MASTERARBEIT

Titel der Masterarbeit

„Impact of flooding on bug communities (Heteroptera) on meadows of the Morava River floodplains, Eastern Austria“

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Abstract

Lowland floodplains in Europe have been altered radically by human activities during the last century. One of Central Europe`s last semi-natural lowland floodplains remained along the Morava River on the border between Austria and Slovakia. In this riparian landscape the annual flood dynamics still represent a determining factor in shaping different habitats. Especially terrestrial arthropods of the soil and herb layer are permanently exposed to flooding events. In this study we quantified effects of flooding on richness, abundance and composition of terrestrial bug assemblages (Heteroptera), considering feeding guild affiliation, host plant specialization of herbivorous species and flight ability, on floodplain meadows in the nature reserve "Untere Marchauen" (Lower Austria) and its close proximity. Bugs were sampled by sweep netting on meadows with different flooding regimes ranging from meadows only occasionally flooded by a rising ground-water level to meadows usually flooded for several weeks per year. A total of 11,950 individuals, 5,312 of them adults belonging to 118 species, were collected. Species richness and abundance of bugs were negatively affected by flooding duration and species composition differed between meadows of different flooding regimes. Meadows flooded for longer periods of time were characterized by a higher relative abundance of predacious species. Relative species richness and abundance of host plant specialists (mono- and oligophagous bugs) and relative abundance of brachypterous bug species increased towards meadows with lower flooding intensity. Our study proved that flooding does not only affect abundance, richness and species composition of bug assemblages but also has an impact on the relative importance of trophic guilds and negatively affects species with lower dispersal abilities. Therefore, river restoration measures changing the hydrological dynamics of adjacent floodplains do not only affect diversity of terrestrial arthropods but may have a significant ecological impact. It remains to be studied to what extent such changes in the feeding guild composition and the trophic structure of arthropod communities are capable to affect ecosystem processes in the entire floodplain ecosystem.

Keywords: terrestrial arthropods, species composition, species richness, flooding intensity, floodplain ecosystem, dispersal ability, feeding guilds, trophic structure

Zusammenfassung

Besonders während des letzten Jahrhunderts wurden Europäische Tieflandauen radikal durch menschliche Eingriffe in Mitleidenschaft gezogen. Eine der letzten naturnahen Auensysteme Mitteleuropas erstreckt sich entlang der March an der Grenze zwischen Österreich und der Slowakei. In dieser Flusslandschaft stellen jährliche Überschwemmungsereignisse immer noch einen entscheidenden Faktor bei der Gestaltung verschiedener Lebensräume dar. Terrestrische Arthropoden, die den Boden oder bodennahe Schichten der Vegetation bewohnen, sind permanent Hochwasserereignissen ausgesetzt. In dieser Studie wurden Auswirkungen der Überschwemmungen auf Artenreichtum, Abundanz und Artenzusammensetzung terrestrischer Wanzen (Heteroptera) auf Auenwiesen im Naturschutzgebiet "Untere Marchauen" (Niederösterreich) – unter Berücksichtigung von Gildenzugehörigkeit, Wirtspflanzenspezifität herbivorer Arten und Flugfähigkeit – untersucht. Die Wanzen wurden mittels Streifkescher in Wiesen mit unterschiedlichen Überflutungsregimen gefangen. Untersucht wurden Wiesen, die nur gelegentlich durch den Anstieg des Grundwasserspiegels unter Wasser stehen, bis hin zu solchen, die in der Regel für mehrere Wochen im Jahr überflutet werden. Insgesamt wurden 11.950 Individuen, darunter 5.312 adulte, gefangen, die 118 verschiedenen Arten zugehörten. Überschwemmungsdauer wirkte sich negativ auf Artenreichtum und Abundanz aus und die Artenzusammensetzung unterschied sich signifikant zwischen Wiesen mit unterschiedlichem Überflutungsregime. Wiesen, die über längere Zeiträume unter Wasser stehen, waren gekennzeichnet durch eine höhere relative Abundanz von räuberischen Arten. Relativer Artenreichtum und relative Abundanz von herbivoren Nahrungsspezialisten (mono- und oligophage Arten) und die relative Abundanz von brachypteren Wanzenarten nahm mit abnehmender Überschwemmungsintensität zu. Unsere Studie belegt, dass sich Überschwemmungen nicht nur auf Abundanz, Artenreichtum und -zusammensetzung, sondern auch auf die relative Zusammensetzung trophischer Gilden auswirken. Zunehmende Überflutungsintensität hat außerdem einen negativen Einfluss auf Arten mit geringer Ausbreitungsfähigkeit. Maßnahmen zur Flussrevitalisierung, die auf Änderungen der hydrologischen Dynamik der angrenzenden Auen abzielen, könnten somit nicht nur die Diversität terrestrischer Arthropoden beeinflussen, sondern auch ökologische Effekte nach sich ziehen. Es bleibt

