LONG-TERM REACTIONS OF PLANTS AND MACROINVERTEBRATES TO EXTREME FLOODS IN FLOODPLAIN GRASSLANDS

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Abstract. Extreme summertime flood events are expected to become more frequent in European rivers due to climate change. In temperate areas, where winter floods are common, extreme floods occurring in summer, a period of high physiological activity, may seriously impact floodplain ecosystems. Here we report on the effects of the 2002 extreme summer flood on flora and fauna of the riverine grasslands of the Middle Elbe (Germany), comparing pre- and post-flooding data collected by identical methods. Plants, mollusks, and carabid beetles differed considerably in their response in terms of abundance and diversity. Plants and mollusks, displaying morphological and behavioral adaptations to flooding, showed higher survival rates than the carabid beetles, the adaptation strategies of which were mainly linked to life history. Our results illustrate the complexity of responses of floodplain organisms to extreme flood events. They demonstrate that the efficiency of resistance and resilience strategies is widely dependent on the mode of adaptation.

Key words: carabid beetles; extreme event; flood; floodplain; grassland; mollusks; resilience; resistance; river Elbe; vegetation.

INTRODUCTION

Although the question is still being debated, there is evidence that greenhouse gas-induced climate changes could modify the hydrology of European streams, leading to an increase in severe summertime flooding (Christensen and Christensen 2003, Mudelsee et al. 2003). Flood disturbances are an integral component of functioning floodplain ecosystems (Ward 1998). Flow variations structure the riverine ecosystems (Scott et al. 1997), maintain the dynamic equilibrium (Junk 2005), and so contribute to the maintenance of the biodiversity in the floodplains (Adis and Junk 2002). The alluvial vegetation and fauna display a large range of resistance and/or resilience strategies, involving life history as well as behavioral and morphological adaptations to survive floods (Lytle and Poff 2004). In temperate regions, flood timing rather than magnitude is critical for the floodplain inhabitants (Junk 2005). Floods occurring in winter and early spring, a period of low physiological activity, have little effect on most plant and animal species. Summer flood events, on the contrary, may severely disturb both vegetation and faunal communities. However, the effects of unusual and extreme floods on floodplain ecosystems and their communities are largely unknown. Studies quantifying the effects of such catastrophic events are rare as in almost all cases no precise data describing the pre-flood situation are available (Hering et al. 2004).

Here we present the effects of the 2002 extreme summer flood on the biodiversity of the Middle Elbe (Germany) floodplain grasslands. The flood was extreme in terms of its timing and height, leading to the inundation of the whole active floodplain area (see Plate 1). We examine the response of three contrasted taxonomic groups with different degrees of mobility (plants, mollusks, and carabid beetles), considering abundance, diversity, and community composition. We compare pre-flood data from 1998 and 1999 with post-flood data from 2003 and 2004 collected by identical sampling methods. We test the hypothesis that groups with lower mobility were more severely affected by the flood as they were unable to escape. Further, we test the expectation that groups with lower mobility are slower colonizers and therefore show delayed resilience.

METHODS

Study site

The Elbe is one of the largest rivers in Europe with a length of 1165 km and a catchment area comprising 150,000 km². The flow regime is characterized by higher
discharge and some heavy floods during the winter and early spring months and a lower tide from June to November. Due to the absence of dams in the German reach, the floodplain of the Middle Elbe in central Germany still contains a large proportion of seminatural areas with a hydrological regime close to the natural state (Scholten et al. 2005).

All sampling plots are located in a 0.9-km$^2$, seasonally flooded grassland and under the direct influence of the river Elbe hydrodynamics. They are managed with medium intensity and have small-scale relief features, including hollows as well as lower and higher areas with different flood frequencies and groundwater levels. In August 2002, the complete floodplain was affected by the highest Elbe flood ever recorded (Fig. 1), with a statistical recurrence interval of 168 years (Schiermeier 2003), and all sampling plots were inundated for at least two weeks. Water height ranged from 2.4 to 5.4 m above soil level. However, no soil erosion or deposition was observed for the sampling plots. The nutriment load of the 2002 Elbe flood was similar to those carried during the usual winter and spring flows (Bachor et al. 2005).

Using a differential global positioning system, we were able to survey exactly the same plots after the flood in 2003 and 2004, following the stratified sampling design developed within the RIVA project (Henle et al. 2006).

Survey

Plants, carabid beetles, and mollusks were surveyed on 36 plots in spring and autumn of 1998, 1999, 2003, and 2004 (Henle et al. 2006), following well-established sampling methods for each taxonomic group.

