

Effects of Extreme Weather Events on Plant Productivity and Tissue Die-Back are Modified by Community Composition

Juergen Kreyling,^{1,2,3*} Mike Wenigmann,³ Carl Beierkuhnlein,³ and Anke Jentsch^{1,2}

¹*Disturbance Ecology and Vegetation Dynamics, Helmholtz Centre for Environmental Research – UFZ, Permoserstr. 15, 04318 Leipzig, Germany;* ²*University of Bayreuth, 95440 Bayreuth, Germany;* ³*Biogeography, University of Bayreuth, 95440 Bayreuth, Germany*

ABSTRACT

Extreme weather events are expected to increase in frequency and magnitude due to climate change. Their effects on vegetation are widely unknown. Here, experimental grassland and heath communities in Central Europe were exposed either to a simulated single drought or to a prolonged heavy rainfall event. The magnitude of manipulations imitated the local 100-year weather extreme according to extreme value statistics. Overall productivity of both plant communities remained stable in the face of drought and heavy rainfall, despite significant effects on tissue die-back. Grassland communities were more resistant against the extreme weather events than heath communities. Furthermore, effects of extreme weather events on community tissue die-back were modified by functional diversity, even though conclusiveness in this part is limited by the fact that only one species composition was available per diversity level within this case study. More diverse grassland

communities exhibited less tissue die-back than less complex grassland communities. On the other side, more diverse heath communities were more vulnerable to extreme weather events compared to less complex heath communities. Furthermore, legumes did not effectively contribute to the buffering against extreme weather events in both vegetation types. Tissue die-back proved a strong stress response in plant communities exposed to 100-year extreme weather events, even though one important ecosystem function, namely productivity, remained surprisingly stable in this experiment. Theories and concepts on biodiversity and ecosystem functioning (insurance hypothesis, redundancy hypothesis) may have to be revisited when extreme weather conditions are considered.

Key words: climate change; functional diversity; Central Europe; grassland; heath; EVENT-experiment; plant functional types; drought; heavy rainfall.

INTRODUCTION

It is widely acknowledged that frequency and magnitude of extreme weather events will increase

during ongoing global climate change (Easterling and others 2000; Meehl and others 2000; IPCC 2007). Changes in drought regime and heavy rainfall have already been reported for Europe according to climate data series (for example, Beck and others 2001; Schönwiese and others 2003; Schmidli and Frei 2005), and are furthermore proposed from

Received 21 February 2007; accepted 25 March 2008; published online 17 May 2008

*Corresponding author; e-mail: juergen.kreyling@uni-bayreuth.de

predictive modeling (for example, Raisanen and Joellsson 2001; Christensen and Christensen 2003; Sanchez and others 2004; Semmler and Jacob 2004). The effects of extreme weather events on vegetation and ecosystem functioning are likely much stronger than the effects of changes in mean values of temperature and precipitation (Easterling and others 2000; Meehl and others 2000). However, extreme weather events have not yet received much attention in vegetation-related climate impact research (Jentsch and others 2007). Furthermore, the few existing experimental studies on extreme weather events often lack details on magnitude or extremeness (Jentsch 2006) of applied manipulations relative to local mean conditions. Objectively choosing realistic extremeness and describing extremeness in relation to local conditions is crucial to allow for the identification of general mechanisms of ecosystem response to extreme weather events. Especially the insurance hypothesis (Yachi and Loreau 1999) which states that communities which are more diverse in species or functional groups can be expected to be more resistant against environmental perturbations, and questions such as complementarity and redundancy (Naeem 1998) need to be re-addressed in this context.

Here, we study the effects of drought and prolonged heavy rainfall in artificial communities of two vegetation types (grassland and heath) of different functional composition. European grassland and heath communities are widespread, deliver economic value, provide many ecological services such as ground water recharge, and are important for nature conservation.

Extreme Weather Events and Plant Response

Drought and prolonged heavy rainfall are expected to affect plants via modified soil moisture. Water shortage leads to a decline in water potential and to water stress. In contrast, excess of water in soil pores creates oxygen deficits and produces a reducing milieu in the soil which is connected with effects on nutrient availability. The lack of oxygen can cause substantial short-term fine root mortality, even though species reactions differ considerably (Crawford and Braendle 1996). Both mechanisms are capable of reducing productivity or even of killing plants if exceeding certain magnitudes. As both extreme events, drought and heavy rainfall, generate highly stressful conditions, we hypothesize that both lead to immediate tissue die-back and reduced aboveground productivity over the growing season.

Differences in Vegetation Types: Grassland Versus Heath

In temperate grasslands, evidence suggests that drought events cause reduced biomass productivity (Sternberg and others 1999; Grime and others 2000; Kahmen and others 2005), reduced reproductive success (Fox and others 1999; Morecroft and others 2004), and ultimately result in alterations of species composition (Grime and others 2000; Buckland and others 2001). Heavy rainfall events have received considerably less interest, even in well-studied vegetation types such as temperate grasslands. It has been reported from a North American prairie, though, that heavy rainfall events, combined with elongated drought periods in between, are more effective in decreasing productivity and changing species composition than an overall decrease in precipitation by 30% (Fay and others 2002; Knapp and others 2002). However, compared with simulated extreme heat, one brief extreme rainfall resulted only in slight changes of species composition in New Zealand grassland communities (White and others 2000).

European heath systems have also been found to show sensitive responses to extreme weather conditions. Heathland reacts to drought with decreased productivity (Gordon and others 1999; Filella and others 2004; Llorens and others 2004; Penuelas and others 2004), reduced reproductive success (Gordon and others 1999; Lloret and others 2004; Llorens and Penuelas 2005), and ultimately with changes in species composition (Lloret and others 2005).