zu prüfen, in welchem Maße Veränderungen in der Zusammensetzung trophischer Gilden von Arthropoden Auswirkungen auf Ökosystem-Prozesse in Aulandschaften haben.

Schlüsselwörter: terrestrische Arthropoden, Artenzusammensetzung, Artenreichtum, Überflutungsintensität, Flussaue, Ausbreitungsfähigkeit, Nahrungsgilden, trophische Struktur

Introduction

In floodplains, flood events play a key role in shaping and maintaining the complex mosaic of riparian and associated aquatic and semi-aquatic habitats (Tockner et al. 1998; Hughes & Rood 2003). However, recurrent flooding represents a serious threat for terrestrial invertebrates and special survival strategies have to be developed to adapt to such catastrophic events. Many species are not able to survive flooding for a longer period of time and as flooded meadows hardly provide any refuge the ability to fly, in order to escape from inundation and re-colonize dry areas again after the flood, seems to be crucial. Additionally, for a more effective production of offspring sophisticated reproduction strategies or life cycles, synchronized to the likely appearance of flooding events, have been evolved in certain groups of arthropods (Zulka 1999a; Rothenbücher & Schaefer 2005).

In this study, we investigated effects of flooding events on bugs (Heteroptera). Bugs represent the most diverse group of hemimetabolous insects. Globally over 38,000 species in 75 families are described (Schuh & Slater 1995), in Central Europe about 1,100 species are known (Günther & Schuster 2000). Bugs inhabit most terrestrial and aquatic habitats and are ecologically very diverse, including phytophagous species with a high number of host plant specialists as well as zoophagous species (Dolling 1991). Due to their sensitive response to environmental changes, bugs have a great potential as indicator organisms in evaluating the quality of habitats (Morris 1979; Otto 1996; Zurbrügg & Frank 2006). Some species are very closely related to certain ecological parameters, such as host plants, soil structure or microclimate (Duelli & Obrist 1998; Friess et al. 1999). About half of Central Europe`s phytophagous bugs are specialists which feed on one or two plant genera within one plant family only (Brändle et al. 2000). Furthermore, bugs proved to be a good indicator group of total insect species richness in human-dominated habitats (Duelli & Obrist 1998).

Using terrestrial bugs, we studied effects of flooding duration on species assemblages of meadows embedded in a landscape still shaped by natural floodplain dynamics. Lowland floodplains belong to Europe`s most diverse ecosystems. In Austria about 12,000 animal and plant species live in floodplain areas (Gepp 1985). Today, about half of the European human population lives on former floodplains and the remaining wetlands have been highly modified through construction of locks, levees and dams, through the impacts of farming, gravel mining, timber harvesting, species extinctions, the invasion of alien species and other direct or indirect anthropogenic disturbances (Brinson & Malvarez 2002; Tockner et al. 2009).

