davis et al. 1998, Harrington et al. 1999, Penuelas and Filella 2001, Visser and Helleman 2001). Particularly strong disruption is likely if the average sensitivity of species differs systematically between trophic levels since, in this case, trophic in-

teractions will be fundamentally altered. This kind of differential trophic sensitivity to climate has not yet been demonstrated in field communities because of the great difficulty and expense of long-term studies of multispecies assemblages, trophic groups, or entire communities. Some studies have, however, implicitly invoked interactions (Ives and Gilchrist 1993, Root and Schneider 1995, Fox and Morin 2001) or experimentally manipulated communities in the laboratory (Harrington and Stork 1995, Jones et al. 1998, Petchey et al. 1999, Fox and Morin 2001) or in the field (Brown et al. 1998, Grime et al. 2000, White et al. 2000). Simply scaling up the results of small-scale experiments is insufficient since real communities contain so many organisms with a multitude of complex interactions (Scholes 1990, Peters 1992, Root and Schneider 1995, Harrington et al. 1999, Lawton 2000). Nevertheless, the available evidence from short-term model systems (Jones et al. 1998, Petchey et al. 1999) indicates that such differential sensitivity exists.

We therefore analyzed extensive long-term field data on plants and animals from a real ecosystem including several functional groups on three trophic levels to determine whether trophic levels differed systematically in their sensitivity to climate variations. We used a statistical approach to assess the degree of correlation between the variation in species abundance and natural climatic variation and examined patterns in the strength of these correlations between trophic levels.

METHODS

The species data were gathered over two decades from xerothermic calcareous grassland habitats at two different sites near Jena, Germany (50.9° N, 11.6° E,

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⁴ E-mail: winfried.voigt@uni-jena.de

⁵ Present address: Faculty of Biology/Chemistry, Department of Ecology, University of Osnabrück, 49069 Osnabrück, Germany.

TABLE 1. The numbers of species and individuals within sites, trophic levels, and functional groups.

Site, trophic level, and functional group	Collection method				
	Cover-abundance (No. species)	Sweep-net		Pitfall trap	
		No. species	No. individuals	No. species	No. individuals
Leutratal					
Producers					
Annual forbs	18				
Grasses	18				
Mosses	40				
Perennial forbs	86				
Woody plants	31				
Herbivores					
Cell-tissue suckers		72	16 864		
Lifetime chewers		11	4 832		
Miners		115	5 622		
Stage-specific chewers		217	22 173		
Vascular suckers		101	38 350		
Carnivores					
Attacking chewers		5	488		
Biting suckers		100	1 236		
Parasitoids		31	131		
Sucking hunters		11	296		
Stuednitz					
Producers					
Annual forbs	30				
Grasses	17				
Mosses	16				
Perennial forbs	36				
Woody plants	14				
Herbivores					
Miners		92	28 436	32	1760
Stage-specific chewers		144	2 977		
Vascular suckers		84	68 549		
Carnivores					
Biting suckers		93	6 954	77	2780
Chewing hunters		74	1 160		
Web-spinners		87	12 794		

Note: The total number of species recorded was 1295, of which 254 (193 in Leutratal [L], 113 in Stuednitz [S]) were producers, 656 (L = 518, S = 325) herbivores, and 385 (L = 147, S = 295) carnivores.

145 m above sea level). One site, Leutratal (south of Jena), is a nature reserve of seminatural calcareous grassland dominated by the grass species *Bromus erectus* Huds., *Brachypodium pinnatum* (L.) P.B., and, in the drier parts, *Sesleria varia* (Jacq.) Wettst. The other site, Stuednitz, 18 km further north, is similar but was heavily disturbed in the past by industrial air pollution. Both sites are described in detail elsewhere (Heinrich 1998, Heinrich et al. 2001; also see Appendix I).

These data derive from 254 producer species (vascular plants and mosses), 656 species (189 563 individuals) of arthropod herbivores, and 385 species (25 839 individuals) of arthropod carnivores (Table 1, Appendices A–C, H) and represent a substantial part of the whole grassland community. Plant species abundance was assessed by the Braun-Blanquet method (Kent and Coker 1994), a combined cover-abundance estimation technique. Invertebrate abundance was determined by collections from regularly maintained pitfall traps and by standardized sweep-net sampling ev-

ery two weeks throughout the annual period of vegetation growth.

