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Submersion tolerance in floodplain arthropod communities

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Summary

River floodplains in Europe have been altered radically by river regulation resulting in a destruction of floodplain habitats. Today, it is the aim of restoration projects to counteract these negative ecological impacts. Arthropods living in floodplains have to cope with a regular cycle of wet and dry conditions. In the floodplain of the Lower Oder we investigated whether the typical wetland fauna recolonises the floodplain after each flooding event or survives winter submersion in the habitat. Furthermore, we analysed whether flooding regimes affect the distribution and migration patterns of arthropod species. With receding water levels in May 2002, gauze-covered exclosure tents were placed at sites subject to different flooding regimes to prevent arthropod colonisation. In July samples were taken from underneath the tents and from adjacent uncovered control plots. Additionally, nearby plots were sampled at biweekly intervals during the whole vegetation period. Planthoppers, leafhoppers (Auchenorrhyncha), spiders (Araneida) and ground beetles (Carabidae) were studied in detail. Most species of plant- and leafhoppers [70%] tolerated submersion and overwintered in the floodplain, whereas most spiders [63%] and carabids [73%] immigrated with receding water level. A high proportion of submersion tolerant species overwintered in the egg stage, whereas only few species hibernating as juveniles or adults were submersion tolerant. Submersion tolerant plant- and leafhoppers as well as spiders occurred in high densities in sites affected by long-lasting winter floods. Many of these species were specialists. Immigrating species of all three groups had highest densities in sites subject to high flooding impact. We conclude that restoration measures in river floodplains should also provide suitable non-inundated overwintering sites for immigrating species. Restoring a natural flooding regime is essential for creating and maintaining a high diversity of habitats and specialists among the fauna.

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Zusammenfassung

In der Vergangenheit wurden in Europa Auen im Zuge des Flussausbaus stark verändert, so dass die Flussauen weitgehend zerstört wurden. Heute versucht man durch Renaturierungsmaßnahmen diesen negativen ökologischen Folgen entgegenzuwirken. Arthropoden, die diesen Lebensraum besiedeln, müssen an diese Bedingungen angepasst sein. Im Nationalpark "Unteres Odertal" wurde untersucht, welche Arten der typischen Flussauenfauna im überfluteten Gebiet überwintern, welche die Aue nach jedem Hochwasser wieder neu besiedeln und ob das Überflutungsregime Migrationsmuster der Arten und deren Verteilung in der Flussaue beeinflusst. Kurz nach Rückgang des Winterhochwassers im Mai 2002 wurden Gazezelte in der Flussaue aufgestellt, um die Wiederbesiedlung der darunter liegenden Flächen durch Arthropoden zu verhindern. Im Juli wurde die Besiedlung der mit Gaze abgedeckten Untersuchungsflächen sowie von daneben liegenden Kontrollflächen durch Zikaden, Spinnen und Laufkäfer erfasst. Während der gesamten Vegetationsperiode wurden auf angrenzenden Flächen zusätzlich Proben genommen, um zu untersuchen, welcher Anteil der typischen Flussauenfauna mit Hilfe des Experiments erfasst wurde. Die meisten Zikadenarten [68%] tolerierten die überflutung und überwinterten in der Flussaue, während die meisten Spinnen [60%] und Laufkäfer [70%] die Flussaue in jedem Frühjahr neu besiedelten. Überflutungstolerante Spinnen- und Zikadenarten wurden in hohen Dichten vor allem auf im Winter lange überfluteten Flächen nachgewiesen. Viele dieser Arten haben einen hohen Spezialisierungsgrad. Einwandernde Arten aller drei Taxa wurden vor allem auf Flächen, die im Winter und im Sommer überflutet werden, gefunden. Da ein Großteil der typischen Flussauenfauna den Lebensraum nach jedem Hochwasser neu besiedelt, sollten im Rahmen von Renaturierungsmaßnahmen die typischen nicht überschwemmten Überwinterungshabitate dieser Arten mit berücksichtigt werden. Weiterhin hat die Untersuchung gezeigt, dass für einige seltene Auenarthropoden besonders regelmäßige und lange andauernde Überflutungsereignisse von besonderer Bedeutung sind.