Only few studies tried to investigate the impact of flooding events on communities of terrestrial arthropods in floodplain landscapes of the temperate zone (e.g. Nickel & Hildebrandt 2003, Rothenbücher & Schaefer 2005). We studied effects of flooding events on richness and composition of bug assemblages in meadows of the floodplain of the Morava River in Eastern Austria. Therefore, bugs were sampled on meadows with different flooding regimes ranging from meadows only occasionally flooded by a rising ground-water level during strong flooding events to meadows usually flooded for several weeks per year. In particular, we tested the following hypotheses:

(1) Abundance and species richness of terrestrial bug assemblages are declining with flooding duration due to a resulting high mortality of many species not adequately adapted to this disturbance. Furthermore, flooding causes a reduction of plant biomass production (Pezeshki 2001). This can correspond to a decline in vegetation height and structural diversity (Morris 2000). Hence, flooding is expected to diminish food supply and microhabitat diversity for bugs (e.g. Zurbrügg & Frank 2006; Rabitsch 2007). Both should additionally decrease richness and abundance of bug assemblages.

(2) The proportion of juvenile bugs decreases with the frequency of flooding events. A higher mortality of bugs on meadows with longer flooding duration should disrupt the population cycles of species. Although bugs are r-strategists, which should be able to produce a high number of offspring in short periods of time after a flooding event (Parry 1981; Brown & Southwood 1983), the abundance ratio of adult to juvenile stages should be shifted towards adults on meadows exposed to a higher flooding intensity. Less mobile juvenile stages should face a higher mortality than most adults which can escape flooding by flight.

(3) We expect that flooding events represent a selective force with the potential to structure bug assemblages by promoting species which are better adapted to this disturbance. Consequently, species composition is expected to differ distinctly between meadows with a different flooding regime.

(4) The ratio of brachypterous to macropterous species is changing in response to flooding duration. Due to their better dispersal ability macropterous insect species will more easily re-colonize strongly flooded meadows after local extinction (Roff 1994; Rothenbücher & Schaefer 2006).

(5) The ratio of predacious to herbivorous species declines with the frequency of flooding events. After flood events plant growth will first enable the re-colonization of herbivorous species, which will be followed by their predators (e.g. Siemann 1998; Knops et al. 1999). Longer and more frequent flooding will, therefore, perhaps more effectively prevent the recovery of predators.

(6) Foodplant specialists may be more dominant in stable environments while generalists (e.g. polyphagous species) may be more prominent in regularly disturbed habitats (Novotný 1994; Marvier et al. 2004), such as flooded meadows.

Methods

Study area and study sites

Fieldwork was conducted in summer 2010 and spring 2011 in Lower Austria on meadows located in the nature reserve "Untere Marchauen" (48°18′31″N, 16°53′34″E) and its close proximity (Fig. 1). The reserve along the Morava River covers an area of 1,166 hectares of lowland floodplains with meadows, semi-natural forests and wetlands as dominant landscape structures (Manzano 1999; WWF Österreich 2012). Combined with the floodplain of the river Thaya, the Thaya-Morava region has the largest remaining area of semi-natural lowland floodplains in Central Europe (Zuna-Kratky 1995; Weigand & Wintersberger 1999).

The study area is located on the right bank of the river Morava between the village Zwerndorf in the north and the city Marchegg in the south. In the east the river Morava marks the frontier to Slovakia and at the western border of the reserve a flood-protection dam prevents the adjacent area from being affected by natural flood dynamics caused by the river (Fig. 1). Inside the nature reserve, meadows account for 160 hectares of the total area (WWF Österreich 2012). According to the Ramsar Convention the reserve is part of the protected area “Donau-March-Auen”. It is furthermore, part of the Natura 2000 Site "March-Thaya-Auen" and was identified as an "Important Bird Area" (Manzano 1999; Amt der Niederösterreichischen Landesregierung 2007a). The area west and south of the nature reserve is dominated by cropland. The lowland river Morava is characterized by a simple flow regime with a maximum runoff in April (Zulka & Lazowski 1999). In spring 2010 the water level was above and in spring 2011 below the mean high water (Amt der Niederösterreichischen Landesregierung 2007b). Despite several river engineering measures, especially in the middle of the 20th century, the dynamics of annual flooding events are still a determining factor for the different habitats along the Morava (Zulka 1999b).

