

# The acid taste of climate change: 20th century acidification is re-emerging during a climatic extreme event

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**Abstract.** The current state of an ecosystem results from the complex interaction of abiotic and biotic drivers jointly influenced by their dynamics and the legacy of a systems' history. Negative synergies between emerging climatically extreme events and past environmental impacts are expected to shift ecological communities to alternative stable states or towards hysteretic successional trajectories. However, knowledge on mutual effects of environmental stressors is scarce especially for not experimentally controlled, natural ecosystems.

We investigated the effect of a prolonged drought and heat wave occurred during 2003 on the short-term vegetation responses of forest springs, a waterlogged type of ecosystem which is highly abundant in Central European siliceous mountains. These landscapes experienced strong impairment by 20th century atmospheric acidification. For different levels of acidification, we investigated plant community composition and water chemistry of 57 springs before (1996) during (2003) and after (2004–2006) the summer of 2003 and quantified ecological resilience and elasticity related to this extreme event for single plant species and species assemblages of whole communities.

The extreme dry and hot summer 2003 significantly decreased discharge, increased water temperature and affected water chemistry of the investigated springs. Ecological resilience and elasticity against the climatic extreme event differed significantly between communities dependent on their previous impact by acidification. Springs which were less affected by acidification performed higher resilience and elasticity than strongly acidified springs.

Our study shows that strong negative synergies between emerging climatic extreme events and past environmental impairments occur on landscape scale. Hitherto, such interactions between climate change, hydrochemistry, and the responses of ecosystems have been neglected.

**Key words:** climate change modelling; crenal habitats; ecosystem stability; extreme weather events; heat spell; insurance hypothesis; summer drought; response diversity; tipping point.

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## INTRODUCTION

A multitude of abiotic and biotic non-linear dynamics and interactions modified by historical

events qualify ecosystems to be complex adaptive systems (Gell-Mann 1994, Levin 1998, Norberg 2004). One major aim in ecology is to increase the basic understanding and, thus,

establish a proper concept of ecosystems by quantifying the characteristics and drivers of these complex dynamics (Potts et al. 2006). Although complexity is inherent in every ecosystem and complex ecosystem dynamics are a major topic in experimental ecology since the introduction of this concept (Standish et al. 2014), the interaction between abiotic triggers and biotic community response remains rarely studied for uncontrolled, natural systems.

Strong temporal dynamics in ecological communities are triggered by disturbances, discrete events in time which change abiotic environmental conditions and significantly disrupt ecological community structure (Pickett and White 1985, White and Jentsch 2001). The temporal response of an ecological community to a certain disturbance can be simplified in a two dimensional model characterized by ecological resilience and elasticity (cf. Holling 1973). Whereas elasticity quantifies the ability of an ecosystem to return to a stable state after disturbance (Grimm and Wissel 1997), ecological resilience defines the amount of disturbance an ecosystem can absorb without changing its actual state (Holling 1973, Gunderson 2000).

During the last three decades of research, climate change is reported to have strong detrimental ecological effects on species, communities and ecosystems (Walther et al. 2002, Bonan 2008). But still, gradual shifts in temperature are in the main focus of climate change research. However, anthropogenically enhanced climatic variability and occurrence of extreme climatic events like heavy rainfall events or severe and extensive droughts that dramatically increased in frequency and severity in recent years (Ciais et al. 2005, Reichstein et al. 2007) are now widely recognized to be more disruptive in terms of ecosystem functioning (Jentsch and Beierkuhnlein 2008, IPCC 2014).

An extreme heat wave combined with a severe drought descended on large parts of Europe during the summer of 2003, with July temperatures exceeding long-term means by up to 6°C, combined with severe droughts expressed in annual precipitation deficits up to 300 mm year<sup>-1</sup>, which were 50% below the long-term average (Luterbacher et al. 2004, Ciais et al. 2005). Such climatic events like in 2003 are expected to interactively cause strong adverse

ecological effects with other stressors like historical environmental pollution (Lovejoy and Hannah 2005, Brook et al. 2008, Fordham and Brook 2010). However, such kind of mutual interactions between historical and emerging environmental stressors can hardly be accounted for in experimental studies and are difficult to identify in most terrestrial ecosystems (Heino et al. 2009).

Forest springs exhibit the advantage of low human disturbance in combination with a close relation between site conditions and species assemblages. Plant communities of springs are assumed to be especially susceptible to climatic extreme events like extensive droughts (Smith and Wood 2002, Wood et al. 2010) as these hybrid ecosystems linking groundwater to the uppermost section of surface running waters are commonly reported to exhibit very constant abiotic environments in terms of discharge, temperature and water chemistry to which species are evolutionary adapted to (Odum 1971, van der Kamp 1995, Cantonati et al. 2006, Gerecke et al. 2011). As springs occur in a high spatial frequency in the mountainous regions of Central Europe they provide a unique study system to assess ecological effects of climatic extreme events on landscape scale by taking into account the full range of natural system complexity.