Introduction

The aim of restoration ecology is to re-establish the original structure, diversity and dynamics of degraded ecosystems (Young, 2000). Natural and semi-natural floodplains contain a high biodiversity of both plant and animal species and have important functions for the water and nutrient budget of riverine landscapes. Nonetheless, most European river valleys have been altered by river straightening and dyke construction during the last 150 years. To counteract the negative ecological impacts of these changes, restoration of river valley habitats is of great interest today. Floodplains of natural rivers are shaped and characterised by the flooding dynamics. Hence, all species living in floodplains have to cope with a more or less regular cycle of wet and dry conditions throughout the year. The main problems terrestrial arthropods have to face during submersion are low oxygen concentrations in the water, danger of cell destruction due to swelling and passive drift with high water (Hildebrandt, 1997). The occurrence of terrestrial invertebrates in periodically submerged habitats suggests that these species have specific adaptations enabling them to survive the adverse conditions during submersion (Adis, 1992). In general, two types of adaptations can be distinguished: migration activity before and after the flooding period, and submersion tolerance. Hildebrandt (1997) defined submersion tolerance as physiological and/or morphological adaptations, which enable the species to survive in their inundated habitat. For example, ground beetles of the genus *Dicheirotrichus* reduce oxygen consumption by lowering their metabolic rates during submersion (Foster & Treherne, 1976). Survival in the flood-resistant egg stage is a common (pre-)adaptation in terrestrial floodplain invertebrates rendering them submersion tolerant (Adis & Junk, 2002). While many studies on survival strategies of terrestrial invertebrates inhabiting floodplains have been carried out in the Amazon basin (Adis & Junk, 2002), surprisingly little is known about adaptations of European arthropods to flooding (Weigmann & Wohlgemuth-von Reiche, 1999). However, when restoring river valley habitats it is crucial to know how the typical wetland fauna copes with the regular floods, because species might not be able to survive long periods of submersion and need structures such as trees, shrubs or elevated areas nearby for shelter.

Using catches of planthoppers, leafhoppers, spiders and ground beetles, we tested the following hypotheses: (1) A high proportion of submersion-tolerant species overwinters in the egg stage. (2) Only a low proportion of species hibernating as juveniles or adults is submersion-tolerant. (3) Submersion-tolerant species preferably occur in sites with a regular flooding cycle. (4) Immigrating species prevail in sites with high flooding intensity.

Materials and Methods

Study area

The floodplain of the Lower Oder River (Fig. 1) is dominated by grasslands. It is a typical lowland river of Central Europe, where flooding occurs frequently in winter and spring, but rarely in summer. At present, inundation is regulated by floodgates, which are integrated into the dykes along the river. Due to this regulation, only winter floods can inundate the polder areas, but this winter flooding occurs under nearly natural conditions.

Figure 1. Location of the Lower Oder Valley National Park.

Colonisation experiment and sampling procedure

With receding water levels in May 2002, three gauze-covered exclosure tents (mesh size: 250 μm; each covering an area of 1 m^2) were placed at sites subject to each of three flooding regimes. The three flooding regimes included high flooding impact (river banks: summer and winter flooding), medium flooding impact (depressions in the polders: long-lasting winter floods; winter 2001/02: approximately 130 days) and low flooding impact (high elevations in the polders: short-lasting winter floods; winter 2001/02: approximately 100 days), respectively. The base of the tents was placed about 10 cm deep into the soil and all further openings were sealed with sticky tape. The exclosure tents prevented arthropods from entering the space underneath but still allowed plants to grow.

When setting up the tents (May 2002), samples were taken in adjacent uncovered control plots and in nearby plots to record arthropod species that were active at the beginning of the experiment, because early immigration by some species might have already occurred. Samples were taken using a motor driven suction apparatus (STIHL SH 85) and pitfall traps (preservative: 50% ethylene glycol). Control plots each covered an area of 1 m^2 and were marked by barrier tape. In July 2002, suction samples were taken from underneath the exclosure tents as well as from the control plots. In addition, one pitfall trap was installed per tent and control plot, respectively (Table 1). After sampling, the tents were removed. Further, samples were taken from nearby plots during the whole growing season using again suction samples and pitfall traps as sampling methods (Table 1).

Overall, nine groups, each consisting of one exclosure tent, one control plot and one nearby plot, were installed in an area measuring 20 × 3 km. The tents and their respective control plots were no more than 1 m apart; the distance to the respective nearby plot was not larger than 5 m. The distance between two groups was not less than 100 m.

