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Simulating the Future – Responses of Ecosystems, Key Species, and European Provenances to Expected Climatic Trends and Events

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With 4 Figures and 1 Table

Abstract

Future climate change is expected to rapidly modify the long-term average and variation in temperature and precipitation regimes. The local climate that has been experienced by organisms and ecosystems does no longer exist. More frequent and more pronounced extreme weather conditions are expected in the near future. Monitoring both future climate and the ecological responses will be important. However, monitoring can not supply the necessary insights for the design of adaptation strategies in time. Ecological modeling is heuristically limited due to the simple fact of hitherto not available evaluation and adjustment of results. Thus, the experimental simulation of climatic trends and events is urgently needed in order to identify responses of important communities and species that are exposed to a novel climate. Experimental approaches are artificial to some degree, but they can yield fundamental insights into crucial mechanisms of response to rapid climate change. In the EVENT experiments (EVENT I to V), we simulate expected future climatic conditions including extreme weather events along a gradient ranging from highly standardized and replicated pot experiments over manipulation of strongly controlled artificial plant communities (with defined number of specimen and with standardized substrate) to manipulation of semi-natural established grassland communities on old-grown soils. We are testing the effects of summer warming, winter warming, increased winter precipitation, recurrent extreme summer drought, excessive summer rain, and modified frost-thaw-cycles. In addition, we are combining different drivers in multi-factor experiments (e.g. land use intensity and warming or more extreme precipitation regimes). The main focus of the EVENT-experiments is on grasslands, but also shrubland (heath) on the community level and important tree species on the within-species diversity level are experimentally exposed to future climatic scenarios. The role of biodiversity – in terms of species richness and richness of various growth forms and functional groups – for the buffering of extreme weather events is of special interest for us. Surprises occur! Total biomass did not respond as strongly as expected, but single species performance was very specific. For particular species, significant effects of drought, heavy rain and increased freeze-thaw cycles were found in parameters related to e.g. nutrient cycling, gas exchange, phenology and reproductive fitness. Biodiversity did both, buffer extremes in some cases and accelerate stress in other cases.

Zusammenfassung

Der zukünftig erwartete Klimawandel wird mit Veränderungen regionaler Temperatur- und Niederschlagsregime einhergehen. Der Rahmen bisheriger Klimabedingungen, welchen Organismen und Ökosysteme ausgesetzt waren, wird in vielen Regionen verlassen. Zusätzlich werden häufigere und stärkere Extremwetterbedingungen erwartet. Die Beobachtung ökologischer Antworten ist wichtig. Dennoch kann diese nicht die Einblicke vermitteln, die für die rechtzeitige Entwicklung von Anpassungsstrategien benötigt werden. Die Möglichkeiten ökologischer Modellierung sind erkenntnistheoretisch limitiert, da noch nicht auftretende Bedingungen zur Evaluierung und Anpassung der Modelle benötigt würden. Folglich wird eine experimentelle Simulation von erwarteten Trends und Events benötigt, um die Antworten wichtiger Lebensgemeinschaften und Arten unter neuartigen Bedingungen erkennen zu können. Experimentelle Ansätze sind immer zu einem gewissen Grad artifiziell, aber sie können signifikante Aussagen zeitigen. In den EVENT-Experimenten (EVENT I bis V) simulieren wir in naher Zukunft erwartete Klimabedingungen inklusive extremer Wetterereignisse in einem Gradienten unterschiedlicher Naturnähe, von stark kontrollierten Topfexperimenten über kontrollierte Feldexperimente (mit definierter Zahl von Pflanzen und einheitlichem Substrat) hin zu naturnahen Experimenten in etablierten Lebensgemeinschaften auf gewachsenen Böden. Wir testen die Auswirkungen von Sommererwärmung, Wintererwärmung, erhöhtem Winterniederschlag, Sommertrockenheit, sommerlichem Starkregen, veränderten Frost-Auftau-Zyklen. Zusätzlich kombinieren wir verschiedene Steuergrößen in Multifaktor-Experimenten (z. B. veränderte Landnutzungsintensität und Erwärmung mit dem Auftreten extremer Wetterereignisse). Hauptsächlich konzentrieren wir uns auf Grünland, doch berücksichtigen wir auf der Ebene der Lebensgemeinschaften auch Strauchvegetation (Heide) und Bäume verschiedener europäischer Herkünfte als Schlüsselarten. Die Rolle der Biodiversität – sowohl der Artenzahl als auch der Vielfalt von Wuchsformen und funktionellen Eigenschaften – in der Modulation der Effekte des schnellen Klimawandels ist für uns von besonderem Interesse. Überraschende Ergebnisse zeigen sich! Die Gesamtbiomasse von Pflanzengemeinschaften reagiert nicht so stark wie erwartet, aber einzelne Arten werden zum Teil stark ausgelenkt und reagieren komplementär. Biodiversität trägt nicht nur zur Pufferung von Extremen bei. In einigen Fällen führt sie zur Verstärkung des auftretenden Stresses.