In this study we take advantage of the outstanding climatic event during 2003 to examine the effects of abrupt environmental changes on the response characteristics of single species and whole communities of central European forest springs (helocrenic springs sensu Thiennemann 1924). Among all morphological types of springs these springs host the most specialized and taxon-rich communities (Cantonati et al. 2012). Numerous studies on this type of springs showed that inhabiting plant species strongly respond to changes in water temperature and water chemistry and, thus, energetic and chemical shifts in their catchments (Kraeuchi 1993, Beierkuhnlein and Gollan 1999, Cantonati et al. 2006, Hájková et al. 2008, Audorff et al. 2011, Kubíková et al. 2012, Schweiger and Beierkuhnlein 2014). But still the multifarious effects of anthropogenic climate change in these complex, natural systems are neglected.

As the outstanding heat wave combined with a severe drought certainly affected water depen-

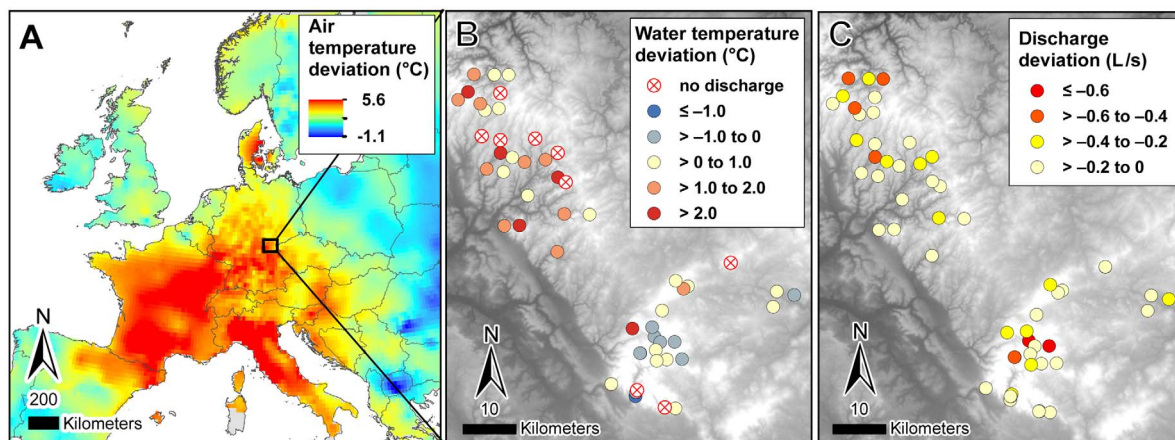


Fig. 1. Location of the studied soft water springs in Central Europe. (A) Map of Central Europe depicting the deviation of the bimonthly mean air temperature for July/August 2003 from the long-term bimonthly mean for July/August (1950–2013, data source: ENSEMBLES Observations gridded dataset (E-OBS), Haylock et al. 2008). Deviation of water temperature (B) and discharge (C) of the studied springs in September 2003 from the September water temperatures/discharge rates averaged for the whole study period (1996–2006).

dent communities (Zwolsman and van Bokhoven 2007), we expect strong and lasting effects on single species occurrence and whole plant community composition in the surveyed springs. Based on the assumed evolutionary adaptation of spring communities to long-term environmental stability we hypothesize low ecological resilience and elasticity to this extreme climatic event as well for single species as for whole plant communities.

## METHODS

### Study sites

The studied springs ( $n = 57$ ) are located in the lower mountain ranges of Central Germany (latitude 49.9–50.6° N, longitude 11.2–12.2° E) and were strongly exposed to the heat wave and the severe drought (see Fig. 1A) which occurred during summer and autumn of 2003 (Schaer et al. 2004). All springs are fed by surface-near run-off (interflow) which leads to constant but rather low discharge rates mainly below 2 L/s.

The parent material in the catchments is characterized by siliceous bedrock (schists and granite), which causes the low buffering capacity against acidification and nutrient load of these springs under pristine conditions. The predominantly forested catchments are characterized by Norway spruce (*Picea abies* (L.) H. Karst),

intermixed and only partly substituted by European beech (*Fagus sylvatica* L.) (further details see Audorff et al. 2011, Schweiger and Beierkuhnlein 2014).

Caused by the low buffering capacity in combination with high loads of acidifying pollutants all investigated springs/catchments were strongly affected by acidification caused by the unfiltered emission of acidifying pollutants, which culminated in the 1970s and 1980s (Matzner and Murach 1995). Since then, impact and effects of former acidification have slowly decreased but are still effective.

The year 2003 featured an extraordinary climatic situation in Central Europe. Precipitation deficits in combination with an early greening of vegetation in springtime caused high losses of soil moisture during spring which significantly intensified drought during summer of this climatically very extreme year (Fischer et al. 2007). The subsequent extreme drought period caused a decline in carbon sequestration at continental scale (Ciais et al. 2005). The discharge and even water quality of Central European rivers was therefore significantly affected (Zwolsman and van Bokhoven 2007).