Selected study sites were hay meadows inside or just outside the nature reserve. Meadows between the flood-protection dam and the river Morava have various phenotypes and are characterized by a heterogeneous relief with deeper humid and elevated dry formations. Roughly, these meadows can be classified as periodically flooded, semi-humid grassland with sub-continental character, belonging to the Cnidion dubii alliance (Zuna-Kratky 1995). Without regular mowing or grazing, the fallow grassland evolves into hydrophilous tall herb fringe communities and, subsequently, into dense layers of reed canary grass (*Phalaris arundinacea*) or, at the transition zone to waterbodies, to reed beds (*Phragmites australis*) (Zuna-Kratky 1995). Most of our selected meadows are mowed once a year, some even less frequently, a fact that leads to a gradual change in plant species composition. The selected meadows outside the dam are not directly influenced by flooding but can be affected by rising groundwater level during strong flooding events.

According to their annual duration of flooding, the studied meadows were classified as non-flooded (NF) meadows, infrequently (not annually) flooded (IF) meadows, meadows with annual flooding for a short period of some days (SF) and meadows annually flooded for a longer period of some weeks (LF). NF meadows were exclusively located outside the flood protection dam. Six to eight meadows were selected per meadow type resulting in a total of 28 study sites, all between one and three hectares large (Fig. 1; Appendix Table A1).