1. Heuristic Value of Ecological Experiments in the Face of Climate Change

Humans will be affected by direct climatic impacts. Even more important, indirect effects that are mediated by organisms can severely restrict the societal benefits from ecosystem services. Resources such as drinking water, food and raw materials can be impaired. Pest outbreaks and other natural hazards are promoted. In addition, declining biodiversity is expected to reduce functional resilience of ecosystems.

However, ecological effects of climate change are largely unclear. Of course, we can learn from the past. Paleo-ecological records are valuable. However, their temporal resolution is quite often very coarse. First of all, the expected climate of the future will be surpassing historical records, at least for the last 10,000 years of ecosystem development and memory relevant in Central Europe.

As a consequence, the modeling of biotic responses suggests to be applied. By generalizing ecosystems and biomes in a low spatial resolution at the global scale, conclusions on carbon cycles can be drawn. A higher resolution is constricted partly due to the fact that regional ecosystems and key species perform individual traits and responses. First of all, it is hypothetical to model responses to hitherto not experienced conditions and to project biotic performance outside of the historic range of regional biota. In case of novel site conditions modeling options are limited.

However, "novel" has to be defined. Here, we apply the ecological perspective, meaning environmental conditions that were not imposed to either a given gene-pool of a species (regional populations) or to a given species composition of an ecosystem. Ecological evidence shows that summarizing ecosystems to biomes such as "tropical rain forest" or "broad-leaved deciduous forest" does only support a preliminary and shallow approach but cannot contribute substantially to the understanding of possible responses.

Actual comparisons between local populations and populations that are found under different climates can not be translated into the evaluation of the natural adaptive capacity. Climatic envelopes, which are derived from recent records of species across a range of site conditions, ignore the genetic variability within species. The occurrence of a species in a warmer climate than the one that is in focus for a certain place, does not guarantee the survival and vitality of local populations of this species. Adapted ecotypes within species must not be morphologically distinct. Conclusions from pattern to process can be misleading and support the illusion of safety, as far as key species for ecosystem functioning are concerned.

However, in the face of the drastic climatic changes, which are projected for the 21st century to occur worldwide, we urgently need a better understanding of possible responses of natural systems. Coping and adaptation strategies have to be developed and implemented, soon.

Traditional approaches of ecology and biogeography are aiming to investigate organisms and ecosystems in nature. This is self-evident, because natural systems are addressed with conceptual, theoretical and practical questions.

In the face of climate change, ecological findings can hardly be derived from observations and monitoring. Too many pitfalls are waiting for the investigation of climate change effects on ecosystems, organisms and local populations. These pitfalls include a locally varying history, delayed response and inertia, small-scale site differences and gradients, and autocorrelation. There is an inherent need to prove the results of monitoring approaches in experimental setting. Records and measurements in natural systems have to be seen as a contribution to the generation of hypotheses.

Due to the complexity of nature, a true testing of hypotheses in natural and diverse ecological systems is almost impossible. We can only get a first glimpse on processes, functioning and mechanisms that create a certain pattern, but these cannot be verified in a natural science understanding.

Experiments, on the other hand, can only pick up a selected and very limited number of variables (Fig. 1). The epistemological approach of experiments is indispensably reductionist. Many aspects of natural systems have to be ignored in order to install replicates and controls. But, only then new unbiased insights can be gained when the design of a study allows hypotheses to be falsified or, in the case of non-falsifiable null-hypothesis, that the correlation between the quality of an exposed system (e.g. ecosystem, community, population) and the conducted treatments is significant.