### Data collection

We investigated spring plant community composition and hydrochemistry before (1996),

during (2003) and in the three consecutive years (2004–2006) after the extreme summer of 2003. Hydrochemical data were collected in September of each year at the uppermost point of the seepage area with visible water movement to avoid any kind of short-term distorting effects caused by water-atmosphere interactions. We conducted measurements of water temperature, electrical conductivity and pH by using a portable pH-conductivity multimeter (WTW Wissenschaftlich-Technische Werkstaetten GmbH, Weilheim, Germany). Furthermore we visually estimated the water discharge rate based on a seven point ordinal scale reaching from 0 L/s up to >1.5 L/s. To quantify the buffering capacity against acidification we measured acid neutralizing capacity (ANC) ex-situ by titration (0.01 m HCL to pH = 4.3). Water sampling was not possible for nine springs in 2003, two springs in 2004 and one spring in 2005 and 2006 because of insufficient discharge (see Fig. 1B for 2003).

Vegetation was surveyed once per year between July and August. Therefore we recorded presence/absence of all vascular plant species, mosses and liverworts for each spring along a permanently marked line-transect with a 10 cm resolution (see also Kapfer et al. 2012). Transects, which vary between 1.1 m and 24.7 m in length, span the full seepage area perpendicular to the direction of main discharge at the largest width of the well-differentiated spring site. Plants, which grew on microsites like rocks or dead wood and, thus, had no contact to the water saturated ground, were excluded from the analyses. To eliminate the bias in between site comparisons caused by differing transect lengths, species abundance along transect was standardized by dividing the number of line sections with species presence by the total number of line sections examined for the particular spring.

#### Data analyses

We analyzed whole community response by using a Principal Component Analysis (PCA) based on the recorded abundances of all species co-occurring along the transects of the investigated springs (vegan R package, v. 2.0-10; Oksanen et al. 2013). We quantified the extent of plant community response by calculating the Euclidean distances of each spring site in the multi-dimensional ordination space between the

investigated years as well as the cumulative distance for all investigated years. Species and environmental parameters which significantly characterize the investigated springs were selected post-hoc by fitting the respective parameters on the ordination with a goodness-of-fit threshold of  $r^2 > 0.4$  (*envfit()*-command with 1000 permutations). We used k-means clustering to differentiate response groups of plant communities in the multi-dimensional ordination space (*kmeans()*-command based on a maximum of 1000 iterations).

For each of the selected, characteristic species we quantified the pairwise interspecific overlap of occupied environmental space with all other characteristic species before, during and after the climatic extreme event of 2003. To quantify the occupied environmental space for each of the selected species we conducted kernel-density estimations based on the five environmental parameters characterizing the spring sites where the particular species occurred: water temperature, pH, electrical conductivity, ANC and discharge (hypervolume-package for R, v. 0.9.9.7, Blonder 2014).

We tested statistical differences between our variables of interest by using the non-parametric Mann-Whitney (U) test for non-paired samples and the Wilcoxon (W) test for paired samples. Potential relatedness between the variables of interest was tested by using Pearson correlation. We conducted all analyses with the software environment R (version 3.0.2; R Development Core Team 2013) with a level of significance of  $\alpha = 0.05$ .

## RESULTS

### Effects on environmental conditions

Mean discharge in 2003 of  $0.14 \text{ L/s} \pm 0.2 \text{ L/s}$  (arithmetic mean  $\pm$  SD) was clearly lower compared to the long-term mean discharge of  $0.34 \text{ L/s} \pm 0.28 \text{ L/s}$  calculated for the whole study period (1996 to 2006, Mann-Whitney  $U = 551$ ,  $n = 57$  springs,  $P < 0.001$ ). Water temperature was higher in 2003 compared to the long-term mean ( $9.1^\circ\text{C} \pm 1.9^\circ\text{C}$  compared to  $8.5^\circ\text{C} \pm 1.2^\circ\text{C}$ ,  $U = 1613.5$ ,  $P = 0.12$ ). Deviations from long-term average conditions were also found for pH ( $5.9 \pm 0.8$  compared to  $5.6 \pm 0.6$ ,  $U = 1596$ ,  $P = 0.14$ ), acid neutralizing capacity (ANC:  $0.27 \text{ mmol/L} \pm$