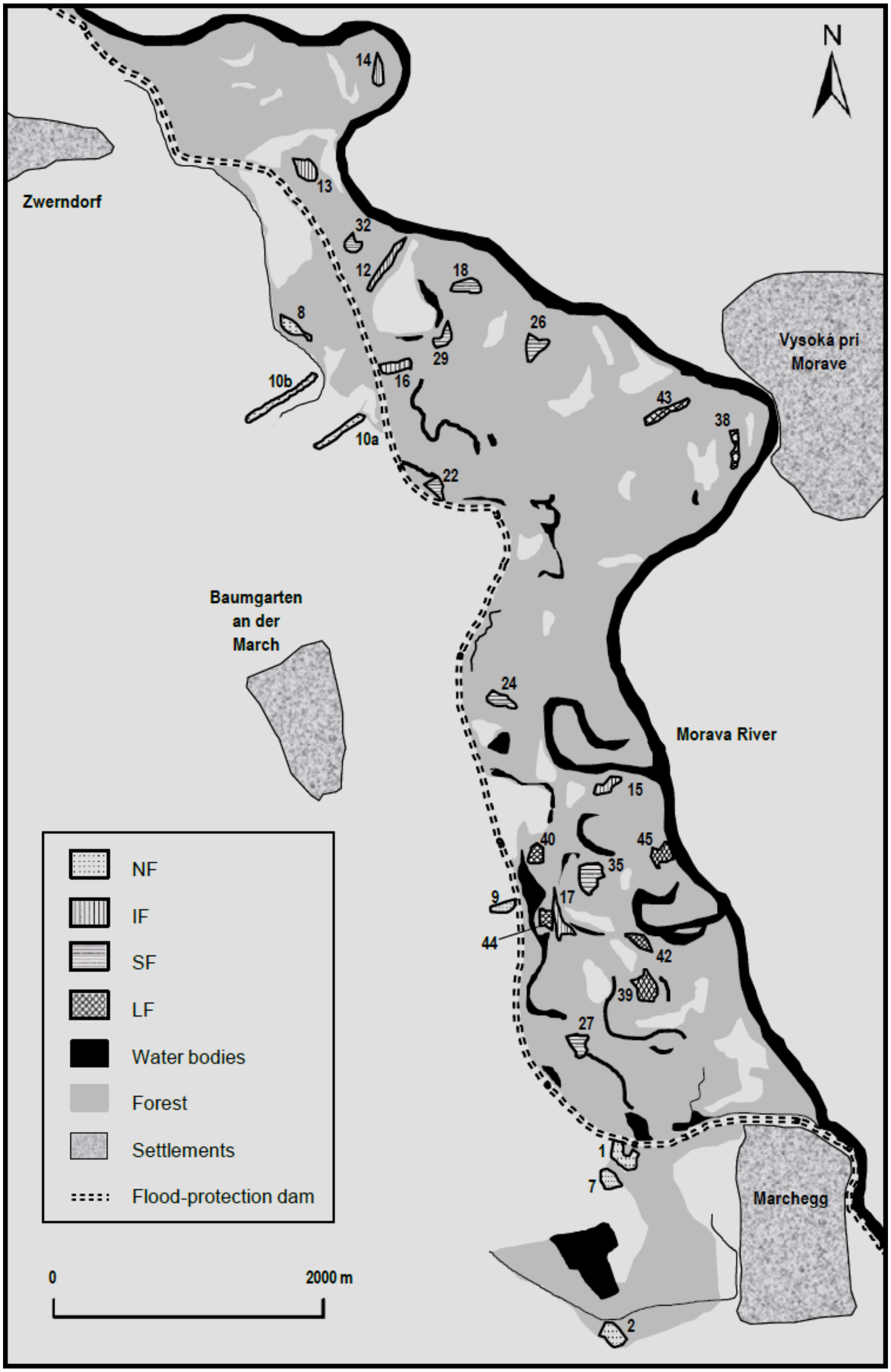

Figure 1. Study area and sampled meadows. Meadow types: NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks. Sampled meadows are indicated by code numbers.

Sampling of bugs

On each meadow bugs were sampled once in July 2010, August 2010, May 2011 and June 2011, respectively (for sampling dates see Appendix Table A1). A sampling unit consisted of 300 sweep net samples, roughly evenly distributed over the meadow area, per sampling date. The sweep net method is commonly used to assess bug communities of meadows (Schwab et al. 2002; Zurbrügg & Frank 2006; Torma & Császár 2012). Individuals belonging to the group of Heteroptera were collected from the net using an exhaustor and were killed in glas tubes moistened with ethyl ether.

The determination of bugs was based on a variety of sources (Wagner 1952, 1966, 1967; Bantock & Botting 2010; Strauß 2011). Juvenile bugs, some adult specimens of the genera *Anthocoris*, *Lygus*, *Orius*, *Orthops*, *Orthotylus*, *Polymerus* and *Psallus* and all female specimens of the genera *Nabis* and *Notostira* – all together 574 adult individuals – could not be identified to species level.

Biological traits

All bugs were affiliated to one of the following three feeding guilds: herbivores, omnivores or predators. Herbivorous bugs were classified as monophagous (feeding on only one plant genus), oligophagous (feeding on only one plant family) or polyphagous. Species were defined as brachypterous when their adults are flightless or adult morphs with partly reduced wings occur, which could be recorded during our surveys. Around 20% of all sampled species were classified as brachypterous (Appendix Table A4). All these biological traits were extracted from various sources (Wagner 1952, 1966, 1967; Bantock & Botting 2010; Strauß 2011).

Data analysis

Because our study had a focus on effects of flooding on bugs occurring on meadows, we excluded all exclusively arboreal species (Appendix Table A4) from our analyses. For all calculations on species richness only adult bugs which could be identified on the level of species were considered.

One-way ANOVAs were calculated to test for effects of flooding regime on total abundance and species richness, proportion of juveniles, richness and abundance of different feeding guilds, richness and abundance of herbivorous bugs with different host plant specificity and the ratio brachypterous to macropterous species. To approach a normal distribution of data, log or arcsin square-root transformations were used. Least significance difference (LSD) tests were calculated to test for significant differences of variables between meadow types. All statistical analyses mentioned above were performed using the program Statistica 7.1 (StatSoft, Inc. 2005). All results of one-way ANOVAs listed in Tables 1 and 3 were controlled for false discovery rate (FDR) using the algorithm provided by Benjamini & Hochberg (1995). FDR-adjusted *p*-values were calculated by a spreadsheet program of Pike (2011).

Species richness for a largest shared sample size was estimated with the software Ecological Methodology version 5.2 (Krebs 1999), species accumulation curves were calculated using the program PAST (Hammer et al. 2001).