All adult planthoppers, leafhoppers, spiders and ground beetles, occurring in the samples were

Table 1. Sampling design

Plots	Suction samples		Pitfall traps	
	Time	Area (m^2)	Time (days)	Traps per plot
Experimental plots	May (Co)	1	3	1
Experimental plots	July (Co & Ex)	1	14	1
Nearby plots	May, June, August, September	0.15	14	3

The sampling time per plot type and sampling method, the area sampled by the suction apparatus and the number of pitfall traps per site are listed.
Co = control plot, Ex = exclosure tent.

identified to species. For all three taxa, analyses of species numbers were based on the combined results of suction and pitfall samples. Analyses of plant- and leafhopper abundance only considered suction samples, while for spiders and ground beetles only pitfall traps were taken into account.

Ecology of species

Information on the ecology of plant- and leafhoppers was taken from Nickel (2003). H. Nickel (pers. comm.) provided further information on flight capability and habitat preferences of plant- and leafhoppers. For spiders Locket and Millidge (1975), Locket, Millidge, and Merrett (1974), Schaefer (1976), Platen et al. (1991) and Lang and Pütz (1999) were used and ecological information for ground beetles was extracted from Barndt et al. (1991), Lang and Pütz (1999) and Turin (2000).

Categories of habitat preferences are based on the classification by Platen et al. (1991) and Barndt et al. (1991) and these were adopted for all three groups. We distinguished species from open habitats as being either hygrophilous (hy; occurring preferably in moist to wet habitats), euryhygric (eu; occurring in different habitats independent of moisture conditions) or xerophilous (xe; occurring preferably in dry habitats). Furthermore, species occurring preferably in wooded habitats or on trees or shrubs were regarded as forest species (fo).

Classification of the species: Submersion tolerance versus immigration

As emphasised above, two general strategies can be distinguished that help species to cope with the annual long winter flood: (1) hibernation in the floodplain in a flood-resistant egg, juvenile (larval) or adult stage (*submersion tolerance*), and (2) (re)colonisation of the floodplain with receding water levels (*immigration*) after emigration and/or death in autumn and winter.

According to sampling results, species were assigned to four groups: (A) Species, which were found as adults in the exclosure tents in July but were not recorded in May, were classified as submersion tolerant. (B) Species, which were caught as adults in the control plots in July but not in May and not in the exclosures, were categorised as immigrating species. (C) Species recorded as adults at the beginning of the experiment (control plots and nearby plots, May) and (D) those found in nearby plots after July but not recorded earlier could be either submersion tolerant or immigrants.

In a second step, we checked the plausibility of our classification using information on the ecology of the species which resulted in a regrouping of a few species. For example, the planthopper *Anakelisia fasciata* and the leafhopper *Metalimnus formosus* were classified as submersion tolerant, although they had been collected in the control plots in July but not underneath the exclosure tents. Both species overwinter in the flood-resistant egg stage and typically occur in temporarily flooded sites (Nickel, 2003). Their distribution in the study area is, however, patchy since they are associated with sedges, which did not occur underneath the exclosure tents.

In a third step we used all available published data on submersion tolerance and immigration activity to validate our classification (Fuellhaas, 1997; Wohlgemuth-von Reiche, Griegel, & Weigmann, 1997; Lang and Pütz, 1999; Wohlgemuth-von Reiche & Grube, 1999; Turin, 2000; Nickel, 2003). In cases where clear evidence for one of the strategies was found in the literature while our own data were rather weak, we used the published data for classifying species. As could be expected, some species obviously follow both strategies. So, in the end, we differentiated between three categories: "submersion tolerance", "immigration" and "submersion tolerance and immigration". For a detailed description of the classification of all species see Rothenbücher (2005).

Statistical analyses

The impact of flooding intensity [high, medium, low] on the distribution of "submersion tolerant", "immigrating" and "submersion tolerant and immigrating" species and individuals sampled in the nearby plots were tested using analysis of variance (ANOVA, Tukey test). Normality of data was tested using the Shapiro-Wilk Test and homogeneity of variances using the Fmax Test. If necessary, data were transformed to approximate normality and homogeneity of variances.

Results

Between May and July, 30 species of plant- and leafhoppers (1079 individuals), 69 species of spiders (1694 individuals) and 63 species of ground beetles (2006 individuals) were collected as adults in exclosure tents, control plots and nearby plots. In the plant- and leafhoppers these species represented about 63% and in spiders 83% and in carabids 85% of the total species numbers recorded (Auchenorrhyncha 47, Araneida 83, Carabidae 74) throughout the growing season. The abundances of the most common plant- and leafhoppers, spiders and ground beetles are given in Appendix 1 along with information on their ecological characteristics.