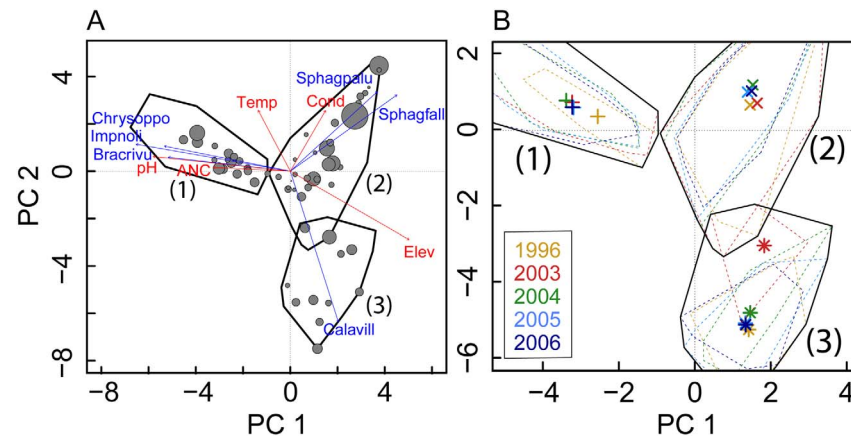


Fig. 2. Short-term vegetation response of springs in community composition to the climatic extreme summer 2003 (results of a Principal Component Analysis). (A) The three different community groups (black hulls, 1: neutral lowland springs, 2: acidified lowland springs and 3: upland springs) are mainly differentiated by temperature (Temp: water temperature and Elev: elevation) as well as by the acidity regime (pH, and ANC: acid neutralizing capacity) reflected in different character species (blue arrows). (B) Temporal shifts in species composition within the three community groups. Depicted are group centroids (plus signs: neutral lowland springs, crosses: acidified lowland springs and asterisks: upland springs) and outer margins (dashed lines in different colours) for the particular years. Size of grey points (A) depicts the extent of initial community reaction (2003–2004) in the particular springs. Abbreviations are Chrysoppo: *Chrysosplenium oppositifolium*, Impnoli: *Impatiens noli-tangere*, Bracrivu: *Brachythecium rivulare*, Sphagpalu: *Sphagnum palustre*, Sphagfall: *Sphagnum fallax*, Calavill: *Calamagrostis villosa* and Cond: electrical conductivity.

0.30 mmol/L compared to  $0.19 \text{ mmol/L} \pm 0.22 \text{ mmol/L}$ ,  $U = 1589$ ,  $P = 0.15$ ) and electrical conductivity ( $112.4 \text{ } \mu\text{S/cm} \pm 107.14 \text{ } \mu\text{S/cm}$  compared to  $133.3 \text{ } \mu\text{S/cm} \pm 137.4 \text{ } \mu\text{S/cm}$ ,  $U = 1201$ ,  $P = 0.28$ ) although differences were not significant.

We observed a significant negative correlation between the deviation of water temperature in 2003 compared to the long-term mean and the elevation of the studied springs (Pearson  $r = -0.31$ ,  $df = 55$ ,  $P = 0.02$ ). In other words, the lowland springs tended to be warmer in 2003, thus, strongly affected by the heat wave, whereas the upland springs tended to be less warmed up during 2003 (see also Fig. 1B). Deviation in pH during 2003 compared to the interannual mean was significantly decreased with increasing elevation ( $r = -0.32$ ,  $P = 0.02$ ). We observed no such correlation between deviation in discharge and elevation, which means that the effect of drought was similar for lowland and upland springs ( $r = -0.14$ ,  $P = 0.3$ ; Fig. 1C).

#### Plant community response

Principal Component Analysis (PCA) com-

bined with the k-means clustering demarcated three groups of spring plant communities which can be seen as a result of impairment caused by previous acidification. Cumulative explanatory power of the first three axes of the principal component analyses was 38.6% of total variation. The first ordination axis, which explained 19.3% of total variation, was mainly correlated with pH and ANC. Both parameters are closely related to the acidity regime and separate neutral lowland springs from anthropogenically acidified lowland springs. The second axis, which explained 10.1% of total variation, was mainly correlated with elevation and water temperature and delimited cool, naturally acid highland springs from the springs of lower elevations.

The community groups, named in the following: neutral lowland springs, acidified lowland springs and upland springs, showed significant differences in the response to the extreme climatic event of 2003 in terms of species assemblage and characteristic species (Fig. 2A). Species which significantly characterize the three community groups are *Chrysosplenium oppositifolium*-

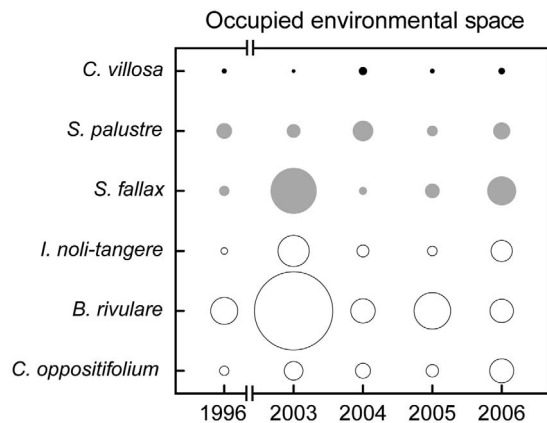


Fig. 3. Temporal variation in occupied environmental space for the plant species characterizing soft water springs in Central Germany. Point size depicts the volume of occupied environmental space in the particular year (based on the  $n$ -dimensional hypervolume for the particular species). The different colors depict the community groups which are characterized by the different species (white: neutral lowland springs, grey: acidified lowland springs, black: upland springs).