These findings suggest that both grassland and heath would respond similarly to extreme weather events. This is remarkable, because grassland and heath communities are composed of different species with very different functional traits such as, for example, mean life span or lignification of the predominant species. Differing from grasses, dwarf shrubs do not die back completely over winter and can more effectively control transpiration rates. On the other hand, grasses are known to perform only weak stomata control.

Therefore, we suppose that grassland productivity is resilient in the face of the applied weather manipulations, whereas heath productivity is resistant. Here, resilience shall be defined as the ability of a system to absorb a disturbance event and return to pre-disturbance characteristics after a short period of time, whereas resistance shall be defined as the ability of a system to remain almost unaffected (compare Grimm and Wissel 1997). This notion of grassland productivity being resilient and

heath productivity being resistant thus implies higher vulnerability of grassland to extreme weather events in the short run.

Species Composition and Stability in Face of Extreme Weather Events

There is a long lasting debate about whether the stability against environmental fluctuations is related to the diversity of communities (summary in Beierkuhnlein and Jentsch 2005). According to the insurance hypothesis (Yachi and Loreau 1999), McGrady-Steed and others (1997) point at the higher predictability of diverse communities and Naeem (1998) stresses that in the face of sudden changes, high diversity increases the “reliability” of communities. The general idea is that diverse systems may be more stress tolerant because a higher number of species means a greater likelihood that there will be plant species to take over if other species suffer or die. Shifts in dominance and species-specific reactions therefore draw attention.

It has been questioned, however, if the described effects are caused by species numbers or rather by key species or functional types (Hooper and others 2005). In biodiversity experiments, facilitation of ecosystem functioning by legumes was found (Spehn and others 2002; Beierkuhnlein and Neshoever 2006). Mainly, the presence of legumes resulted in a higher productivity of communities via increased nitrogen availability. In most temperate ecosystems, available soil nitrogen is a limiting factor for plant growth. An increased supply of nitrogen can promote tolerance against other stressors (Larcher 2003). Here, we cannot test the insurance hypothesis comprehensively, but we compare the reactions of communities differing in

their functional and species compositions. For example, we expect that communities containing legumes are more stable in productivity and stress response after experimentally applied extreme weather events than communities only including non-legumes.

Our objectives were to test (1) the ecological effects of climatological extreme events. We furthermore asked (2) whether community composition is an important driver of system performance after extreme weather events in relation to two vegetation types with contrasting functional types of their predominant species (grassland versus heath), and (3) whether more diverse communities in our case study are more tolerant against the applied 100-year drought and heavy rainfall events.

MATERIALS AND METHODS

Experimental Design

The field experiment (EVENT-experiment, Jentsch and others 2007) was carried out in a three-factorial design manipulating (1) weather events (drought, heavy rainfall, control), (2) vegetation type, and (3) diversity level (Table 1). The design consisted of 90 plots, each 2 × 2 m in size, with every factorial combination replicated five times. Experimental plant communities (vegetation type × diversity level) were blocked and randomly assigned within each weather manipulation. Original species composition was maintained by periodical weeding. Prior to the experiment an area of 50 × 70 m was prepared with homogenized substrate (about 80 cm in depth) and drainage facilities to avoid soil-related heterogeneity. Texture of the soil body consisted of loamy sand (82% sand, 13%

Table 1. Experimental Plant Communities of Two Vegetation Types (Grassland, Heath) were used in Three Functional Diversity Levels, Resulting in Six Species Combinations

Abbreviation	Vegetation Type	Description	Species
G2 ⁻	Grassland	Two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	Grassland	Four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	Grassland	Four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	Heath	Two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	Heath	Four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	Heath	Four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

G = grassland; H = heath; 2/4 = number of species; -, without legume; +, with legume.

silt, 5% clay) with $\text{pH}_{(\text{KCl})} = 4.5$ and total N = 0.07% in the upper and $\text{pH}_{(\text{KCl})} = 6.2$ and total N = 0.01% in the lower soil layer. Data acquisition was carried out in the central square meter of each plot only, to circumvent edge effects. The experiment is located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19"N, 11°34'55"E, 365 m asl). Mean annual temperature is 7.8°C; mean annual precipitation 709 mm (data: German Weather Service). Usually, annual precipitation is distributed bimodally with a major peak during June/July and a second peak during December/January.

Extreme Weather Manipulations

The weather manipulations consisted of extreme drought, prolonged heavy rainfall, and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category; that is, we used a defined extremeness of weather events to measure ecological response, because we were interested if ecological response to the same weather event will differ between different plant communities. Vegetation periods (March–September) 1961–2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated. Drought was defined as the number of consecutive days with less than 1 mm daily precipitation. Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during the peak growing season in June 2005 (drought manipulation: days of the year 160–191; heavy rainfall manipulation: 178–191). Maximum values in the historical data set were 33 days without rain during June and July 1976 and 152 mm of precipitation during 14 days in June 1977.

Drought was simulated using rain-out shelters, constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany), and covered with a transparent plastic sheet (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany), which permitted nearly 90% penetration of photosynthetically active radiation. Near-surface air temperature was slightly (mean + 1.2°C), but not significantly (pairwise *t*-test with Bonferroni correction: $P = 0.12$), increased by the roofs during the weather manipulation period. Strong greenhouse effects were avoided by starting the roof at 80 cm height, allowing for near-surface air exchange.

Heavy rainfall was realized using portable irrigation systems. Drop size and rainfall intensity

resembled natural heavy rainfall events through application by Veejet 80100 nozzles, commonly used in erosion research. At 0.03 MPa water pressure this system resulted in 2.8 mm water per minute. The whole amount of added water was divided into two applications per day to constantly ensure high soil water saturation. If natural precipitation occurred, then the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of small plastic sheet pilings around treated plots.