Ecology of species: submersion tolerance versus immigration

The results presented in the following paragraphs give the classification of the species after all three classification steps (see Materials and Methods). For the detailed steps of the classification see Rothenbücher (2005).

Species group A – sampled in exclosure tents in July

In July, 21 species of plant- and leafhoppers but only five species of spiders and one carabid species, all of them not recorded in the control plots or nearby plots in May, were found underneath the exclosure tents (Table 2, Appendix 1). The most abundant species of plant- and leafhoppers were *Arthaldeus pascuellus*, *Streptanus aemulans* and *Megamelus notula* (Appendix 1). All plant- and leafhopper species collected underneath the exclosure tents overwinter in the egg stage (Fig. 2A), and almost all show reduced capability to fly (Fig. 2A). Both hygrophilous and euryhygric species comprise about 40% of the species recorded (Fig. 2A). All the plant- and leafhoppers of species group A and the spider *Microlinyphia impigra* overwinter in the floodplain and thus tolerate submersion. The spider *Oedothorax apicatus* tolerated submersion and overwintered in the floodplain, but also immigrates into the floodplain in spring. Accordingly, this spider species seems to follow both strategies, i.e. submersion tolerance and immigration. For the remaining spider species and the ground beetles data were not sufficient to assign them to one of the three categories. In summary, 22 species tolerated submersion, one species followed both strategies and for four species the overall strategy remains unclear.

Species group B – sampled in control plots in July

Three species of plant- and leafhoppers, 11 species of spiders and two species of ground beetles were found in the control plots in July, but were neither found in May nor underneath the exclosure tents in July (Table 2). These species appear to

Table 2. Numbers of species (*S*) and adult individuals (*n*) of plant- and leafhoppers (Auchenorrhyncha), spiders (Araneida) and ground beetles (Carabidae) sampled in the exclosure tents in July but not recorded in control plots or nearby plots in May (A), in the control plots in July but not recorded in May nor in the exclosure tents in July (B), in the control plots and nearby plots in May (C) and in the nearby plots later than July (D)

	Type of spatio-temporal distribution	Auchenorrhyncha		Araneida		Carabidae	
		S	*n*	*S*	*n*	*S*	*n*
Exclosure tents July	A	21	273	5	9	1	6
Control plots July	B	3	3	11	17	2	8
Control plots and nearby plots May	C	7	37	53	1309	61	1318
Nearby plots after July	D	17	116	8	432	7	41