*lium* L., *Impatiens noli-tangere* L. and *Brachythecium rivulare* Schimp. for the neutral lowland springs as well as *Sphagnum fallax* (H. Klinggr.) H. Klinggr. and *S. palustre* L. for the recently acidified lowland springs. *Calamagrostis villosa* (Chaix) J.F.Gmel. characterizes the upland springs. We observed a high resilience of neutral lowland springs to the climatic extreme event of 2003 (expressed by relatively small point size and shifts of convex hulls in Fig. 2A and B, respectively). In contrast, we observed strong initial response, thus low resilience for the acidified lowland springs. For the upland spring communities, we found the strongest response in 2003, thus, lowest resilience among all three community groups. Community composition of these upland springs shifted towards the acidified lowland springs. However, the highland communities showed high elasticity by returning to the initial pre-2003 state right after the extreme in 2004 and overall shift in community composition was lower than for the acidified lowland springs.

#### Single species response

For the characteristic species of the three

community groups demarcated by the PCA we observed a strong but not uniform change in the volume of occupied environmental space during the extreme summer of 2003 (Fig. 3). The strongest increase in occupied environmental space was found for the moss *Brachythecium rivulare*, followed by the moss *Sphagnum fallax* and the annual herb *Impatiens noli-tangere*. The perennial clonal herb *Chrysosplenium oppositifolium* showed a slight increase during 2003. In contrast, we observed losses in occupied environmental space for the moss *Sphagnum palustre* and the perennial clonal grass *Calamagrostis villosa*.

Temporal variation in occupied environmental space (coefficient of variation [cv]) was highest for *Sphagnum fallax* (cv = 0.74) followed by *Impatiens noli-tangere* and *Brachythecium rivulare* (cv = 0.62 and 0.61, respectively). Lowest temporal variation was observed for *Sphagnum palustre* (cv = 0.24), while *Chrysosplenium oppositifolium* and *Calamagrostis villosa* performed intermediate temporal variation in occupied environmental space (cv = 0.36 and 0.32, respectively).

Significant impacts of the climatic extreme summer of 2003 on the interspecific overlap of occupied environmental space were detected (Fig. 4). We observed a decrease in the overlap between *Calamagrostis villosa*, which characterizes upland springs, and all other lowland spring species from 32% in 1996 to 16% in 2003 (mean difference 16%,  $W = 15$ ,  $P = 0.06$ ). In contrast, overlap between *Sphagnum fallax* and common species such as *Chrysosplenium oppositifolium*, *Brachythecium rivulare* and *Impatiens noli-tangere* increased in 2003 on average from 18% to 37% (mean difference 19%,  $P = 0.25$ ).

## DISCUSSION

Biotic responses to climatic extreme events are extensively studied for experimentally controlled, artificial ecosystems on spatially restricted, local scale (Smith 2011 and references therein, Jaeschke et al. 2014). Knowledge is scarce when it comes to uncontrolled, natural ecosystems on larger spatial scales (Easterling et al. 2000, Smith 2011). Here we show for an uncontrolled ecosystem on landscape-scale that biotic response of plant communities to the extreme