Data preparation

The arthropod data were standardized to unit sample vector length (sample norm) to adjust for different sample sizes:

$$x'_{ij} = \frac{x_{ij}}{\left(\sum_{j=1}^r x_{ij}^2\right)^{1/2}}$$

where x_{ij} is the original abundance of species i in sample j (for r sampling years). Logarithmic transformation was applied where necessary to improve normality of variances and avoid distortions (Fig. 1). Rare species of invertebrate taxa (≤ 5 individuals) were omitted to reduce noise. Likewise, two data sets for the parasitoid Diptera, both from Stuednitz, were also excluded because of the very low abundances of the few species

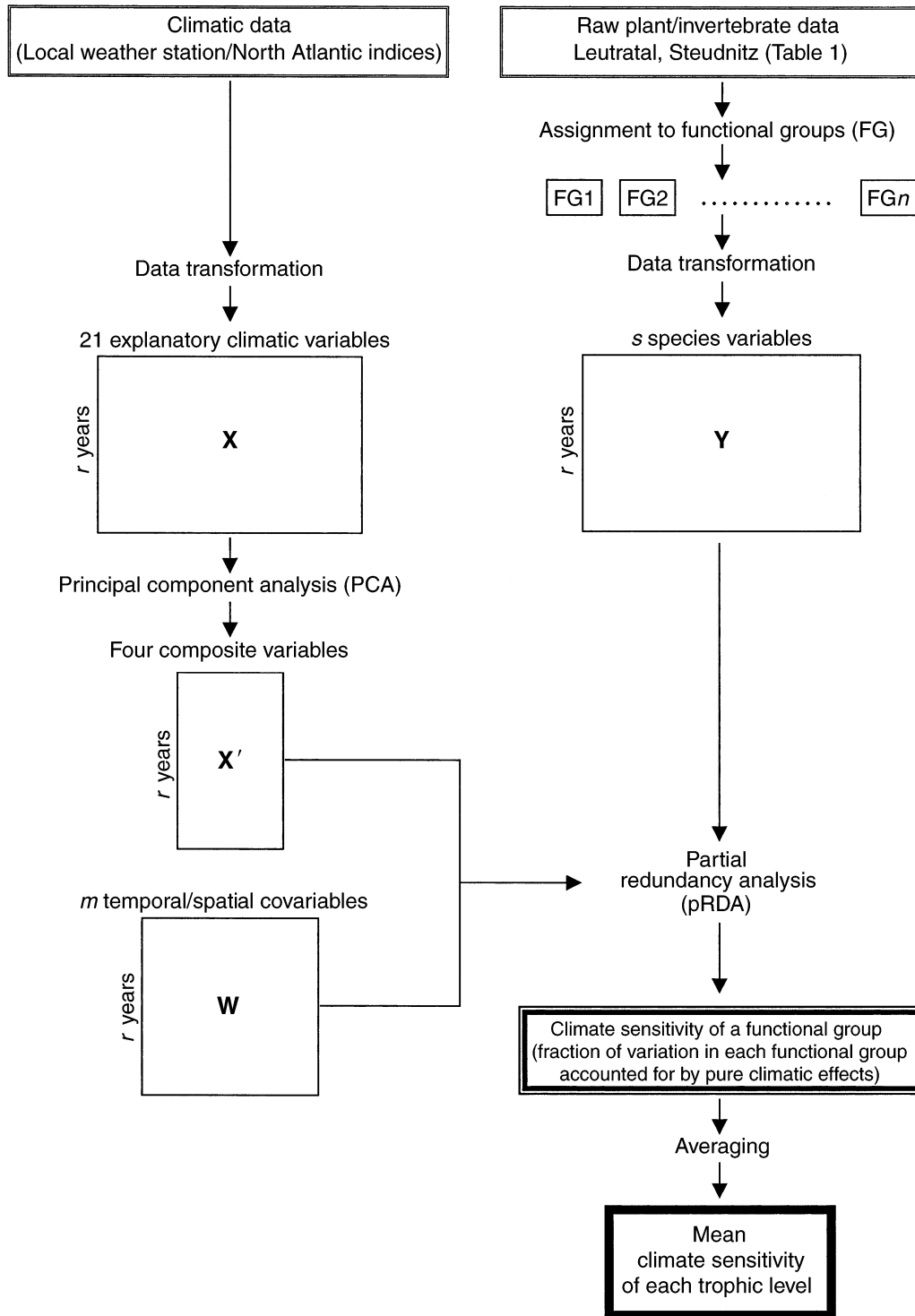


FIG. 1. Organization of data analysis (W , X , Y , Z denote data matrices).

they contained. Standardization of plant data was unnecessary because of the uniform sample size and the relative abundance scale used (Braun-Blanquet method; Kent and Coker 1994).