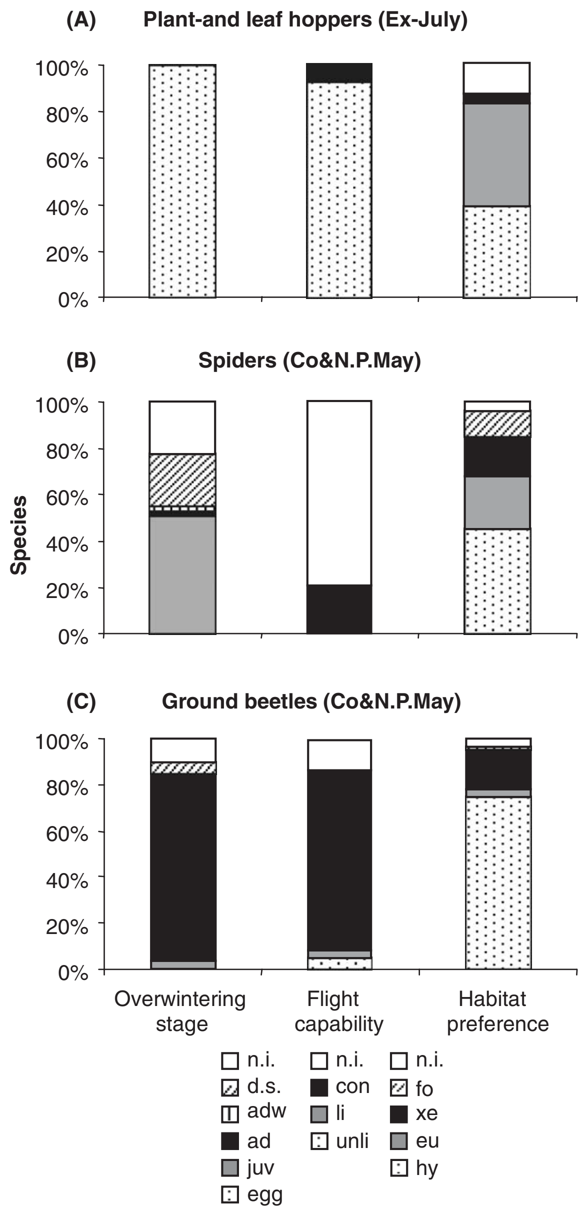

Figure 2. Ecological characteristics of plant- and leafhoppers ($S = 21$) that were recorded from the exclosure tents in July (Ex-July) but not in control and nearby plots May (A), and of spiders ($S = 53$) (B) and ground beetles ($S = 61$) (C) that were recorded in control and nearby plots in May (Co & N.P. – May). Proportion of species overwintering in the egg stage (egg), as juveniles (juv), adults (ad), adults active in winter (adw) or in different developmental stages (d.s.). Proportions of species, for which flight capability is unlikely (unli), likely (li) or confirmed (con) are shown in the second column. Proportions of hygrophilous (hy), euryhygric (eu), xerophilous (xe) and forest (fo) species are given in the right column. n.i.: no information.

have immigrated into the floodplain after the tents were set up. Most of the species are hygrophilous, three overwinter as eggs, and four are capable of flight or ballooning (Appendix 1). Most species occur in sites that are situated either close to the dyke or close to trees and shrubs, which provide non-flooded overwintering sites. According to the literature, three species of group B were classified as submersion tolerant. To summarise, three submersion tolerant and 13 immigrating species were identified.

Species group C – sampled in control plots and nearby plots in May

Seven plant- and leafhopper species, 53 spider and 61 carabid species were recorded from the floodplain at the start of the experiment in May (Table 2). These species either hibernated in the inundated site or immigrated early. Most spiders found in May overwinter as juveniles or adults (Fig. 2B). For about 20% of them ballooning activity is reported, and more than 40% of the species are hygrophilous (Fig. 2B). 58% are smaller than 5 mm, thus ballooning is likely. The most abundant spiders were *Pardosa prativaga*, *P. palustris* and *Erigone atra* (Appendix 1). About 80% of the carabid species overwinter as adults (Fig. 2C). Only *Poecilus lepidus* and *Pseudoophonus rufipes* overwinter as larvae and thus must be submersion tolerant. For approximately 80% of the species flight activity is reported (Fig. 2C). Only *Carabus granulatus*, *Dyschirius globulosus* and *Harpalus autumnalis* are not able to fly. In May the ground beetle community was clearly dominated by hygrophilous species (Fig. 2C), the most abundant species were *Agonum afrum*, *Poecilus versicolor* and *Carabus granulatus* (Appendix 1). Most species of group C immigrated into the floodplain with receding water level.

In summary, two species were submersion tolerant, 88 immigrated into the floodplain, seven followed both strategies and for 24 species data were not sufficient for classification.

Species group D – sampled in nearby plots after July

As previously mentioned, not all species present in the floodplain were sampled during the experiment. Those that were caught with more than four individuals in nearby plots after the end of the experiment are listed in Appendix 1 (species group D). Out of the species of group D, seven plant- and leafhopper species and two spider species overwinter in the egg stage, for nine species flight activity is reported, and all except the spider *Marpissa radiata* and the ground beetle *Amara plebeja* are adult from summer until autumn. The ground beetle *Patrobus atrorufus* hibernates as adult, is not capable of flight and was found in sites that were further away from possible non-flooded overwintering sites. Thus, the seven plant- and leafhopper species, the two spider species and the ground beetle *Patrobus atrorufus* were classified as submersion tolerant. The planthopper *Stenocranus major* and four carabid species are capable of flight, for the spider *Kaestneria pullata* ballooning is assumed and *Calathus fuscipes* was found near sheltered areas. Thus, these species were classified as immigrating species.

Hence, in the nearby plots 10 submersion tolerant and seven immigrating species were identified, while for 15 species data were not sufficient for classification.

Summarising the findings of all four species groups, 38 submersion tolerant and 108 immigrating species were identified (Table 3). Furthermore, eight species follow both strategies and for 42 species no classification was possible (for details see Table 3).

Impact of flooding on the distribution of submersion tolerant and immigrating species

Most recorded plant- and leafhopper species tolerated winter submersion (Fig. 3A). No differences in the proportions of immigrating or submersion tolerant species due to flooding impact were found. The relative number of individuals indicates that the few immigrating species clearly dominated in sites subject to high flooding impact (ANOVA: $F = 7.5$, $p < 0.05$, transformation: arcsin $[x^{0.5}]$), whereas submersion tolerant species dominated in sites subject to medium flooding impact (ANOVA: $F = 12.7$, $p < 0.05$, transformation: arcsin $[x^{0.5}]$) (Fig. 3A).