Analyses of similarity (ANOSIM; number of permutations: 999) were calculated with the program Primer v5 (Clarke & Gorley 2001) to test for differences in bug species composition between meadow types. Similarity of species composition was quantified by Bray-Curtis similarities (calculated using square-root transformed abundances). Similarity relationships between bug assemblages of the sampled meadows were visualized in a two-dimensional plot using non-metric multidimensional scaling (NMDS). A stress value of <0.20 was considered as appropriate for displaying similarity relationships (Clarke 1993). A Spearman matrix rank correlation relating spatial distances between meadows and faunal similarity (Bray-Curtis indices) calculated with Primer v5 (Clarke & Gorley 2001) was used to test for spatial autocorrelation.

Results

Species richness and abundance

A total of 11,950 individuals, of that 5,312 adults belonging to 118 species, were sampled. Only 15 individuals of 9 arboreal species, which were excluded from all subsequent analyses, occurred in our samples (Appendix Tables A2 – A4).

Bug abundance was significantly affected by meadow type (Table 1). NF and IF meadows showed higher bug abundances than meadows characterized by longer flooding durations (Fig. 2a). The relative abundance of juveniles did not differ significantly after being controlled for false discovery rate (FDR) (Table 1). The mean number of species recorded per study site decreased from NF sites to IF sites and, further, to meadows flooded for longer durations (Fig. 2b). However, mean species richness estimated for a largest shared sample size (N = 37 individuals) did not differ between meadow types (Table 1).

Table 1. Results of one-way ANOVAs testing for differences of number of individuals (log x transformed), relative abundance of juveniles (arcsin √x transformed), recorded species and species estimated for a largest shared sample size (N = 37 individuals) between meadows with different flooding regime. Results printed bold remained significant after controlled for false discovery rate (FDR) (Benjamini & Hochberg 1995).

Dependent variable	**One-way ANOVA**	**FDR-adjusted *p***
Individuals	$\boldsymbol{F_{3,24} = 14.04, p = 0.001}$	**0.003**
Relative abundance juveniles	$F_{3,24} = 3.11, p = 0.045$	0.064
Recorded species[1]	$\boldsymbol{F_{3,24} = 13.24, p = 0.001}$	**0.003**
Rarefied richness[1]	$F_{3,24} = 1.65, p = 0.205$	0.256

[1] only adult specimens considered

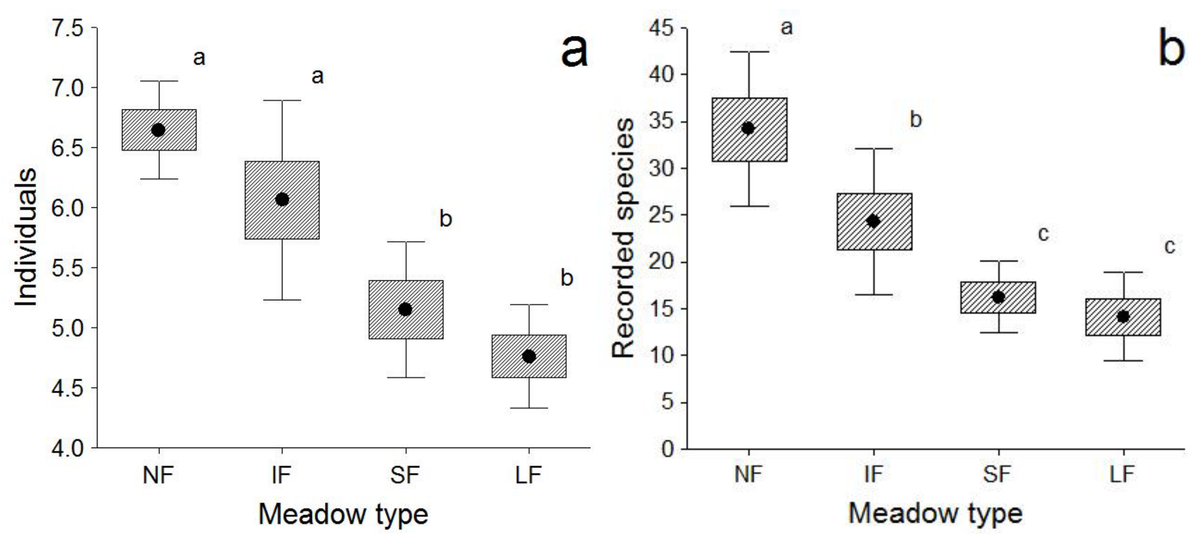

Figure 2. (a) Mean number of individuals (log x transformed) and (b) species ± SE (box) and 95% CI (whiskers) sampled on meadows with different flooding regime. Different letters indicate significant differences (LSD tests). Meadow types: NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks.