Within each plot, plants were surveyed in 100-m$^2$ quadrats, according to the method of Braun-Blanquet (Braun-Blanquet 1964). The Braun-Blanquet score of each species from each year and plot was transformed into cover categories (Table 1).

Carabid beetles were caught using five pitfall traps per plot (Gerisch et al. 2006). The traps were filled with a 7% solution of acetic acid and detergent, exposed for four weeks, and emptied biweekly during each sampling season. Sampling occurred in spring and autumn, when ground beetles are most active (Lindroth 1986). All adult ground beetles were determined to species level. Data are expressed as mean numbers of individuals per species, trap, and exposure day for each plot and year.

Mollusk samples were collected by sampling five 1000-cm$^2$, 5 cm depth, soil samples at each plot and season (Foeckler et al. 2006). For the flooded plots, the procedure was similar but the sampling was done with a sieve. After sieving, the mollusks were dried, sorted, and identified to the finest taxonomic level possible. The data of the five samples were pooled and log-transformed prior to data analysis.

Table 1. Conversion of Braun-Blanquet scores into cover categories of plants on the Elbe River floodplain in central Germany.

<table>
<thead>
<tr>
<th>Braun-Blanquet score</th>
<th>Mean cover (%)</th>
<th>Cover category</th>
</tr>
</thead>
<tbody>
<tr>
<td>r</td>
<td>&lt;0.01</td>
<td>1</td>
</tr>
<tr>
<td>+</td>
<td>0.1</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>2.5</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>37.5</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>62.5</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>87.5</td>
<td>7</td>
</tr>
</tbody>
</table>
We used β-diversity to determine species turnover between the different sampling years. β-diversity was measured using one minus the Sorensen index (C). 

\[ C = \frac{2j}{a+b} \]

where j is the number of taxa found in both years, a is the number of taxa found in year a, and b is the number of taxa found in year b (Magurran 1988). This β-diversity measure ranges from 0, indicating identical taxa composition, to 1, indicating that no taxa are common between the compared years. The α-diversity values were used to assess potential loss of diversity due to the flood and to evaluate whether flood-induced changes in species composition were due to species changes, species increase, or species loss.

Vegetation and invertebrate data were processed by correspondence analysis (CA; Legendre and Legendre 1998) to study the effects of this extreme flood on community composition and to detect possible shifts in populations. Plant species represented by fewer than four occurrences and invertebrate species represented by only one occurrence were not included in the analyses. All multivariate analyses were performed with the ADE-4 software (Thioulouse et al. 1997).

**Results**

Our results show that the mollusk and carabid beetle communities were most affected by the flood. The total number of mollusk species increased from 26 taxa in 1998–1999 to 31 taxa after the flood. Both mollusk taxon richness and abundance per sampling plot increased significantly after the flood (Fig. 2, Table 2). Land snails were not negatively affected by the flood. The abundance increase and the mollusk species
turnover occurring after the flood (Table 3) are explained mainly by the colonization of truly aquatic species leading to a shift toward a community with a higher moisture requirement and increased flood tolerance (Fig. 3). Although $\alpha$-diversity decreased in 2004, mollusk density remained considerably higher than in the years prior to the flood.

In contrast, the total number of carabid beetle species decreased from 117 species in 1998–1999 to 88 species in 2003. However, already in 2004, the number of species was similar to the pre-flood years (115 species). The populations decreased significantly in abundance and $\alpha$-diversity after the flood but also displayed high recovery capability (Fig. 2, Table 2). Despite abundance and $\alpha$-diversity reaching pre-flood values, obvious differences in carabid beetle community composition still remained in 2004 (Fig. 3). Surprisingly, the populations adapted to wet conditions, found in hollows and lower areas, were the most affected, losing >40% of their species but also showed the fastest recovery.

The vegetation was least impacted by the flood. There was no significant change in plant abundance despite a decrease of the total number of species from 113 in 1998–1999 to 107 after the flood (Fig. 2, Table 2). Despite a significant decrease in $\alpha$-diversity (Fig. 2, Table 2) and an increased species turnover (\(\beta\)-diversity) (Table 3) after the flood (Fig. 2), no important change in the vegetation structure was observed (Fig. 3). The flood rather affected single species, leading to the loss of diversity observed in 2003.