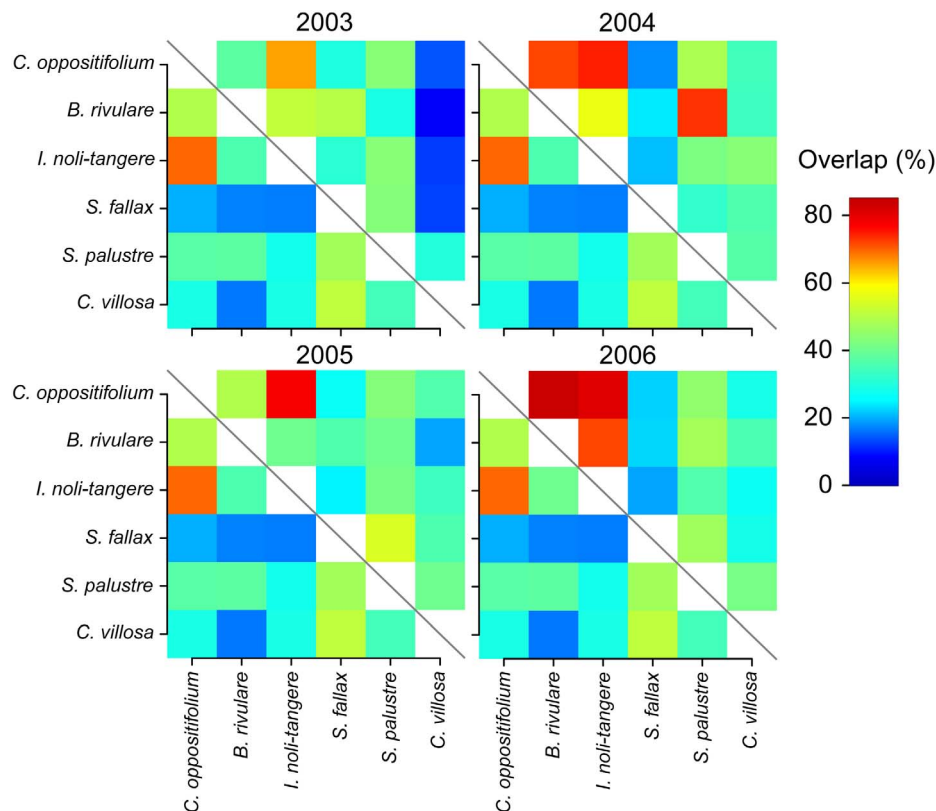


Fig. 4. Temporal variation of overlap in occupied environmental space (2003–2006) between species characterizing neutral lowland springs (*C. oppositifolium*, *B. rivulare*, *I. noli-tangere*), acidified lowland springs (*S. fallax*, *S. palustre*) and upland springs (*C. villosa*). Overlap of the particular year is depicted in the upper right half of each plot, whereas pre-2003 niche overlap (1996) is shown as reference in the lower left half of each plot.

conditions of the year 2003 is clearly related to the systems' history in terms of anthropogenic acidification. This was found for single species as well as for species assemblages and plant communities.

Extensive and prolonged summer drought has been reported for freshwater systems to significantly interact with acidification (Schindler et al. 1996, Schindler 1997). Here, we show that spring communities previously impaired by anthropogenic acidification clearly differ in terms of ecological resilience and elasticity compared to springs previously less affected by acidification. We observed high community resilience for neutral lowland springs unaffected by historic pollution but low resilience for lowland springs that were exposed to acidification. In other words, pristine lowland springs which were previously not strongly affected by acidification

were significantly more resilient, thus, more prone to prolonged summer droughts than springs which are already destabilized by acid rain. Upland springs which were affected in discharge (drought) similar to lowland springs but were significantly less affected in water temperature (heat wave) showed lower resilience but higher elasticity than lowland springs.

In contrast to anthropogenic atmospheric acidification, natural acidification is a consequence of long-term processes that require time spans such as millennia. Podzolic traits in upper soils are formed under high precipitation combined with low temperature and subsequently low carbon turnover. Spring communities that are located in catchments with these properties had enough time to adapt to the naturally acidic conditions. Comprehensibly, upland springs which are characterized by naturally acid condi-

tions showed lowest resilience but high elasticity to the climatically extreme summer of 2003. The strong initial reaction of the upland spring community is linked to water temperature as the direction of the water temperature effect in the ordination follows the same direction as the shift of this community.

Extreme climatic events will affect the performance of individual species in different ways and, thus, alter community composition (Parmesan and Yohe 2003, Thibault and Brown 2008). However, communities exposed to fluctuating environmental conditions are more prone to abrupt climatic changes than communities adapted to environmental stability (Walther et al. 2002). Spring plant communities are commonly expected to consist of very specialized taxa that are evolutionary confined to stable environmental conditions and, thus, should reveal low ecological resilience and elasticity in face of extreme climatic events. Although we observed the community response to the extreme climatic event to be dependent on acidification history, we observed surprisingly high elasticity of single species populations and whole spring plant communities to the climatic extreme summer of 2003.

Biotic compensation against the climatic extreme summer 2003 on community level results from the variance in response characteristics of single plant species. Species-specific responses within the neutral low-land spring community were characterized by high heterogeneity in the extent of reaction. Both, the moss *Brachythecium rivulare* and the annual herb *Impatiens noli-tangere* performed high elasticity but low resilience, whereas high resilience was observed for the perennial and clonal herb *Chrysosplenium oppositifolium*. Similar patterns were found for the acidified lowland springs, where *Sphagnum fallax* showed higher response flexibility compared to *S. palustre*. This is in accordance with the conceptual idea of the insurance hypothesis, which states that asynchronous responses of different species contribute to overall community stability against environmental fluctuations (Folke et al. 1996, Naeem and Li 1997, Yachi and Loreau 1999).

*Chrysosplenium oppositifolium* is known from several studies to be closely associated to neutral lowland springs in mountain ranges of Central

Germany. In these lower elevations, *Sphagnum fallax* indicates anthropogenic acidification (Auldorff et al. 1999). Furthermore, *Sphagnum fallax* is known to be significantly promoted by nutrient input (Twenhoeven 1992) and can be classified as a competitive species which profits from the consequences of acidification and nutrient deposition (Limpens et al. 2003). In addition, this species which is rather tolerant to desiccation (Sagot and Rochefort 1996) and is able to actively enhance local acidification in its habitat through cation exchange processes (Soudzilovskaia et al. 2010). All these characteristics enable *Sphagnum fallax* not only to temporally invade neutral lowland springs during prolonged drought periods but also permanently shift these systems towards novel ecological states. According to that, the significant increase in the interspecific overlap of occupied environmental space we observed for all of the characteristic species of neutral lowland springs with *S. fallax* indicates that this competitive moss is increasingly interacting with these species in times of environmental changes (and stress). This increase in the interspecific overlap for the species of neutral and acidified lowland springs, which occurred after 2003, supports evidence for invasion processes.