Species accumulation curves for samples pooled on the level of meadow types indicate significant higher species richness for non-flooded meadows compared to all other three meadow types, which apparently were characterized by relative similar species richness as indicated by similar shapes of their species accumulation curves and a strong overlap of the associated 95% confidence intervals (Fig. 3).

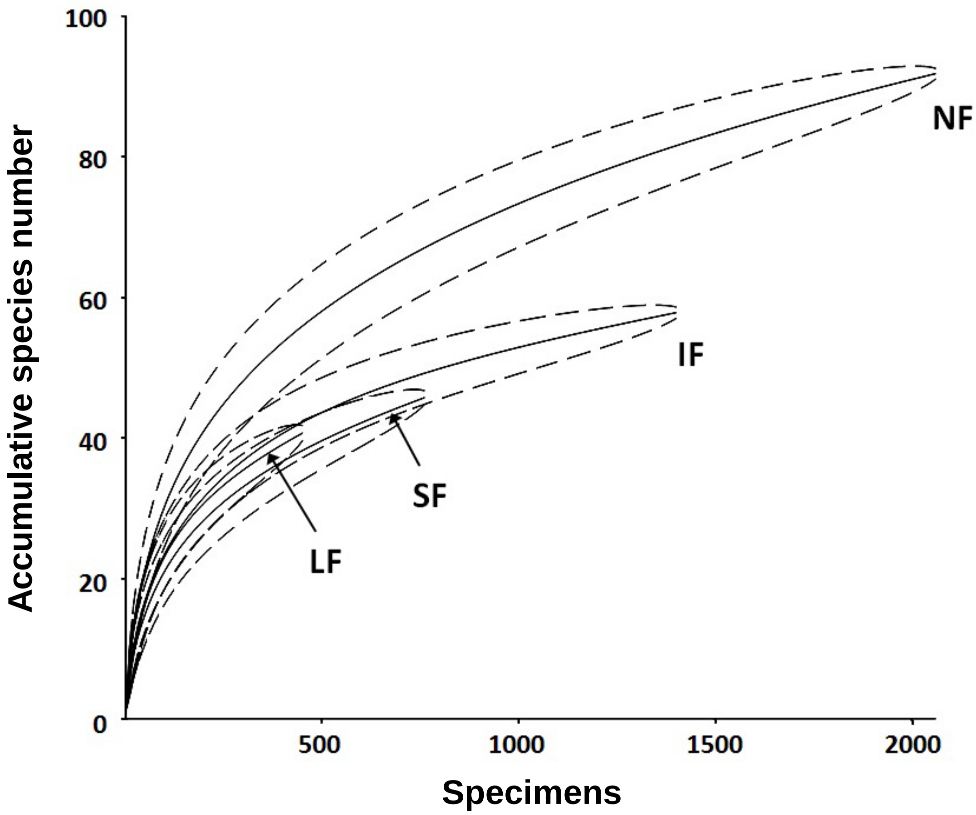

Figure 3. Species accumulation curves ± 95 % CI (dashed lines) for four different meadow types: NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks.

Species composition

The similarity relationships (quantified by Bray-Curtis similarities) between species assemblages of the sampled meadows are visualized in a NMDS plot (Fig. 4). Dimension 1 can be interpreted as the flooding duration. NF meadows (predominantly plotted in the right part of the graph) are clearly separated from LF meadows (segregating in the left half of the graph), while the two other meadow types IF and SF are plotted in-between these two extremes (Fig. 4). Dimension 1 values differed significantly between the four different meadow types (one-way ANOVA: $F_{3,24} = 11.78$, $p < 0.001$). A significant effect of flooding regime on bug species composition was also indicated by a one-way ANOSIM (global $r = 0.32$, $p = 0.001$). Pairwise tests to detect differences between meadow types achieved a significant level for the comparisons between NF and SF as well as LF sites and between LF and IF sites (Table 2).