The climate sensitivity of multispecies groups spanning several trophic levels can only be adequately assessed by calculating an index that encapsulates the long-term overall response of the assemblage. We

TABLE 2. Original climatic variables used to produce four explanatory composite variables by a standardized principal component analysis.

No.	Name of variable	Description
1	Tav1-12	mean air temperature, whole year
2	Tav1-3	mean air temperature, January–March
3	Tav4-6	mean air temperature, April–June
4	Tav7-9	mean air temperature, July–September
5	Tav10-12	mean air temperature, October–December (of previous year)
6	Tmax	maximum air temperature (yearly average)
7	Tmin	minimum air temperature (yearly average)
8	dTmax >30	no. days with maximum temperature >30°C
9	dT <0	no. days with minimum temperature <0°C (preceding winter)
10	dT <-10	no. days with minimum temperature <-10°C (preceding winter)
11	dTmax <-10	no. days with maximum temperature <-10°C (preceding winter)
12	PRsum	annual precipitation (mm)
13	PRJanMar	precipitation (mm), January–March
14	PRAprJun	precipitation (mm), April–June
15	PRJulSep	precipitation (mm), July–September
16	PROctDec	precipitation (mm), October–December (of preceding year)
17	SunHour	annual number of sun hours
18	NLI1-3	North Wall Index (mean latitude of Gulf Stream) January–March
19	NLI7-9	North Wall Index (mean latitude of Gulf Stream) July–September
20	NAO11-3	North Atlantic Oscillation (mean November (previous year)–March)
21	EA9-4	East Atlantic Pattern (mean September (previous year)–April)
22	EAJET4-8	East Atlantic Jet (mean April–August)

Note: These variables comprised local meteorological data (University Weather Station, Jena, Germany), three North Atlantic climate indices (NAO, EA, EAJET; Climate Prediction Center, Camp Springs, Maryland, USA) and the mean quarterly latitude of the Gulf Stream (NLI, also called North Wall Index; Marine Laboratory, Plymouth, UK [Taylor 1996]).

therefore assessed the effect of climate fluctuation on long-term changes in species abundances within functional groups (i.e., the interannual variation of functional groups) so as to capture changes in species abundance due to species interactions within groups of ecologically similar species, as well as those due to direct responses to climate. Changes due to species interactions within functional groups would be hidden in background variance if only single species responses were examined. Thus, using functional groups directly links ecological characteristics to climatic sensitivity. We combined species into functional groups, depending on their growth form and life history (producers) or their foraging behavior (herbivores and carnivores), within each site and assigned the groups to trophic level (Table 1 and Fig. 1: FG1 . . . FGn; see also Appendices A–C). The producers were grouped as mosses, grasses, woody plants, annual forbs, and perennial forbs; the herbivores were grouped as vascular suckers (e.g., Auchenorrhyncha), cell-tissue suckers (e.g., Heteroptera), life-time chewers (e.g., Orthoptera), stage-specific chewers (e.g., Coleoptera), and miners (e.g., Diptera); and carnivores were grouped as chewing hunters (e.g., Coleoptera), attacking chewers (e.g., carnivorous Orthoptera), biting-suckers (e.g., Diptera), sucking hunters (e.g., Heteroptera), parasitoids (e.g., Diptera), and web-spinners (e.g., Araneae). Because collections were made over different periods within the 20 years of research and not all species were collected over the whole period, the species composition of functional groups varied with year.