Experimental Plant Communities

Overall, ten plant species were used to install artificial plant communities, which nevertheless represent naturally occurring species combinations in Germany. Species were chosen with respect to their belonging to one of the desired functional groups (grasses, herbs, legumes, dwarf shrubs), to their life-span (perennials), to their overall importance in nearby and central European grassland and heath systems, and to the fact that they can naturally occur on similar substrate. A total of 100 plant individuals per plot were planted in a systematic hexagonal grid with 20 cm distance between neighbors in early April (day of the year 92) from pre-grown individuals acclimated on site since February 2005. Communities were planted in three diversity levels for both vegetation types, resulting in six species combinations (Table 1). Only one species composition was used per diversity level and vegetation type. The reduction of complexity of the experimental systems as well as their strongly controlled environmental conditions are the only way to allow for identification of causal effects of changing variables such as extreme events or species diversity (see detailed discussion in Beierkuhnlein and Nesshoever 2006).

Data Acquisition: Response Parameters

Aboveground net primary productivity (ANPP) had to be quantified in different ways in the grassland and heath communities. For the grassland plots, aboveground harvests were conducted twice a year (1 week after weather manipulations ended, day of the year 200; and in September, day of the year 255), resembling local agricultural routines. ANPP was calculated by subtracting the initial biomass at planting from the sum of biomass over both harvests. Initial biomass was obtained by destructive measurements of 10 representative individuals per species prior to planting. The resulting mean biomass was multiplied by the number of planted individuals per plot. For the heath plots, destructive

sampling was not feasible due to the absence of such a disturbance in their natural environments and the chamaephytic life form of the key species. Instead, a set of non-destructive biometric measures were calibrated by multiple regression analysis against harvested individuals from outside the central plots, but inside the weather manipulations. For each species, a coefficient of correlation of $r^2 > 0.8$ was reached by a combination of two or three biometric measures.

Tissue die-back was quantified by cover measurements of standing-dead plant organs. A pin-point method was applied, recording the presence of plant organs in general and the presence for each species separately at 100 vertically inserted steel needles. These values were treated as percent cover. The measurement was repeated four times over the course of the vegetation period.

Soil moisture was monitored over the growing period by weekly readings with a TDR tube access probe (Diviner 2000, Sentek) at 5, 12, 20, and 28 cm soil depth in every plot. Near-surface air temperature was logged continuously in 10 min intervals in the G4⁻ communities of the drought and control treatments using thermistors (B57863-S302-F40, EPCOS).

Data Analysis

Significant differences between groups were tested for by analysis of variance (ANOVA). Homogeneous groups of factor combinations (weather manipulation, vegetation type, and diversity level) were identified by Tukey HSD post-hoc comparison. Repeated measure ANOVAs were used for measurements repeated over time (for example, tissue die-back). Prior to statistical analysis, data were log or square root transformed, if conditions of normality were not met or to improve homogeneity of variances. Both characteristics were tested by examining pp-qq plots (Faraway 2005). All statistical analyses were performed using SPSS 12.0 for Windows.

RESULTS

Ecological Effects of Climatological Extreme Events

Effects of Weather Manipulations on Soil Moisture Availability. Soil moisture content displayed the effects of the applied weather manipulations on the ecologically relevant parameter water availability (Figure 1). Dry conditions before the beginning of the drought manipulation (only 4 mm of precipitation in the 15 days before manipulation onset)

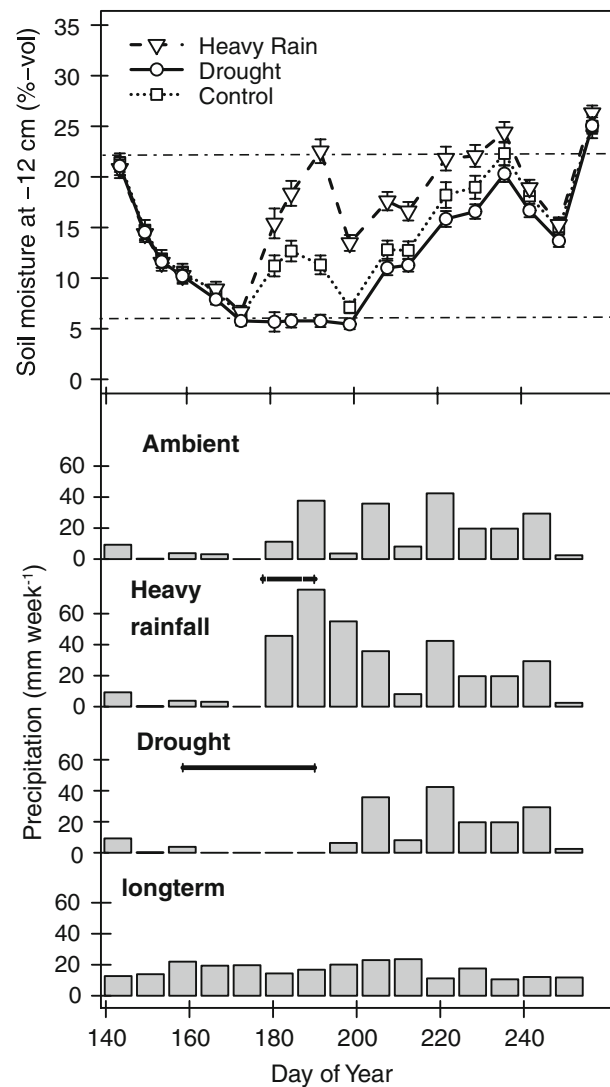


Figure 1. Soil moisture and precipitation in the EVENT experiment during manipulation and recovery after extreme drought and heavy rainfall events. Soil moisture (% volume) at 12.5 cm depth was measured by TDR tube access probe. As no difference in soil moisture as a function of experimental plant community was detected, all plant communities were merged together. Mean values and standard errors are given. Upper *dot-dashed* line indicates field capacity ($pF = 1.8$), lower *dot-dashed* line indicates permanent wilting point ($pF = 4.2$) of the soil substrate (AG Boden 1996). Grey bars show weekly precipitation for the weather manipulations in comparison with ambient conditions (control) and the long-term mean precipitation 1961–2000 (data: German Weather Service, Station Bayreuth). Timing and duration of the weather manipulations is indicated by black horizontal bars.