Combining the output and projections of climate models with manipulation experiments is very promising. But, still, there are deviations between models. Plus, only few larger regions of the earth can be covered by regional models at higher resolution. In Europe, WETTREG, STAR, CLM and REMO are providing informative regional projections for a plenitude of climatic parameters. But scenarios on the future frequency and magnitude of extreme weather events are very limited. Uncertainties exist concerning the most probable global emission scenarios. The IPCC has developed such scenarios based on demographic, technological, political, and societal projections. The COP 15 conference in Copenhagen has clearly demonstrated that even if there is conviction and will for decision, the requirements of internal policy are stronger than for international agreement.

2. Overview on Previous Experimental Approaches in Field Ecology

Although hypotheses can hardly be tested in nature, traditional ecology and biogeography were very much orientated to field research, exploring and analyzing patterns. Early experimental studies, important for hypotheses testing, such as the extinction and recolonization experiment on Florida Keys mangrove islands by Simberloff and Wilson (1970), were not criticized for being artificial but for being destructive (e.g. Farnsworth and Rosovsky 1993).

The major problem when experimentally manipulating communities and ecosystems is the complexity of biotic interactions. Ecological systems are not sealed and often diffuse in their spatial extent. This is why influential historical case studies preferred defined catchments (e.g. Hubbard Brook) or concentrated on other distinct units such as lakes (Likens 1985). As in any field experiment, true controls and true replicates are impossible. Unavoidably, noise and variance sets may hide the targeted response patterns.

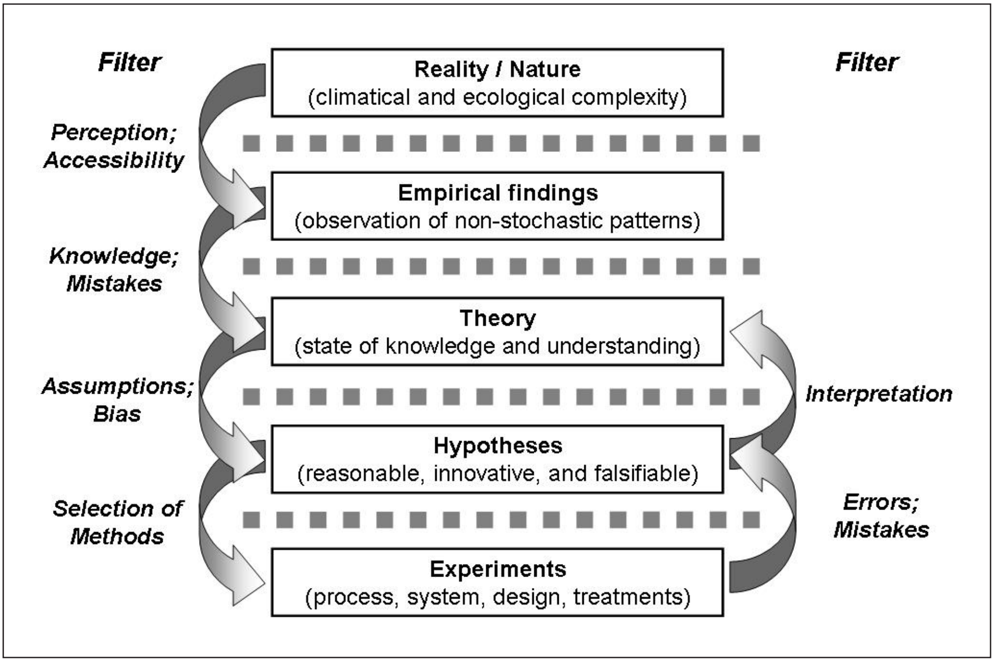

Fig. 1 The development of scientific understanding is mostly stimulated by filtered observation of natural patterns. However, in case of expected future developments a more heuristic and experiment-oriented approach is needed. Restrictions (filters) have to be considered but, with every loop, hypotheses can be refined and theoretical understanding will be improved. Another advantage is the reduction of complexity in experiments by concentrating on a certain mechanism, ecosystem or simulations of expected climatic changes.