Climatic data were derived from 22 variables including both local and global meteorological indices (matrix **X** in Fig. 1; Table 2). By including many climate measures we greatly reduce the possibility of omitting signals that are weak but biologically important (Taylor et al. 2002). To condense these data and to avoid nonorthogonality, we summarized these climatic variables as the four major axes (matrix **X'** in Fig. 1) of a standardized principal component analysis (PCA). Since PCA axes are, by definition, orthogonal and so independent of one another, this procedure creates composite independent climate variables and so avoids the danger of spurious correlations (i.e., multicollinearity) inherent in a multivariate design using nonorthogonal climate factors. Very little information was lost by this process since the first four PCA axes explained nearly all of the total variance in the original climate data (mean 93.7%, range 81–100%, $n = 9$; i.e., nine different year-sequences for which PCA axes were calculated). All further analyses therefore were carried out using the combined and condensed climate information represented by the interannual fluctuations of these four axes. These composite variables fluctuated widely over time and showed no particular long-term trends (Appendix D). The principal component coefficients (loadings) for all the standardized original climatic variables (Table 3) show that the first PCA axis primarily represents temperature (many temperature variables, number of hours of sunshine, and the winter signal of the North Atlantic Oscillation [NAO]) but the second PCA axis mainly represents the interannual var-

TABLE 3. The eigenvector coefficients (loadings) of a standardized principal component analysis of original climatic variables for the entire period 1970–1996.

No.	Climatic variable	Axis 1	Axis 2	Axis 3	Axis 4
1	Tav1-12	-0.9509	0.1687	0.1043	0.0736
2	Tav1-3	-0.8021	0.1912	0.3772	-0.3433
3	Tav4-6	-0.1724	0.4766	-0.5625	-0.0937
4	Tav7-9	-0.7523	-0.0127	-0.3489	0.1989
5	Tav10-12	-0.2237	-0.0049	0.3026	0.7233
6	Tmax	-0.9562	-0.0054	-0.0506	0.0547
7	Tmin	-0.5802	-0.1280	0.6287	0.1848
8	dTmax >30	-0.6741	-0.1350	-0.3200	-0.0630
9	dT <-10	0.6843	-0.0463	-0.4180	0.4371
10	dTmax <-10	0.1892	0.6100	-0.3638	-0.0154
11	dT <0	0.7650	-0.0497	-0.4556	0.1617
12	PRsum	0.3306	0.8506	0.2630	-0.0341
13	PRJanMar	0.0861	0.4151	0.2448	0.5937
14	PRAprJun	0.2404	0.3627	0.2367	-0.1865
15	PRJulSep	0.4415	0.7329	0.0215	-0.2592
16	PROctDec	0.0845	0.6990	0.2354	-0.1260
17	SunHour	-0.6888	-0.3695	-0.5307	-0.0878
18	NLI1-3	-0.3253	0.5829	-0.1000	-0.1995
19	NLI7-9	-0.2545	0.5965	-0.2915	-0.0107
20	NAO11-3	-0.5975	0.3733	-0.3842	-0.0669
21	EA9-4	-0.3672	0.6018	0.2283	0.3795
22	EAJET4-8	-0.2371	0.3656	-0.4294	0.4709

Note: The eigenvalues of the first four axes are: axis 1 = 0.2981, axis 2 = 0.1920, axis 3 = 0.1227, and axis 4 = 0.0838 (sum = 70% of total variance explained). Loadings >0.45 are shown in boldface type to highlight the meanings of the respective axes. A mean eigenvalue sum of 0.94 (93.7% variance explained) was calculated for the shorter periods during which organism abundance was recorded within the total 26-year study (see *Methods: Data preparation*).

iation of local precipitation and the impact of general weather processes (North Wall Index [NLI], East Atlantic Pattern [EA]). PCA axis 3 accounts for the effects of spring temperature (Tav4–6) and cold weather in general (Tmin), number of hours of sunshine, and the impact of East Atlantic Jet [EAJET], but axis 4 predominantly represents the winter temperature of the preceding year (Tav10–12), as well as spring precipitation (PRJanMar) and the effect of EAJET.