## CONCLUSIONS

An increasing frequency of severe droughts, which is expected for the near future (IPCC 2014), is very likely to weaken pristine spring plant communities and stimulate the immigration of species. Such enhanced establishment of new species will lead either to homogenization of communities or trigger community shifts into alternative stable states.

As frequency and intensity of drought periods and heat waves will significantly increase during the next decades, interactions between abiotic and biotic non-linear dynamic processes and historical legacies leading to tipping points and subsequent alternative states are likely to become important in many ecosystems. However, the threat to local biodiversity is especially high in less disturbed and isolated plant communities such as springs.

The environmental parameters measured in this study seem to be all those necessary to



sustain the argumentation of our study. However, future studies about the interaction of abiotic and biotic elements in these ecosystems should also elaborate on other environmental factors like nutrient availability and toxic elements to fully understand community responses to abrupt climatic shifts.

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## LITERATURE CITED

- Audorff, V., W. Durka, and C. Beierkuhnlein. 1999. Vegetation der Waldquellen im Fichtelgebirge. Pages 197–207 in C. Beierkuhnlein and T. Gollan, editors. *Ökologie silikatischer Waldquellen in Mitteleuropa*. Bayreuther Forum Ökologie 71, BITÖK, Bayreuth, Germany.
- Audorff, V., J. Kapfer, and C. Beierkuhnlein. 2011. The role of hydrological and spatial factors for the vegetation of Central European springs. *Journal of Limnology* 70:9–22.
- Beierkuhnlein, C., and T. Gollan. 1999. *Ökologie silikatischer Waldquellen in Mitteleuropa*. Bayreuther Forum Ökologie 71:1–8.
- Blonder, B. 2014. Hypervolume: High-dimensional kernel density estimation and geometry operations. R-package version 0.9.9.7. <http://CRAN.R-project.org/package=hypervolume>
- Bonan, G. B. 2008. Forest and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449.
- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23:453–460.
- Cantonati, M., R. Gerecke, and E. Bertuzzi. 2006. Springs in the Alps—sensitive ecosystems to environmental change: From biodiversity assessments to long-term studies. *Hydrobiologia* 562:59–96.
- Cantonati, M., L. Füreder, R. Gerecke, I. Jüttner, and E. J. Cox. 2012. Crenic habitats, hotspots for freshwater biodiversity conservation: Toward an understanding of their ecology. *Freshwater Science* 31:463–480.
- Ciais, P., et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Kalr, and L. O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. *Science* 289:2068–2074.
- Fischer, E. M., S. I. Seneviratne, P. L. Vidale, D. Lüthi, and C. Schaer. 2007. Soil moisture - atmosphere interactions during the 2003 European summer heat wave. *Journal of Climate* 20:5081–5099.
- Folke, C., C. S. Hollings, and C. Perrings. 1996. Biological diversity, ecosystems, and the human scale. *Ecological Applications* 6:1018–1024.
- Fordham, D. A., and B. W. Brook. 2010. Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation* 19:329–342.
- Gell-Mann, M. 1994. *The quark and the jaguar: Adventures in the simple and the complex*. W.H. Freeman, San Francisco, California, USA.
- Gerecke, R., M. Cantonati, D. Spitale, E. Stur, and S. Wiedenburger. 2011. The challenges of long-term ecological research in springs in the northern and southern Alps: Indicator groups, habitat diversity, and medium-term change. *Journal of Limnology* 70:168–187.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334.
- Gunderson, L. H. 2000. Ecological resilience: in theory and application. *Annual Review of Ecology, Evolution, and Systematics* 31:425–439.
- Hájková, P., M. Hájek, I. Apostolova, D. Zelený, and D. Díte. 2008. Shifts in the ecological behaviour of plant species between two distant regions: evidence from the base richness gradient in mires. *Journal of Biogeography* 35:282–294.
- Haylock, M. R., N. Hofstra, A. M. G. Klein Tank, E. J. Klok, P. D. Jones, and M. New. 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation. *Journal of Geophysical Research* 113:D20119. doi: 10.1029/2008JD10201
- Heino, J., R. Virkkala, and H. Toivonen. 2009. Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews* 84:39–54.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology,*