had already led to a minimum in soil water content. During the drought treatment, soil water content remained at this minimum at and below the permanent wilting point of this substrate

($pF = 4.2$, AG Boden 1996). During the rainfall manipulation, it took nearly 2 weeks until soil moisture had reached its maximum, and field capacity of the substrate ($pF = 4.2$, AG Boden 1996) was surpassed only transiently. After the end of the manipulation, however, soil moisture remained above the control level for several weeks, which resulted in about 20 days of water saturation in August, whereas the naturally wet conditions during this time led to moisture levels above field capacity for only 1 week in the control.

Plant Community Productivity and Tissue Die-Back in Response to the Weather Manipulations. Overall, simulated drought and prolonged heavy rainfall had no significant effect on community aboveground net primary productivity (ANPP), except in the heath community composed of grasses and dwarf shrubs ($H4^-$, Figure 2). Here, heavy rainfall resulted in an increase in ANPP compared to control. The increase in biomass was due to the performance of one grass species, *Agrostis stolonifera* (Figure 3), which is known to profit from increased soil moisture. Two other species showed significant alterations in ANPP: *Vaccinium myrtillus*, which decreased, and *Geranium pratense*, which increased ANPP after drought.

Community plant tissue die-back, recorded as cover percentage of dead fiber, is used here to express stress response. In the grassland communities,

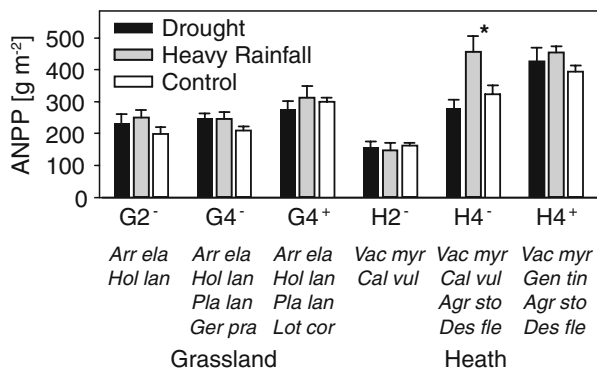


Figure 2. Effects of weather manipulations on community aboveground net primary productivity (ANPP) are small. Significant deviations from control within each experimental plant community are marked with an asterisk (ANOVA, Tukey's post-hoc comparison, $P < 0.05$). Shown are mean values and standard errors over five replications of the biomass gain between day of the year 92 (planting date) and 255. For the grassland communities, two destructive harvests were conducted (day of the year 200 and 255). Regressions with non-destructive, biometric measurements, validated outside the plots, were used in the heath-plots. Abbreviations of the respective species names are provided below the graph.

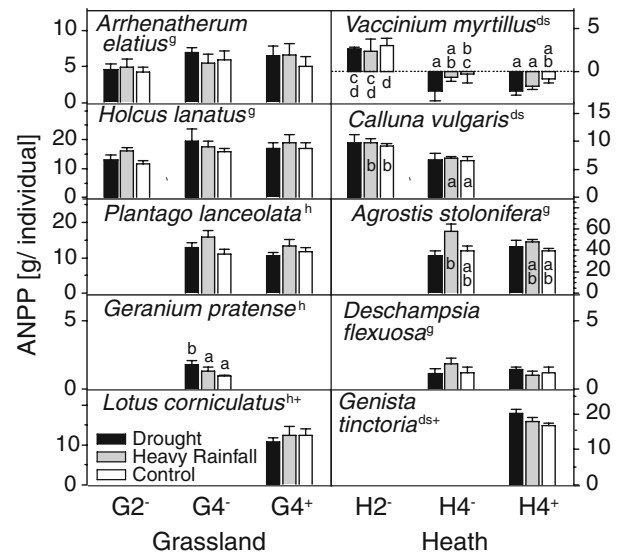


Figure 3. Mean species-specific aboveground net primary productivity (ANPP) per planted individual after planting date (day of the year 92). Grassland plots (species on the left side) were harvested twice (day of the year 200 and 255). ANPP of heath plots (species on the right side) was determined by correlations of non-destructive biometric measurements, validated against destructively harvested control plants outside the plots. Homogeneous groups according to Tukey HSD post-hoc comparison are indicated by letters (a, b, c, d) only if significant effects of weather manipulation and community composition occurred (ANOVA, $P < 0.05$). Mean values and standard errors of five replications are shown. *g* grass; *h* herb; *ds* dwarf shrub; +, legume; *G* grassland; *H* heath; 2⁻, two species, one growth form; 4⁻, four species, two growth forms; and 4⁺, four species, two growth forms containing legumes.

die-back rates were significantly higher after both drought and heavy rainfall as compared to controls. In heath communities, die-back rates were only increased after drought (Figure 4, Table 2). After drought, five species showed significant negative stress response, four of them in heath communities (Figure 5).