Data analysis

We derived a measure for climate sensitivity of each functional group as the percentage of its total species variation explained by the four composite climatic variables (PCA axes) by partial redundancy analysis (pRDA; Jongman et al. 1995, Legendre and Legendre 1998; performed with CANOCO 4.5, Ter Braak and Smilauer [2002]). RDA is a canonical extension of PCA that uses, instead of the original values (matrix \mathbf{Y} in Fig. 1), the fitted values of a multiple linear regression of each species data on the set of explanatory variables (here the composite climate variables). As it combines PCA and multiple regression analysis, the axes extracted by RDA are linear combinations of the explanatory variables involved (matrix \mathbf{X}' in Fig. 1), and so the amount of species variation accounted for by this model is restricted solely to that fraction explained by the four composite climate variables (the sum of the canonical eigenvalues; Jongman et al. [1995]). Partial RDA controls for the effects of one or

more covariables and is comparable to partial correlation or partial regression techniques. In our pRDA analysis, we constructed two covariables reflecting differences in species composition and abundance that arise, even if climate is invariant, merely from the arrangement of the collections. These covariables represent either spatial position, which might give rise to small topographical differences (e.g., the relative position in the study site) or the temporal sequence of collections, which might show successional changes (e.g., sampling years). The remaining variance is that due predominantly to climatic effects. All the functional groups were significantly associated with climate (at $\alpha = 0.05$, Monte Carlo permutation test) except Steudnitz mosses, Leutratal annual forbs, and chewing hunters. All the functional groups were then grouped by trophic level, and trophic climatic sensitivity was derived as the mean climate sensitivity of all the functional groups within a particular trophic level (Fig. 1).

ANOVA models could not be appropriately used to analyze differences in sensitivity between trophic levels because normal distributions and homogeneity of variances were neither present nor could they be satisfactorily achieved by data transformation. We therefore applied a Jonckheere-Terpstra trend test (Jonckheere 1954, Sachs 1999; in SPSS 10.0; SPSS, Chicago, Illinois, USA) to test for trends in the sensitivity to climate across trophic levels. This test is a powerful k -sample extension of the Mann-Whitney U test, a more

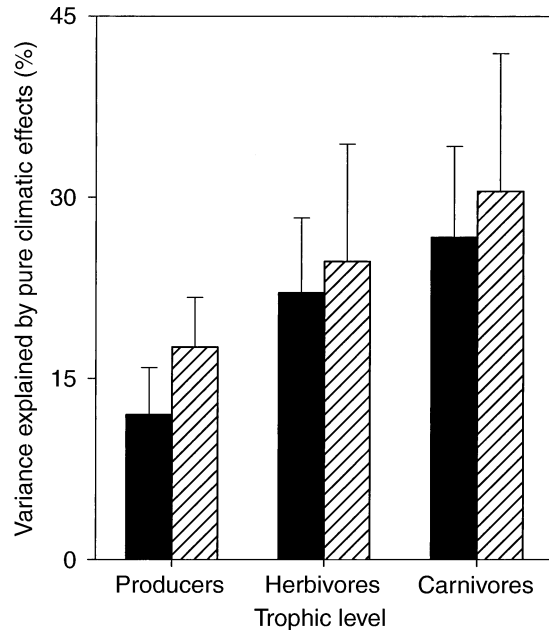


FIG. 2. Climatic sensitivity of different trophic levels at two separate grassland sites (solid bars, Leutratal; hatched bars, Steudnitz; means + 1 SD). Sensitivity is the mean temporal variation (averaged over functional groups within trophic levels) in organism abundances explained by climate (four major axes of a principal component analysis [PCA] based on 21 local and global climatic indices; for more details see *Methods: Data analysis*).

appropriate alternative to the Kruskal-Wallis test when assuming an a priori rank order in the data.

To exclude the possibility that trophic sensitivities resulted from differences in mean species richness of functional groups within trophic levels, we conducted a Jonckheere-Terpstra trend test on the size of functional groups within trophic levels. In addition, we used a model I regression to test whether functional group sensitivity was related merely to group size. Sensitivities in species-rich functional groups might be higher because large groups are more likely to contain strongly responding species or lower because of statistical averaging, the reciprocal canceling out of individual species fluctuations (Doak et al. 1998), the effects of which are greater the greater the number of species a functional group contains.

To indicate the relative importance of each of the four axes, and thus the relative importance of different aspects of climate, we also calculated the functional group sensitivity to each of the axes separately.