Flooding intensity did not affect the occurrence of submersion tolerant and immigrating species of spiders (Fig. 3B). In all study sites species richness was highest for immigrating species. Regarding the proportion of individuals, submersion tolerant species significantly dominated in sites subject to medium flooding impact (ANOVA: $F = 63.8$, $p < 0.001$) (Fig. 3B).

Species richness of immigrating carabid species was highest in all study sites. In terms of abundance, however, the proportion of immigrating species was significantly lower in sites subject to low flooding intensity than in sites subject to more intense flooding (ANOVA: $F = 5.9$, $p < 0.05$) (Fig. 3C). Considering the proportion of individuals, the dominance of immigrating species is still evident in sites subject to high and medium inundation (Fig. 3C). Furthermore, in sites subject to low flooding intensity, higher proportions of species were found that follow both strategies, i.e. immigration and submersion tolerance, as compared to all other study sites (ANOVA: $F = 23.3$, $p < 0.001$) (Fig. 3C).

Discussion

Ecology of species: Submersion tolerance versus immigration

The present study demonstrated, that the floodplain arthropod fauna consists of submersion tolerant and immigrating species as well as of species that follow both strategies.

Most species of plant- and leafhoppers tolerate submersion during winter. All but one of these species overwinter in the egg stage, which is considered as rather flood resistant (see Tamm, 1986). According to Weigmann & Wohlgemuth-von Reiche (1999) it is unlikely that Central European arthropods evolved specific adaptations to cope with submersion as it has been found, for instance, in Central Amazonian arthropods (see Adis & Junk, 2002). In temperate regions river floodplain systems are comparatively young and flooding events

Table 3. Species numbers (S) of sampled plant- and leafhoppers (Auchenorrhyncha) spiders (Araneida) and ground beetles (Carabidae) classified as "submersion tolerant", "immigrating" or "submersion tolerant and immigrating" species

Life strategy	Auchenorrhyncha		Araneida		Carabidae	
	S	%	S	%	S	%
Submersion tolerant	32	66	5	6	1	1
Immigrating	7	15	48	62	53	75
Submersion tolerant and immigrating	0	0	2	3	6	8
Uncertain	9	19	22	29	11	16
Sum	48	100	77	100	71	100

For each taxon the proportion of species assigned to one of the life strategy categories is listed.