**Discussion**

Floodplain community structures are driven by short- to medium-term hydrological events, such as floods and droughts (Adis and Junk 2002). In the Elbe floodplain grasslands, the hydrological parameters are also key factors determining the structure of vegetation, mollusk, and ground beetle communities with soil and other abiotic factors contributing less to the variation (Follner and Henle 2006). Thus we expected the 2002 Elbe summer flood to have a significant influence on the vegetation, mollusk, and ground beetle communities. Surprisingly, the vegetation structure hardly changed. The high resistance of the vegetation can be explained by the large range of morphological and life-history adaptations displayed by most floodplain plants, such as the development of aerated root tissue, shoot elongation, or timing of reproduction (Blom and Voesen 1996). The high stability of the vegetation structure also suggests that long-term processes rather than an isolated extreme event may drive plant community structure in floodplains (Vervuren et al. 2003). This has been suggested also for mollusks (Castella et al. 1994). However, the changes between extreme pre- and post-flood years were much stronger than the changes between pre-flood years, and colonization by truly aquatic species played the most important part in the increase of mollusk species diversity and abundance following the flood. Land snails are able to take refuge on floating objects and, by drifting downstream, could colonize new habitats. For hygrophilous land snails especially, the passive concentration of populations in depressions by floods may be important for reproduction and maintenance of

<table>
<thead>
<tr>
<th>Taxonomic group and year</th>
<th>1998</th>
<th>1999</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plants</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>0.095 ± 0.068</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>0.360 ± 0.113</td>
<td>0.350 ± 0.095</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>0.330 ± 0.122</td>
<td>0.330 ± 0.108</td>
<td>0.310 ± 0.123</td>
</tr>
<tr>
<td>Mollusks</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>0.250 ± 0.199</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>0.500 ± 0.174</td>
<td>0.515 ± 0.156</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>0.380 ± 0.175</td>
<td>0.455 ± 0.174</td>
<td>0.400 ± 0.163</td>
</tr>
<tr>
<td>Carabids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>0.335 ± 0.089</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>0.495 ± 0.083</td>
<td>0.445 ± 0.097</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>0.385 ± 0.079</td>
<td>0.540 ± 0.132</td>
<td>0.340 ± 0.085</td>
</tr>
</tbody>
</table>

*Note: Values are median numbers (±SD) of all plots between the different years.*

Table 3. $\beta$-diversity values between the different years for the three taxonomic groups.
gene flow (Jungbluth et al. 1986). Many mollusk species also take advantage of the humidity after a flood to reproduce in higher numbers reestablishing their populations within a short time (Jungbluth et al. 1986). Furthermore, most terrestrial mollusks can well tolerate short flood periods (Künkел 1930). Altogether, the adaptations displayed by the terrestrial and aquatic mollusks to cope with the dynamics of floodplain ecosystems not only enabled them to survive the extreme flood event but also to benefit from it.

In contrast, carabid beetle populations were seriously decimated by the flood, despite the fact that most adult floodplain ground beetles are good swimmers (Siepe 1994, Adis and Junk 2002). They also display different behavioral and life-history adaptations to survive floods, such as emigration to dryer wintering places in autumn (Assman and Starke 1990) and/or hibernation as adults (Riecken 1992, Wohlgemuth-von Reiche and Grube 1999) or physiological adaptations, such as low physiological activity conditioned by low temperature or higher submergence resistance in colder temperatures (Zulka 1994). Most of these adaptations enable survival through the “usual” winter and spring floods. The 2002 flood, however, occurred in summer when several
species, many of which belong to the hygrophilous species, were in a sensitive larval or pupal phase (Müller-Motzfeld 1989), and so less able to cope with the flood.

Our results show that the effects of the 2002 flood as well as the response to this event (i.e., resistance/resilience) varied widely among the different taxonomic groups. Our results demonstrate that resilience/resistance efficiency of an organism to extreme flood events is not only dependant on its degree of mobility but rather linked to the mode of flood adaptation (i.e., life-history, behavioral, or morphological adaptation), which in turn determines its vulnerability. For taxa displaying morphological and behavioral adaptations to inundation, such as plants and mollusks, predictability and duration of the flood event may be more critical than timing. Thus, these taxonomic groups were less vulnerable or even able to benefit from this seasonally atypical flood. The carabid beetles, displaying a large range of life-history adaptations, are more dependent on the timing of a flood event, and therefore were less able to survive the 2002 Elbe summer flood. A rapid immigration of ubiquitous ground beetle species (Szekeres et al. 2006) was responsible for the fast abundance and diversity resilience.

Nevertheless, it can be difficult to quantify the effects of a single extreme event in regard to the long-term variation patterns of the observed communities and taxonomical groups. We believe that long-term monitoring of floodplain ecosystems with standardized methods is essential to assess the consequences of an increased frequency of extreme events on floodplain biodiversity.

Acknowledgments

This work was supported by the German Ministry of Education and Research (project RIVA, no. 0339579) and by the Federal Hydrological Institute (project HABEX, no. RA/V1658). We thank the River Landscape Biosphere Reserve Middle Elbe (Saxony-Anhalt), the nature conservation authorities, and the farmers for their helpful cooperation.

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