RESULTS

Different trophic levels had different sensitivities to climate (Fig. 2), and these sensitivities were highly significantly ordered with increasing trophic rank (producers < herbivores < carnivores: Jonckheere-Terpstra (J-T) trend test, two-tailed $P = 0.001$, $n = 27$, Monte-Carlo significance based on 10 000 samples). The dif-

ferences were the same in both sites (Fig. 2) and the sensitivity trend in Leutratal was also highly significant (J-T test, two-tailed $P < 0.002$, $n = 14$), although that in Steudnitz was not (J-T test, two-tailed $P = 0.075$, $n = 13$). There was no significant tendency in the species richness of functional groups across the three trophic levels (J-T test, two-tailed $P = 0.11$, $n = 28$, Monte-Carlo significance based on 10 000 samples) and the ordering of mean species richness (producers < herbivores > carnivores) was not the same as the ordering of climatic sensitivities. There was also no significant relationship between sensitivity and group species richness (model I regression, total data, $r^2 = 0.06$, $P = 0.21$; Leutratal, $r^2 = 0.03$, $P = 0.55$; Steudnitz, $r^2 = 0.16$, $P = 0.18$; Fig. 3).

Within trophic levels, each of the four climatic variables explains ~25% of the total climatic variance (Appendix E). However, the relative sensitivity to each of the four axes separately differed between functional groups but the differences showed no particular pattern with respect to trophic level except that producers might be more affected by local precipitation and Gulf Stream impact (axis 2) than by temperature (axes 1 and 3; Appendix F). For individual response of species to composite climatic variables, see RDA triplots in Appendix G.

DISCUSSION

The differential sensitivity of trophic levels to climate will have profound effects on the way in which these xerothermic grassland communities respond to climate change. More importantly, however, the differential trophic sensitivities to climate that we found may indicate a general phenomenon in trophic systems, and finding the same differences in sensitivity at both the sites studied strengthens this contention. The species responses at each site are independent because individual arthropod species were not sampled synchronously between sites and because population syn-

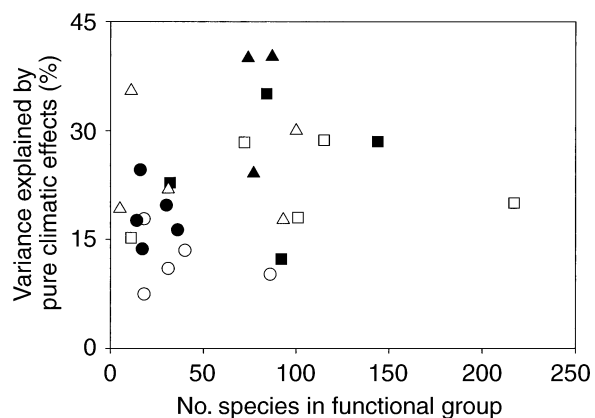


FIG. 3. Relationship between climatic sensitivity in terms of explained variance and species number of functional groups (circles, producers; squares, herbivores; triangles, carnivores; open symbols, Leutratal; solid symbols, Steudnitz).

chronization between sites through the migration of organisms is prevented by the town of Jena and the considerable distance (18 km) that separate the sites. The generality of differential trophic response is also supported by the similar results from controlled aquatic microcosm experiments on the effects of elevated temperatures (Petchey et al. 1999). Furthermore, our data derive from a frequent ecosystem type that is in no way unusual, and it is unlikely that the trophic structure and interactions of other systems differ greatly from those of our grasslands. Differential responses to climate between trophic levels may therefore be widespread.

Our results are likely to be the direct results of climate since we can exclude alternative, nonclimatic causes of differential trophic responses. Differences between trophic levels might arise if each level were represented by few taxa because small groups of taxa might have differences in sensitivity to climate by chance. This phenomenon cannot affect our findings, however, because our data derive from large numbers of species in each level and from a substantial part of highly diverse and real grassland ecosystems. Neither can they be attributed to purely taxonomic effects, as could be the case if the species analyzed were largely taxonomically similar within, but taxonomically distinct between, trophic levels. This is not the case since at Leutratal and Steudnitz the "producers" include a wide range of plant species from different taxa as, similarly, the "herbivores" and "carnivores" include a wide range of arthropod species. In addition, at both sites, the "herbivores" and "carnivores" are not taxonomically distinct since they contain representatives of the same taxonomic groups (e.g., Coleoptera, Diptera, Heteroptera). Differences in plant generation time or arthropod voltinism are also unlikely to be the cause of the differences we report although short-generation organisms might be expected to respond more quickly to climatic changes. The distribution of generation times is similar for the "carnivores" and the "herbivores" but we did find that short-generation plants, i.e., annual forbs, had higher climate sensitivity (Leutratal [Lt], 17.8%; Steudnitz [St], 19.7%) than the mean of all plant functional groups (Lt, 12.0%; St, 17.6%). Nevertheless, these values for short-generation plants are still well below the mean sensitivity of herbivores (Lt, 21.5%; St, 23.6%) so the generally low climate sensitivity of the producers cannot be attributed merely to the inclusion of long-generation, i.e., perennial, plants in this trophic level. There are also no consistent differences in voltinism between the herbivore and carnivore arthropods, each arthropod functional group consisting of both univoltine and multivoltine species with diverse overwintering modes.