As a consequence of the Rio Conference on Biodiversity and the international Convention on Biodiversity, and stimulated by the idea that biodiversity loss may have consequences on ecosystem functioning and services to mankind, a new generation of ecological experiments was installed since the 1990ies (Hector et al. 2007). First of all, the Cedar Creek Experiment in the USA (Tilman et al. 1996) and the European BIODEPTH Experiment (Hector et al. 1999) yielded remarkable results (Beierkuhnlein and Nesshoever 2006) and a follow-up of more and more sophisticated experiments (e.g. Jena-Experiment, Roscher et al. 2004) even manipulating tree species richness (Scherer-Lorenzen et al. 2005).

With some delay but in certain parallelism to the development of biodiversity experiments, climate change experiments evolved. Initially, at the end of the 20th century, mainly CO_2 enrichment and warming were simulated. In first experiments, the majority of manipulations was affected in natural and supposedly sensitive ecosystems (e.g. high mountains, tundra). Simple “Open-Top-Chambers” (OTCs) were established in the International Tundra Experiment (ITEX) in the whole arctic in order to reduce wind speed and thereby increase surface-near air temperature. Harte and Shaw (1995) installed infrared heating devices at wet and dry sites in high mountain ecosystems and found specific responses of plant functional groups on both sites proving that resource availability and functional attributes of plant species have to be considered. In recent years, manipulations of the precipitation regime were carried out in semi-natural ecosystems (e.g. Kahmen et al. 2005). In contrast to slight modifications of temperatures, changes in the temporal availability of water will be directly reflected in the vegetation. It is evident that his field of research is rapidly expanding (Fig. 2).

3. The Simulation of Future Climate and Extreme Weather Events

As far as projections of climatic extremes are concerned, we can only argue on the basis of probabilities. Neither global nor regional climate models are capable of delivering reliable data. There is too much noise in the data stream. Nevertheless, an increase of energy in the atmosphere will necessarily enhance climatic variability in general, making extremes more pronounced and more frequent.

Recognizing the necessity to investigate the effects of rare but possibly influential extreme events, we installed a set of experiments, which are explicitly designed to dissect the role of extreme conditions (Jentsch et al. 2007, Jentsch and Beierkuhnlein 2008). In the EVENT Experiments (I to V, see Tab. 1), we simulate the expected future Central European climate.

Based on experience from field and biodiversity experiments, we organized the experiments along a gradient of naturalness ranging from pot experiments through defined communities to manipulations of established semi-natural ecosystems. The effects of simulated weather extremes are detected in various kinds of replicates and controls (Fig. 3). Modifications of carbon sequestration appear at the ecosystem scale (Mirzaei et al. 2008). Various species-specific responses appear in the vegetation, but surprisingly, biomass productions remains quite stable at the community level (Kreyling et al. 2008a). The same is found true for microbial activity in soils (Kreyling et al. 2008b).

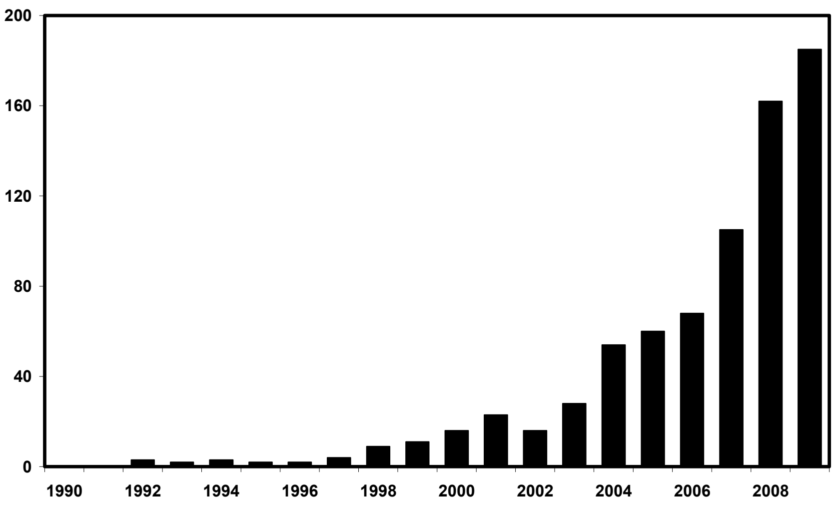

Fig. 2 Development of the number of publications found in peer-reviewed journals for the search string: "climat* change" + biodiversity / "biol* diversity" + experiment* (February 2010, ISI web of knowledge).