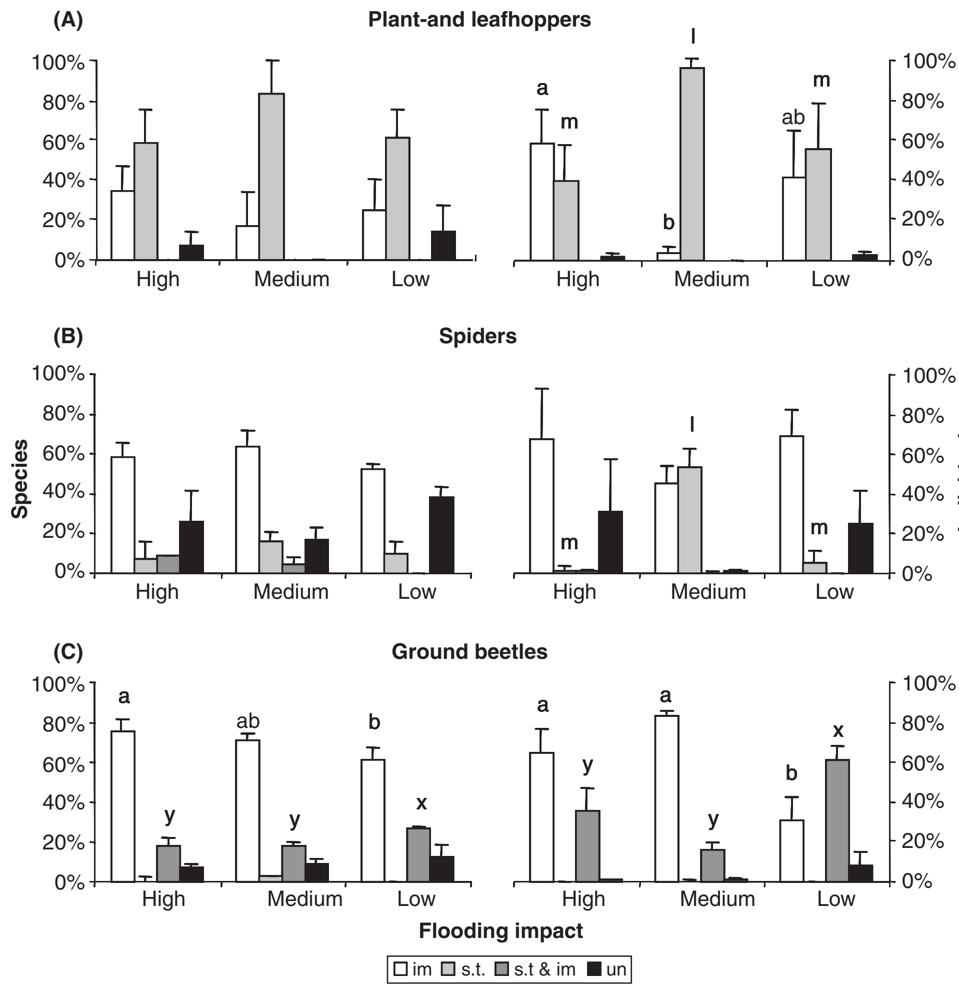

Figure 3. The influence of flooding on the proportions of species and individuals of plant- and leafhoppers ($S = 40$, $N = 920$) (A), spiders ($S = 52, N = 2056$) (B) and ground beetles ($S = 66, N = 4003$) (C), with the following strategies: immigration (im), submersion tolerance (s.t.), submersion tolerance and immigration (s.t. & im) and uncertain (un). For each category of strategy an ANOVA and a Tukey Test were carried out separately. The letters in the diagram indicate the Tukey groupings. In each category of strategy different letters are used to indicate significant differences between bars (immigration: a, b; submersion tolerance: l, m; submersion tolerance and immigration: *x*, *y*).

are less predictable than those in Central Amazonia (see Adis & Junk, 2002). Thus, most adaptations that help Central European arthropods to survive winter floods are considered as "predispositions"; they evolved before the species populated floodplain ecosystems as an adaptation to other environmental conditions than flooding. In Germany more than 60% of all plant- and leafhoppers overwinter in the egg stage (Nickel, 2003), which can be interpreted as an adaptation to avoid unfavourable conditions such as cold and lack of food resources during winter. Thus, concording with hypothesis (1) this phenological predisposition allows many plant- and leafhopper species to become established in floodplain habitats. In the study area submersion tolerance in the egg stage was also found in the spiders *Allomengea scopigera* and *Allomengea vidua*. Such an adaptation was also observed in other arthropods, such as springtails (*Isotoma* spp.), the centipede *Lamyctes emarginatus* and some caeliferan grasshoppers (Weigmann & Wohlgemuth-von Reiche, 1999). Obviously, flood-resistance of eggs is a common (pre-) adaptation of terrestrial arthropods to survive longer periods of submersion (Tamm, 1986; Adis & Junk, 2002).

Most species of spiders and ground beetles and a few plant- and leafhopper species did not hibernate in the floodplain, but (re-)colonised the habitat with receding water levels either from shelters within the floodplain or from outside. All these species overwinter as juveniles or adults. In general, most spiders in temperate climates overwinter in the juvenile or adult stages, only 7% overwinter in the egg stage (Schaefer, 1976). Ground beetles hibernate either as larvae or as adults and only for very few species overwintering in the egg stage is discussed (Thiele, 1977). In general and in accordance with hypothesis (2), the juvenile or adult stages of terrestrial arthropods are less flood resistant than are their eggs. Immigration in spring and emigration in autumn of many species of spiders and ground beetles was found by Lang and Pütz, 1999 at the river Oder. High flight activity of ground beetles was also recorded for populations at the river Elbe (Germany) and the Morava river (Austria) (Zulka, 1994; Bonn, Hagen & Helling, 1997). Thus, species that overwinter in the juvenile or adult stages are not able to tolerate longer winter submersion and avoid the unfavourable conditions by migration into sheltered areas. However, some contradicting results were found as well. The planthopper *Paraliburnia adela*, the spiders *Microlinyphia impigra*, *Oedothorax apicatus* and *Porrhomma pygmaeum* as well as a number of ground beetles were found to tolerate winter submersion in the juvenile or adult stages. At present, possible physiological or morphological adaptations of these species to inundation are still unknown.