Differences in Vegetation Types: Grassland Versus Heath

Community ANPP was not affected by drought in any of the two vegetation types, and it increased after heavy rainfall in one heath community (Figure 2). An interesting, even though not significant, finding is that all species in grassland communities ($G2^-$, $G4^-$) increased in ANPP, whereas almost all species in heath communities ($H2^-$, $H4^-$) decreased in ANPP (Figure 3). Community tissue die-back rates revealed strong

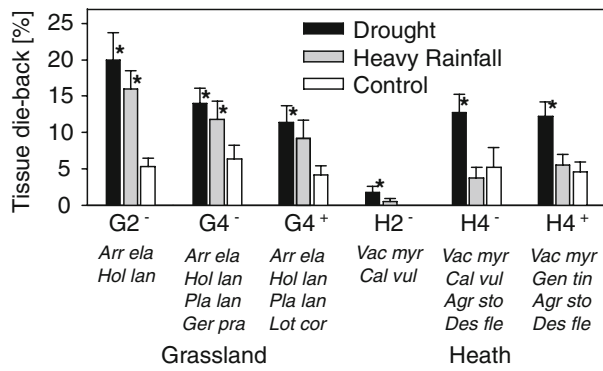


Figure 4. Tissue die-back due to simulated extreme weather events in the experimental plant communities 1 week after the extreme weather manipulations ended (day of the year 195). Asterisks indicate significant differences between weather manipulation and control within each experimental plant community ($P < 0.05$, see Table 1). G grassland; H heath; 2⁻, two species, one growth form; 4⁻, four species, two growth forms; and 4⁺, four species, two growth forms containing legumes. Displayed are mean values and standard errors over five replications.

reactions of grassland communities to both extremes and of heath communities only to drought. By examining the significant species-specific die-back rates (Figure 5), however, grassland com-

munities appeared to be slightly more tolerant with increased tissue die-back of only one species compared to increased tissue die-back of three species in the heath communities.

Community Composition and Stability in the Face of Extreme Weather Events

No significant differences were found between the different community compositions within each weather manipulation in the grassland communities, even though a trend toward increasing community productivity with increasing diversity seems to exist (Figure 2). Community productivity of heath communities differed significantly between community compositions, but no significant interaction between community composition and weather manipulation was found. This indicated that the various community compositions did not differ in their response to the applied weather events for any of the two vegetation types.

Significant reactions to the applied weather manipulations on species ANPP were found only for two dwarf shrubs: *Vaccinium myrtillus* and *Calluna vulgaris* (Figure 3). Both species produced less biomass per planted individual in the more diverse communities. This phenomenon even increased

Table 2. Mean Tissue Die-Back due to Simulated Extreme Weather Events in the Experimental Plant Communities over the Growing Season

Tissue Die-Back (% Cover)		Day of the Year				P (F) versus Control
		166	195	234	252	
G2 ⁻	Drought	0.0	20.0	2.0	4.8	0.006 (10.7)
	Heavy rain	0.0	16.0	5.0	3.2	0.046 (4.1)
	Control	0.0	5.4	1.4	2.2	
G4 ⁻	Drought	0.0	14.0	2.0	3.6	0.031 (3.9)
	Heavy rain	0.0	11.8	5.8	2.8	0.044 (3.2)
	Control	0.0	6.4	0.0	1.8	
G4 ⁺	Drought	0.0	11.4	3.0	1.8	0.041 (3.9)
	Heavy rain	0.0	9.2	4.6	1.0	0.179 (1.8)
	Control	0.0	4.2	4.2	0.6	
H2 ⁻	Drought	0.0	1.8	0.4	1.2	0.029 (3.8)
	Heavy rain	0.0	0.6	0.8	0.2	0.386 (1.0)
	Control	0.0	0.0	0.6	0.0	
H4 ⁻	Drought	0.0	12.8	6.0	4.0	0.035 (5.8)
	Heavy rain	0.0	3.8	0.6	1.2	0.800 (2.7)
	Control	0.0	5.2	1.6	1.6	
H4 ⁺	Drought	0.0	12.2	6.0	5.8	0.011 (7.4)
	Heavy rain	0.0	5.6	0.8	0.6	0.170 (2.2)
	Control	0.0	4.6	1.6	2.8	

Repeated measures ANOVA revealed a significant interaction between time, experimental plant community, and manipulation (Greenhouse-Geisser: $P = 0.002$; $F = 8.2$). Significant treatment effects within one experimental plant community were evaluated in a pairwise *rmANOVA* between one weather manipulation and control. Note that in the grassland communities aboveground biomass was harvested twice (day of the year 200 and 255).

G = grassland; H = heath; 2⁻ = two species, one growth form; 4⁻ = four species, two growth forms; 4⁺ = four species, two growth forms containing legumes. Displayed are mean values over five replications.

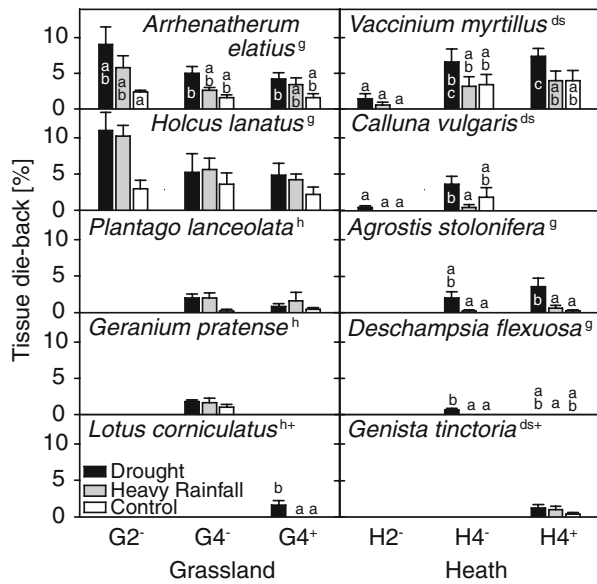


Figure 5. Species-specific tissue die-back 1 week after the extreme weather manipulations ended (day of the year 195). Shown are mean values and standard errors measured by pinpoint method with 100 needles per plot. Homogeneous groups according to Tukey HSD post-hoc comparison are indicated by letters (a, b, c, d) only when significant effects of weather manipulation and community composition occurred (ANOVA, $P < 0.05$). Mean values and standard errors of five replications are shown. *g* grass; *h* herb; *ds* dwarf shrub; +, legume; *G* grassland; *H* heath; 2^- , two species, one growth form; 4^- , four species, two growth forms; and 4^+ , four species, two growth forms containing legumes.

with increasing diversity after drought compared to control.