Tab. 1 EVENT-Experiments at the University of Bayreuth

	EVENT I	EVENT II	EVENT III	EVENT IV	EVENT V (ex BIODEPTH)
Begin	2005	2008	2008	2010	1996/2009
# Replicates	5	5	21	5	2
# Plots (*Pots)	150	225	2,352*	140	64
Communities	grassland, shrubland	grassland	–	grassland, shrubland	grassland
Functional Types	grasses, herbs, legumes, shrubs	grasses, herbs, legumes	grasses, trees, shrubs	grasses, shrubs	grasses, herbs, legumes
Biodiversity					
Gradient of species diversity (# species per plot)	artificial 1, 2, 4	natural 9–32	none	artificial 1, 2, 4	initially artificial 1–6, now 16–26
Gradient of functional diversity	1, 2, 3	none	none	1, 2, 3	1, 2, 3
Total # species	10	55	10	4	54
Simulation of climatic extremes					
Extreme precipitation in summer	×	×	×	–	–
Extreme drought in summer	×	×	×	–	–
Intensified frost-thaw-cycles in winter	×	–	–	×	–
Simulation of climatic trends					
Summer warming	–	×	×	–	–
Winter warming	×	×	–	–	–
Winter-rain	–	×	–	–	×
Types of control					
Ambient control	×	×	–	×	×
Artefact control	×	–	×	–	–
Average control	×	×	–	–	–
Naturalness					
Naturalness of the installed system	intermediate	high	low	low	intermediate
Simulation of land use intensity (mowing)	–	×	–	–	–
Simulation of land use intensity (fertilisation)	–	×	–	–	–
Combined treatments					
Warming / drought	–	×	×	–	–
Warming / heavy rain	–	×	×	–	–
Warming / land use	–	×	–	–	–

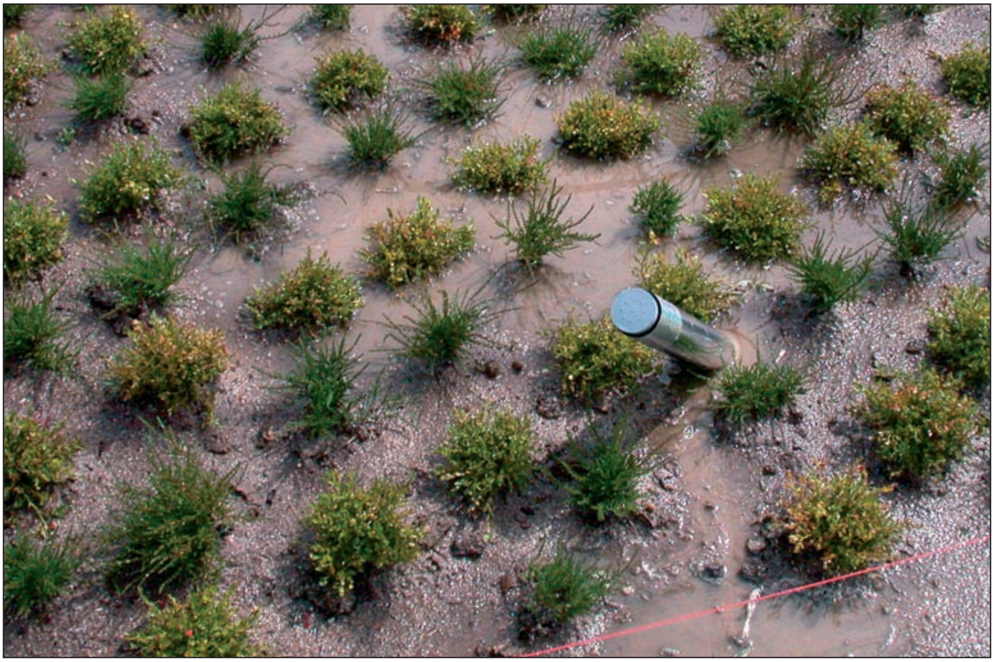

Fig. 3 Newly installed regular distribution of dwarf shrubs in the EVENT I Experiment in the Ecological-Botanical Gardens of the University of Bayreuth after artificial heavy rainfall.

Increased thermal variety in winter time is expected to come along with more frequent changes between freezing and thawing at the soil surface. The repeated melting of insulating snow cover exposes the overwintering parts of plants to night time frost. We interrupted soil frost several times and found strong responses during the following vegetation period. However, the underlying mechanisms are not yet understood (Kreyling et al. 2010).