We can also exclude the possibility that differential climate sensitivity arises because there are different numbers of species within functional groups (McArdle et al. 1990) since there is no relationship between these two quantities (Fig. 3). Furthermore, the variation ex-

plained purely by climate is a fraction of the total variation in the data. There is no reason to believe that the size of this fraction should be determined by the number of species within the functional group from which it was derived even if the total variation (from climate and all other causes) were to be so. In addition, our results do not arise because of statistical averaging because group species richness does not decrease systematically with trophic rank and, in consequence, higher sensitivity to climate is not associated with species-poor groups.

Why trophic levels generally, or only in our grasslands, should be differentially sensitive to climate variation cannot be determined at this stage. It may be possible that differential sensitivity to climate is due to functional groups in different trophic levels responding to different elements of climate. Other possible explanations and foci for further research may lie in different degrees of density dependence, differences in metabolic rates, or in varying resource availability. Populations with weak density dependence are expected to be more sensitive to climate than those with overcompensatory dynamics (Ives and Gilchrist 1993), and this mechanism could operate if density dependence differed systematically between trophic levels. The "carnivores" may be generally more active foragers and so have intrinsically higher metabolic rates than "herbivores," and these in turn, since they have to forage among, and select from, the available vegetation, may have higher metabolic energy expenditure than "producers" (Pianka 1981, Townsend and Hughes 1981). It is also conceivable that response to climatic variations in one trophic level causes the resource availability to vary for the level above. This increased extrinsic uncertainty in resource availability might be amplified along trophic chains causing a reciprocal cascade. Differential sensitivity to climate may be a specific manifestation of the general observation that sensitivity to disturbance of any kind often increases with trophic level (e.g., Morris and Rispin 1987, 1988, Eyre and Rushton 1989, Eyre et al. 1989, Rodriguez et al. 1998, Cagnolo et al. 2002).

Whether caused by intrinsic or extrinsic mechanisms, our findings, from detailed and abundant long-term field data, indicate that different trophic levels respond differently to climate fluctuations and suggest that differential trophic responses are likely to be a common, widespread, and important phenomenon. Communities are, therefore, unlikely to respond as discrete entities to climatic changes, and climate change is likely to disrupt trophic relationships between organisms, prompting trophic cascades (Jones et al. 1998, Petchey et al. 1999). Changes in the trophic structure of communities will affect ecosystem processes such as nutrient cycling and thereby the services these systems provide (De Angelis 1992, Jones et al. 1998) although the proximal mechanisms for these differential sensitivities to climate are still under study. Differential

response of trophic levels will substantially increase the ecological disruption to be expected under global climate change and must therefore be incorporated into existing models (Root and Schneider 1995) if the prediction of ecosystem responses to climate change is to be adequate.

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APPENDIX A

A list of identified plant species and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A1.

APPENDIX B

A list of herbivore species caught and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A2.

APPENDIX C

A list of carnivore species caught and their classification into functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A3.

APPENDIX D

A figure showing the fluctuations of four PCA axes (composite climatic variables = sample scores) over the total study period is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A4.

APPENDIX E

Figures providing the distribution of variance explained by PCA axes (composite climatic variables) for each trophic level are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A5.

APPENDIX F

Figures providing the distribution of the fraction of variance, standardized to 1, independently accounted for by the four composite variables (PCA axes) for all functional groups of different trophic levels are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A6.

APPENDIX G

Redundancy analysis (RDA) triplots for all functional groups analyzed are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A7.

APPENDIX H

Literature used in Appendices A–C is available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A8.

APPENDIX I

A map and pictures of Leutratal and Steudnitz study sites are available in ESA's Electronic Data Archive: *Ecological Archives* E084-060-A9