- Evolution, and Systematics 4:1–23.
- IPCC. 2014. Climate Change. 2014. Fifth Assessment Report (AR5). Cambridge University Press, Cambridge, UK.
- Jaeschke, A., T. Bittner, A. Jentsch, and C. Beierkuhnlein. 2014. The last decade in ecological climate change impact research: Where are we now? *Naturwissenschaften* 101:1–9.
- Jentsch, A., and C. Beierkuhnlein. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience* 340:621–628.
- Kapfer, J., V. Audorff, C. Berkunlein, and E. Hertel. 2012. Do bryophytes show a stronger response than vascular plants to interannual changes in spring water quality? *Freshwater Science* 31:625–635.
- Kraeuchi, N. 1993. Potential impacts of a climate change on forest ecosystems. *European Journal of Plant Pathology* 23:28–50.
- Kubíková, L., O. P. Simon, K. Tichá, K. Douda, M. Maciak, and M. Bílý. 2012. The influence of mesoscale habitat conditions on the macroinvertebrate composition of springs in geologically homogeneous are. *Freshwater Science* 31:668–679.
- Levin, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1:431–636.
- Limpens, J., H. B. M. Tomassen, and F. Berendse. 2003. Expansion of *Sphagnum fallax* in bogs: Striking the balance between N and P availability. *Journal of Bryology* 25:83–90.
- Lovejoy, T. E., and L. Hannah. 2005. Climate change and biodiversity. Yale University Press, New Haven, Connecticut, USA.
- Luterbacher, J., D. Dietrich, E. Xoplaki, M. Grosjean, and H. Wanner. 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. *Science* 303:1499–1503.
- Matzner, E., and D. Murach. 1995. Soil changes induced by air pollutant deposition and their implication for forests in Central Europe. *Water, Air and Soil Pollution* 85:63–76.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–509.
- Odum, E. P. 1971. Fundamentals of ecology. Saunders, Philadelphia, Pennsylvania, USA.
- Norberg, J. 2004. Biodiversity and ecosystem functioning: A complex adaptive system approach. *Limnology and Oceanography* 49:1269–1277.
- Oksanen, J., F. Guillaume Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, H. H. Stevens, and H. Wagner. 2013. vegan: Community ecology package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pickett, S. T. A., and P. S. White. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.
- Potts, D. L., T. E. Huxman, B. J. Enquist, J. F. Weltzin, and D. G. Williams. 2006. Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland. *Journal of Ecology* 94:23–30.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reichstein, M., et al. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: A joint flux tower, remote sensing and modelling analysis. *Global Change Biology* 13:634–651.
- Sagot, C., and L. Rochefort. 1996. Sphagnum desiccation tolerance. *Cryptogamie, Biologie et Lichenologie* 17:171–183.
- Schaer, C., P. L. Vidale, D. Lüthi, C. Frei, C. Haeberli, M. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heat waves. *Nature* 427:332–336.
- Schindler, D. W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes* 11:1043–1067.
- Schindler, D. W., S. E. Bayley, B. R. Parker, K. G. Beaty, D. R. Cruikshank, E. J. Fee, E. U. Schindler, and M. P. Stainton. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lake Area, northwestern Ontario. *Limnology and Oceanography* 41:1004–1017.
- Schweiger, A., and C. Beierkuhnlein. 2014. Water temperature and acidity regime shape dominance and beta-diversity patterns in the plant communities of springs. *Frontiers of Biogeography* 6:132–143.
- Smith, M. D. 2011. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* 99:656–663.
- Smith, H., and P. J. Wood. 2002. Flow permanence and macroinvertebrate community variability in limestone spring systems. *Hydrobiologia* 487:45–58.
- Soudzilovskaia, N. A., J. H. C. Cornelissen, H. J. During, R. S. P. van Logtestun, S. I. Lang, and R. Aerts. 2010. Similar cation exchange capacities among bryophyte species refute a presumed mechanism of peatland acidification. *Ecology* 91:2716–2726.
- Standish, R. J., et al. 2014. Resilience in ecology: Abstraction, distraction, or where the action is?

- Biological Conservation 177:43–51.
- Thibault, K. M., and J. H. Brown. 2008. Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences USA* 105:3410–3415.
- Thienemann, A. 1924. Hydrobiologische Untersuchungen an Quellen. *Archiv für Hydrobiologie* 14:151–189.
- Twenhoeven, F. L. 1992. Competition between two *Sphagnum* species under different deposition levels. *Journal of Bryology* 17:71–80.
- van der Kamp, R. O. 1995. The hydrogeology of springs in relation to the biodiversity of spring fauna: A review. Pages 4–17. *in* L. C. Ferrington, editor. Biodiversity of aquatic insects and other invertebrates in springs. *Journal of the Kansas Entomological Society* 68.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450.
- Wood, P. J., A. J. Boulton, S. Little, and R. Stubbington. 2010. Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? *Fundamental and Applied Limnology* 176:377–390.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the USA* 96:1463–1468.
- Zwolsman, J. J. G., and A. J. van Bokhoven. 2007. Impact of summer droughts on water quality of the Rhine River: A preview of climate change? *Water Science & Technology* 56:45–55.