The two vegetation types showed oppositely directed diversity effects compared to each other for community tissue die-back (Figure 4). Nearly no effect of weather extremes for heath communities composed of dwarf shrubs only ($H2^-$) contrasted strongly with severe effects in communities composed of dwarf shrubs and grasses ($H4^-$) after drought. Thus, the effect size increased with increasing diversity in heath communities after drought compared to control. Grassland communities showed the opposite response. The highest stress values occurred in communities composed of grasses only ($G2^-$), whereas the presence of herbs tended to attenuate the effect size.

Community ANPP showed no significant effect of extreme weather manipulation between communities with legumes (4^+) and without legumes (4^-). For the comparison between heavy rainfall and controls, grassland community die-back rates were significantly increased without the presence of a nitrogen-fixing species, and no longer significantly

increased with a nitrogen-fixing species present. However, this effect seems to be small (Figure 4), and no other reaction supported the idea of increased community stability due to legume presence.

DISCUSSION

Ecological Effects of Climatological Extreme Events

In our experiment, effects of the applied weather manipulations on plant communities were moderate and community productivity appeared to be relatively stable in the face of extreme weather events with a recurrence of 100 years. No species was driven to lethal reactions by the extreme weather manipulations.

As it is the climatological extremeness which changes due to climate change (IPCC 2007), calculating and testing extremeness on this basis is a mechanistic way to conduct experiments (Jentsch and others 2007). But our results show that extreme events in climatological parameters do not necessarily have to be accompanied by strong reactions in the ecosystems. The extremeness in the ecologically relevant steering parameters (here: soil moisture) and their dependence on the proposed changes in climate therefore require attention. Even though the length of time with soil moisture below the permanent wilting point in the drought manipulation and above field capacity in the heavy rainfall manipulation was clearly increased as compared to controls, we cannot provide any number of the extremity of these conditions, as the long-term data basis for such parameters is generally very poor and, of course, strongly site specific.

Die-back numbers and species-specific performance at the community level, however, proved that the applied events generated stress and that species differ in their response. These changes might be driven by direct plant reactions to the applied weather manipulations or through indirect effects. For example, effects of drought and water on plant growth can also be translated through changes in soil and microbial processes (Emmett and others 2004). Such indirect effects are important to study to obtain a mechanistic understanding on the effects of extreme weather events.

Experimental weather manipulations resulted in an immediate severe reduction in productivity due to a single simulated drought in a study by Kahmen and others (2005), but this can be explained by the more extreme manipulation (60% longer rain-free period compared to our study in a comparable

environment). This fact emphasizes the importance of reporting effects of extreme events relative to local mean conditions, as extremeness based on ecologically more meaningful parameters are not commonly available (see above). Comparably small effects on plant productivity when exposed to drought manipulations are found in other experiments during the first year, too (Fay and others 2000; Gorissen and others 2004). In these experiments, effects became much more obvious after repeated weather manipulations. However, such an increase in recurrence describes another, undeniably important dimension of climate change, nevertheless leading away from the study of single events, which was the focus of our study.

Our results imply that a single local 100-year extreme drought or prolonged heavy rainfall event can be tolerated by the studied vegetation types without adverse effects on productivity, despite high stress levels, which are indicated by significant tissue die-back. The significant reactions by single species, however, might be capable of changing community compositions in the long term, potentially leading to even more stable communities in the face of recurrent disturbance events of the same kind as the more tolerant species become more dominant. The applied weather manipulations, however, do not cover drought and heavy rainfall completely, other factors like the minimum amount of rainfall over longer time periods rather than the time without any precipitation, or the recurrence and timing of such events are worth studying as well.

Differences in Vegetation Types: Grassland Versus Heath

The literature suggests similar reactions to drought events for both vegetation types, with reduced biomass productivity in grassland (Sternberg and others 1999; Grime and others 2000; Kahmen and others 2005) and heath (Gordon and others 1999; Filella and others 2004; Llorens and others 2004; Penuelas and others 2004), reduced reproductive success in grassland (Fox and others 1999; Morecroft and others 2004) and heath (Gordon and others 1999; Lloret and others 2004; Llorens and Penuelas 2005), ultimately resulting in alterations of species composition in grassland (Grime and others 2000; Buckland and others 2001) and heath (Lloret and others 2005). Heavy rainfall has not yet been considered nearly as extensively as drought, rendering a literature comparison of both vegetation types with respect to this aspect impossible. We argued that the similarity between two such con-

trasting vegetation types might only be due to the fact that the experiments so far are not comparable in their manipulation magnitudes.

In our experiment, grassland and heath communities reacted differently to the weather manipulations. Overall, grassland remained surprisingly stable. More significant effects of weather manipulations were found in heath species, especially in the dwarf shrubs. These differences cannot be explained by the different treatments in terms of cutting twice only the grassland and not the heath communities. Even though this point complicates direct comparisons between the two vegetation types, our results indicate that vegetation types in their natural disturbance regimes differ in their reactions to extreme weather events.

The different reactions between both vegetation types can probably be explained by the contrasting life strategies of their dominant functional types. Nevertheless, it is surprising that dwarf shrubs with their rather conservative life strategies (longevity, lignification) are more strongly affected than grasses which are known to have a high turnover rate, exploit resources fast and die-back when resource availability is limited until the conditions become favorable again (Larcher 2003). Competitive strength may be an explanation for the observed differences between grasses and dwarf shrubs. Strong competitors could be facilitated as their neighbor's mean competitive power decreases with increasing diversity. This would ultimately result in positive diversity effects only for strong competitors. The studied dwarf-shrub species in the heath communities are especially known to be outcompeted by grasses under nutrient enrichment via nitrogen deposition (Wessel and others 2004).