Flower phenology was found to answer sensitively to short-term extreme events and in a much stronger way than expected for long-term trends (Jentsch et al. 2009).

In accordance with the insurance hypotheses (Yachi and Loreau 1999), species diversity contributes to the buffering of responses and increases resilience due to species-specific responses. In flower phenology, however, we also find counteracting effects of biodiversity. Drought delays phenology of heath (*Calluna vulgaris*) considerably, but only when grasses are present. Grasses are efficient in the development of dense and shallow rooting systems, which intensifies the experienced water shortage in drought treatments for the dwarf shrub (Jentsch et al. 2009).

Community stability is not only controlled by intrinsic responses. Invasion processes may be enhanced by stress that is imposed to the established community. Compared to controls, we found increased community invasibility after heavy rain and reduced invasibility after drought (Kreyling et al. 2008c). Species richness reduced invasibility and contributed to the structural maintenance of established ecosystems.

In addition to approaches at the community and species level, we looked at the genetic variability between populations and their performance in face of climatic extremes. For key species such as *Arrhenatherum elatius* we found a differentiated response, indicating that selecting certain provenances can be seen as an adaptation strategy for the maintenance of ecosystem functioning (Fig. 4).

4. Conclusions

Future experiments on the ecological effects of climate change are needed at larger spatial scales. Ecological complexity can hardly be addressed at small plot sizes. Reliable results can only be achieved in long-term research. However, specific responses are to be expected to a certain year's climate. Also, the climate of early spring may influence the legacy of the whole experiment. Such kinds of singularities can be identified in a stratified design, only, where the start of the experiment is replicated several times in order to produce communities of different ages, which are exposed to climatic manipulations.

Concepts for experimental controls (ambient, artifact, average conditions) and references for manipulations (historical time series, ecological impact, and future projections) are not elaborate and mature until today. Meta-analyses would profit from more standardized and defined approaches. Generality in responses could easier be identified. Obviously, the intensity, duration and also the timing of weather and climate change simulations is decisive – but appropriate data, scales and reference systems are still missing. Finally, we need more multi-factorial experiments, as it is not only one driver that is changing. Interactions between

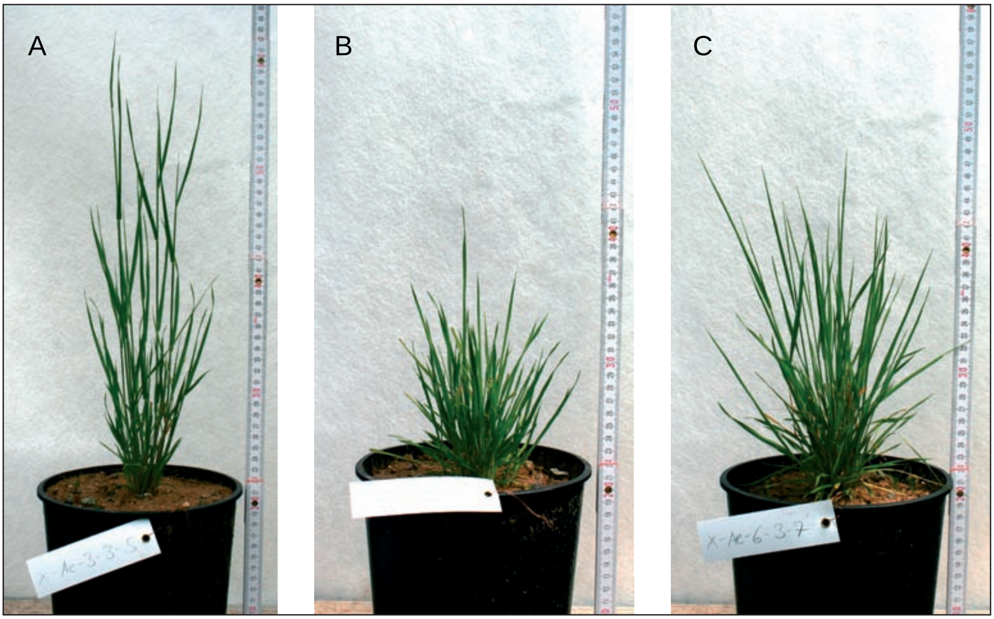

Fig. 4 Comparison of an italian (*A*), hungarian (*B*), and german provenance (*C*) of *Arrhenatherum elatius* (EVENT III). These plants are grown from seed and have been exposed to the same treatment (here combined treatment: warming plus drought). Within the same species, the resilience against climatic stress differs strongly depending on genetically fixed preadaptation.

drivers of ecosystem change are to be expected. Additive effects but also complementary compensation effects are likely to occur and modify the responses to single variables.