Some species of spiders and ground beetles followed both strategies to cope with the annual winter flood. For three species of ground beetles, Fuellhaas (1997) found that the viability of their populations was dependent on immigrating individuals. Possibly, some of the species classified as submersion tolerant in the present study might also be dependent on immigrating individuals to maintain a viable population. Thus, future investigations should focus on the question, whether immigrating individuals of submersion tolerant species are crucial for the survival of the populations.

Impact of flooding intensity

As predicted by hypothesis (4), we found high densities of immigrating species of the three arthropod groups studied in sites subject to summer and winter flooding. In these sites, flooding is unpredictable and can occur at nearly any time of the year. Especially during summer, inundation has a severe impact on the arthropod communities. Shortly after the catastrophic summer flood at the river Elbe (Germany) in 2002, only few pioneer species such as the planthopper *Javesella pellucida* were found in the floodplain (W. Witsack pers. comm.). In these sites, species that are characterised by high mobility and high fecundity are favoured. They emigrate or die during the time of flooding and quickly recolonise the sites with receding water levels. Additionally, increased mortality might be compensated by a high reproductive rate as *J. pellucida* is a bivoltinous species (Nickel, 2003).

In contrast, immigrating species of planthoppers, leafhoppers and spiders were less successful in sites subject to medium flooding impact, i.e. in sites that are regularly flooded for a long time during winter. This might be due to the low competitive ability of the immigrating populations. In these sites, submersion tolerant species of plant- and leafhoppers dominated in terms of numbers of species and individuals, which accords with hypothesis (3). Whereas most of the spiders that occurred in the Lower Oder Valley belonged to the category "immigrating species", the submersion tolerant species *Allomengea scopigera* and *A. vidua* accounted for 50% of the total number of individuals in sites subject to medium flooding impact.

Long lasting winter floods appear to favour the occurrence of specialist arthropod species. Rothenbücher and Schaefer (2005) showed that many of the submersion tolerant plant- and leafhoppers of sites subject to medium flooding impact are specialists, most of which are monophagous, monovoltine, brachypterous and restricted to a narrow range of habitats (Achtziger, Nickel & Schreiber, 1999). Also, the submersion tolerant spider species *A. scopigera* and *A. vidua* typically occur in moist to wet habitats. Heller and Irmler (1997) found that specialised species of spiders and ground beetles were favoured by long lasting winter floods.

In sites subject to low flooding impact we found a high proportion of ground beetles following both strategies. For three species of ground beetles, Fuellhaas (1997) showed that they were not able to maintain large populations only based on overwintering individuals when the habitat was regularly flooded for a long period of time. Here, the survival of the population depended on immigrating individuals. In the Lower Oder Valley the sites subject to low flooding impact were mostly situated close to potential shelter areas, such as dykes, trees and shrubs. Recolonisation out of these areas was possible. Nonetheless, some adult ground beetles seem to be able to tolerate submersion for a short period of time. Zulka (1994) found that the ground beetle *Bembidion dentellum* survived in cold, aerated water for 40 days. The chance of adult ground beetles to survive the annual winter flood depends on the period of submersion and thus is much higher in sites subject to low flooding impact than in sites subject to high or medium inundation influence.

Conclusions for the restoration of river valleys

One important finding of the present study was, that both submersion tolerant and immigrating arthropods were abundant in temporarily flooded grasslands. Many of the submersion tolerant species seem to have a low dispersal capacity. Future research should focus on the exact dispersal range of these species to assess whether they are capable to colonise new suitable habitats created by floodplain restoration. Furthermore, the assemblage of immigrating species is dependent on the regional species pool. In general, immigrating species need suitable non-flooded overwintering sites within as well as in the surroundings of the floodplain as a source of recolonisation with receding water levels each spring. Thus, the surrounding landscape of floodplains should also be taken in account in restoration projects. Additionally, the study revealed, that the distribution of immigrating and submersion tolerant species was dependent on the frequency and duration of flooding events. Among planthoppers, leafhoppers and spiders, specialists particularly occur in sites subject to medium flooding impact, i.e. to long and regular winter inundation (Rothenbücher, 2005). In these sites flooding impact is similar to natural conditions. Many of these specialist plant- and leafhoppers are listed as endangered in Germany according to Remane, Achtziger, Fröhlich, Nickel, and Witsack (1998), the spider *A. vidua* is categorised as "vulnerable" in Germany (Platen, Blick, Sacher & Malten, 1998) and also a number of endangered carabid species were found in sites subject to medium flooding impact. Thus, the restoration of natural flooding conditions appears to be crucial for supporting typical floodplain arthropod communities.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2006.05.005

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