Community Composition and Stability in Face of Extreme Weather Events

Our results concerning the differences in the response to extreme events of different community compositions are limited to one species composition per diversity level and are therefore not conclusive. The results, however, indicate interesting effects that should be further examined. Looking at community tissue die-back (Figure 4), an insurance effect (McNaughton 1977; Yachi and Loreau 1999) occurred in the grassland communities. This increase in stability with increasing diversity, however, was even inverted in the heath communities. Positive diversity effects can be attributed to two classes of mechanisms: sampling effects and complementarity (Huston 1997; Tilman and others 1997; Loreau and Hector 2001). The sampling

effect refers to the greater probability of including (sampling) a highly productive species (or species better adapted to changing environmental conditions) in an assemblage with increasing species richness. Positive reactions were found in our experiment, for example, for *G. pratense* biomass after drought. As many as 8 out of 19 significant species reactions were positive. In contrast, complementarity refers to a class of processes that result in higher performance of a mixture than would be expected from the separate performances of each component species. Complementarity is often attributed to niche partitioning or facilitation (Tilman and others 1997; Loreau and Hector 2001). In our grassland plots, the die-back rates decreased with increasing diversity, and although we are not able to separate between sampling and complementarity in this contribution, this effect can at least partly be explained by facilitation (Callaway and Walker 1997) of the two relevant species (*Arrhenatherum elatius* and *Holcus lanatus*), which both showed decreased die-back rates in the presence of more species (Figure 5).

Independent from diversity, the species-specific reactions show that single extreme events can already alter competitive pressure on particular species. Furthermore, the presence of changes in both directions at the species level together with no effects at the community level illustrates that stability at a higher level of organization may require overcoming stability at lower levels (Berkes and others 2003). Shifts in different directions at the species level can therefore be viewed as an integral part of the stability at the community level.

Species combinations integrating legumes produced the highest amounts of aboveground biomass in both vegetation types, but this was independent from the weather manipulations. Facilitation by legumes, found in diversity experiments where biomass production is addressed as a key function (Spehn and others 2002), could therefore not be proven to have a significant buffering effect against the applied weather events with respect to ANPP and tissue die-back in grassland and heath communities. Species-specific reactions indicated even a higher susceptibility to extreme weather events if legumes were present, especially after drought. Negative effects of increased nitrogen availability on ecosystem functioning are also reported from other systems during periods of water stress. Nitrogen fertilization makes vine plants more susceptible to drought due to decreased root to shoot ratios (Keller 2005). *Populus* species are also found to be more vulnerable to xylem cavitation due to water stress after high

concentrations of nitrogen in the soil (Harvey and van den Driessche 1999).

CONCLUSIONS

One important ecosystem function, community productivity, remained remarkably stable in artificial plant communities exposed to local 100-year extreme drought and heavy rainfall events. This finding poses the question of how the expected increase in magnitude and frequency of extreme climatic events influences ecological extremity. In our experiment, tissue die-back proved to be a strong stress response to the applied intensity of weather manipulations. This response was modified by species composition. Even though diversity levels used here were low and not repeated, the opposing results from the two vegetation types with grassland apparently stabilized against extreme weather events by increasing functional diversity, and heath communities even more adversely affected in more diverse communities hint that contrasting vegetation types or functional groups need to be considered in more detail in the diversity-stability debate. Mechanisms of coexistence and ecosystem functioning such as above-average effects of single species (sampling effect hypothesis), resource-use partitioning, and complementarity gain current importance in the face of dramatically changing environments. To quantify upcoming changes in ecosystems under these circumstances, it is an urgent question whether functional response types are adequate tools or whether species-specific reactions have to be considered.

ACKNOWLEDGMENTS

We thank Katherine Owen for helpful comments on reasoning and language of an earlier version of this article, Henning Schröder for assistance in statistical analyses, and Steve Neugebauer and Jégor Böttcher-Treschkow for their assistance in field work.

REFERENCES

- AG Boden. 1996. *Bodenkundliche Kartieranleitung*, 4th edn. E. Schweizerbartsche Verlagsbuchhandlung, Hannover.
- Beck C, Jacobeit J, Philipp A. 2001. Variability of North-Atlantic-European circulation patterns since 1780 and corresponding variations in Central European climate. In: Brunet India M, López Bonillo D, Eds. *Detecting and modelling regional climate change*. Berlin: Springer. pp 321–31.
- Beierkuhnlein C, Jentsch A. 2005. Ecological importance of species diversity. A review on the ecological implications of species diversity in plant communities. In: Henry R, Ed. *Plant*