References

Beierkuhnlein, C., and Nesshoever, C.: Biodiversity experiments – artificial constructions or heuristic tools? Progress Botany *67*, 486–535 (2006)

Farnsworth, E. J., and Rosovsky, J.: The ethics of ecological experimentation. Conservation Biology *7*, 463–472 (1993)

Harte, J., and Shaw, R.: Shifting dominance within a montane vegetation community. Science *267*, 876–880 (1995)

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H.: Plant diversity and productivity experiments in European grasslands. Science *286*, 1123–1127 (1999)

Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Spehn, E. M., Wacker, L., Weilenmann, M., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell, K., Jumpponen, A., Leadley, P. W., Loreau, M., Mulder, C. P. H., Nesshöver, C., Palmborg, C., Read, D. J., Siamantziour, A. S. D., Terry, A. C., and Troumbis, A. Y.: Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. Functional Ecology *21*, 998–1002 (2007)

Jentsch, A., and Beierkuhnlein, C.: Research frontiers in climate change: effects of extreme meteorological events on ecosystems. Comptes Rendus Geoscience *340*, 621–662 (2008)

Jentsch, A., Kreyling, J., Boettcher-Treschkow, J., and Beierkuhnlein, C.: Beyond gradual warming – effects of extreme weather events on flower phenology of European grassland and heath species. Global Change Biology *15*, 837–849 (2009)

Jentsch, A., Kreyling, J., and Beierkuhnlein, C.: A new generation of climate change experiments: Events, not trends. Frontiers in Ecology and Environment *5*, 365–374 (2007)

Kahmen, A., Perner, J., Audorff, V., Weisser, W., and Buchmann, N.: Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. Oecologia *142*, 606–615 (2005)

Kreyling, J., Wenigmann, M., Beierkuhnlein, C., and Jentsch, A.: Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. Ecosystems *11*, 752–763 (2008a)

Kreyling, J., Beierkuhnlein, C., Elmer, M., Pritsch, K., Radovski, M., Schloter, M., Wöllecke, J., and Jentsch, A.: Soil biotic processes remain surprisingly stable in face of 100-year extreme weather events in experimental grassland and heath. Plant Soil *308*, 175–188 (2008b)

Kreyling, J., Beierkuhnlein, C., Ellis, L., and Jentsch, A.: Invasibility of grassland and heath communities exposed to extreme weather events – additive effects of biotic resistance and fluctuating physical environment. Oikos *117*, 1542–1554 (2008c)

Kreyling, J., Beierkuhnlein, C., and Jentsch, A.: Effects of soil freeze-thaw cycles differ between experimental plant communities. Basic and Applied Ecology *11*, 65–75 (2010)

Likens, G. E.: An experimental approach for the study of ecosystems. Journal of Ecology *73*, 381–396 (1985)

Mirzaei, H., Kreyling, J., Hussain, M. Z., , Li, Y., Tenhunen, J., Beierkuhnlein, C., and Jentsch, A.: A single drought event of 100-year recurrence enhances subsequent carbon uptake and changes carbon allocation in experimental grassland communities. Journal of Plant Nutrition and Soil Science *171*, 681–689 (2008)

Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W. W., Schmid, B., and Schulze, E.-D.: The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. Basic and Applied Ecology *5*, 107–121 (2004)

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G., and Schulze, E.-D.: The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen, M., Körner, C., and Schulze, E.-D. (Eds.): Forest Diversity and Function; pp. 347–376. Berlin: Springer 2005

Simberloff, D. S., and Wilson, E. O.: Experimental zoogeography of islands. Ecology *51*, 934–937 (1970)

Tilman, D., Wedin, D., and Knops, J.: Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature *379*, 718–720 (1996)
Yachi, S., and Loreau, M.: Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. USA *96*, 57–64 (1999)

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