- diversity and evolution: genotypic and phenotypic variation in higher plants. Wallingford: CAB International. pp 249–85.
- Beierkuhnlein C, Nesshoever C. 2006. Biodiversity experiments—artificial constructions or heuristic tools? *Prog Bot* 67:486–535.
- Berkes F, Colding J, Folke C. 2003. Navigating social-ecological systems: building resilience for complexity and change. Cambridge: Cambridge University Press.
- Buckland SM, Thompson K, Hodgson JG, Grime JP. 2001. Grassland invasions: effects of manipulations of climate and management. *J Appl Ecol* 38:301–9.
- Callaway RM, Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–65.
- Christensen JH, Christensen OB. 2003. Climate modelling: severe summertime flooding in Europe. *Nature* 421:805–6.
- Crawford RMM, Braendle R. 1996. Oxygen deprivation stress in a changing environment. *J Exp Bot* 47:145–59.
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–74.
- Emmett BA, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Penuelas J, Schmidt I, Sowerby A. 2004. The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. *Ecosystems* 7:625–37.
- Faraway JJ. 2005. Linear models with R. Boca Raton: Chapman & Hall/CRC.
- Fay PA, Carlisle JD, Danner BT, Lett MS, McCarron JK, Stewart C, Knapp AK, Blair JM, Collins SL. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *Int J Plant Sci* 163:549–57.
- Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. *Ecosystems* 3:308–19.
- Filella I, Penuelas J, Llorens L, Estiarte M. 2004. Reflectance assessment of seasonal and annual changes in biomass and CO₂ uptake of a Mediterranean shrubland submitted to experimental warming and drought. *Remote Sens Environ* 90:308–18.
- Fox LR, Ribeiro SP, Brown VK, Masters GJ, Clarke IP. 1999. Direct and indirect effects of climate change on St John's wort, *Hypericum perforatum* L. (Hypericaceae). *Oecologia* 120:113–22.
- Gordon C, Woodin SJ, Alexander IJ, Mullins CE. 1999. Effects of increased temperature, drought and nitrogen supply on two upland perennials of contrasting functional type: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytol* 142:243–58.
- Gorissen A, Tietema A, Joosten NN, Estiarte M, Penuelas J, Sowerby A, Emmett BA, Beier C. 2004. Climate change affects carbon allocation to the soil in shrublands. *Ecosystems* 7:650–61.
- Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kieley JP. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289:762–5.
- Grimm V, Wissel C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–34.
- Harvey HP, van den Driessche R. 1999. Nitrogen and potassium effects on xylem cavitation and water-use efficiency in poplars. *Tree Physiol* 19:943–50.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35.
- Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–60.
- IPCC. 2007. Climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, Eds. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press. p 996.
- Jentsch A. 2006. Extreme climatic events in ecological research. *Front Ecol Environ* 5:235–6.
- Jentsch A, Kreyling J, Beierkuhnlein C. 2007. A new generation of climate change experiments: events, not trends. *Front Ecol Environ* 5:365–74.
- Kahmen A, Perner J, Buchmann N. 2005. Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct Ecol* 19:594–601.
- Keller M. 2005. Deficit irrigation and vine mineral nutrition. *Am J Enol Vitic* 56:267–83.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–5.
- Larcher W. 2003. Physiological plant ecology. 4th edn. Berlin: Springer.
- Llorens L, Penuelas J. 2005. Experimental evidence of future drier and warmer conditions affecting flowering of two co-occurring Mediterranean shrubs. *Int J Plant Sci* 166:235–45.
- Llorens L, Penuelas J, Beier C, Emmett B, Estiarte M, Tietema A. 2004. Effects of an experimental increase of temperature and drought on the photosynthetic performance of two ericaceous shrub species along a north-south European gradient. *Ecosystems* 7:613–24.
- Lloret F, Penuelas J, Estiarte M. 2004. Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. *Global Change Biol* 10:248–58.
- Lloret F, Penuelas J, Estiarte M. 2005. Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland. *J Veg Sci* 16:67–76.
- Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–6.
- McGrady-Steed J, Harris PM, Morin PJ. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390:162–5.
- McNaughton SJ. 1977. Diversity and stability of ecological communities—comment on role of empiricism in ecology. *Am Nat* 111:515–25.
- Meehl GA, Karl T, Easterling DR, Changnon S, Pielke R, Changnon D, Evans J, Groisman PY, Knutson TR, Kunkel KE, Mearns LO, Parmesan C, Pulwarty R, Root T, Sylvest RT, Whetton P, Zwiers F. 2000. An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bull Am Meteorol Soc* 81:413–6.
- Morecroft MD, Masters GJ, Brown VK, Clarke IP, Taylor ME, Whitehouse AT. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Funct Ecol* 18:648–55.

- Naeem S. 1998. Species redundancy and ecosystem reliability. *Conserv Biol* 12:39–45.
- Penuelas J, Gordon C, Llorens L, Nielsen T, Tietema A, Beier C, Bruna P, Emmett B, Estiarte M, Gorissen A. 2004. Noninvasive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north-south European gradient. *Ecosystems* 7:598–612.
- Raisanen J, Joellsson R. 2001. Changes in average and extreme precipitation in two regional climate model experiments. *Tellus A Dynam Meteorol Oceanogr* 53:547–66.
- Sanchez E, Gallardo C, Gaertner MA, Arribas A, Castro M. 2004. Future climate extreme events in the Mediterranean simulated by a regional climate model: a first approach. *Glob Planet Change* 44:163–80.
- Schmidli J, Frei C. 2005. Trends of heavy precipitation and wet and dry spells in Switzerland during the 20th century. *Int J Climatol* 25:753–71.
- Schönwiese CD, Grieser J, Tromel S. 2003. Secular change of extreme monthly precipitation in Europe. *Theor Appl Climatol* 75:245–50.
- Semmler T, Jacob D. 2004. Modeling extreme precipitation events—a climate change simulation for Europe. *Glob Planet Change* 44:119–27.
- Spehn EM, Scherer-Lorenzen M, Schmid B, Hector A, Caldeira MC, Dimitrakopoulos PG, Finn JA, Jumpponen A, o'Donovan G, Pereira JS, Schulze ED, Troumbis AY, Körner C. 2002. The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos* 98:205–18.
- Sternberg M, Brown VK, Masters GJ, Clarke IP. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. *Plant Ecol* 143:29–37.
- Tilman D, Lehman CL, Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–61.
- Wessel WW, Tietema A, Beier C, Emmett BA, Penuelas J, Riis-Nielsen T. 2004. A qualitative ecosystem assessment for different shrublands in western Europe under impact of climate change. *Ecosystems* 7:662–71.
- White TA, Campbell BD, Kemp PD, Hunt CL. 2000. Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Glob Planet Change* 6:671–84.
- Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci USA* 96:1463–8.