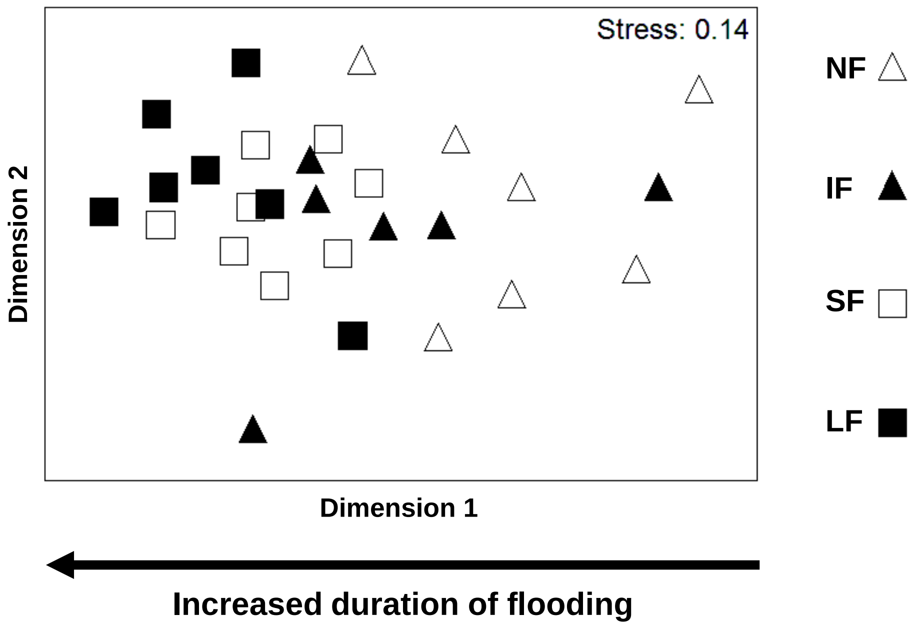

Figure 4. Similarity relationships between species assemblages of meadows with different flooding regime visualized in a NMDS-plot based on Bray-Curtis similarities. Meadow types: NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks.

Table 2. ANOSIMs testing for differences in species composition between meadow types (NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks). Significant differences printed bold.

Pairwise comparisons of meadow types	*R*	*p*
NF vs. IF	0.124	0.090
NF vs. SF	**0.625**	**0.001**
NF vs. LF	**0.705**	**0.003**
IF vs. SF	0.109	0.112
IF vs. LF	**0.250**	**0.024**
SF vs. LF	0.077	0.204

A Spearman matrix rank correlation did not indicate that similarity of species assemblages found on individual meadows was affected by spatial distances between sampled meadows (*Rho* = -0.049, p = 0.784).

Biological traits

The relative abundance of brachypterous species was significantly affected by meadow type (Table 3). NF sites showed a significantly higher relative abundance of brachypterous bugs than the other three meadow types (Fig. 5a). In contrast, relative species richness of brachypterous bugs was not affected by flooding regime (Table 3).

The relative abundance of predacious species was significantly affected by flooding intensity (Table 3). It increased continuously with flooding duration from NF towards IF, SF and LF sites (Fig. 5b). In contrast, the relative abundance of herbivorous species did not differ significantly between meadow types (Table 3). However, the composition of herbivorous bugs was affected by flooding regime, when considering their foodplant specificity (Table 3). The mean relative abundance of mono- and oligophagous herbivorous species was significantly higher at NF sites compared to meadows with a longer duration of flooding (IF, SF and LF sites) (Fig. 5c). The mean relative richness of this group was significantly higher at NF and IF sites compared to SF and LF meadows (Fig. 5d). Because only twelve individuals belonging to three species were classified as omnivorous, this feeding guild was not further considered.

Table 3. Results of one-way ANOVAs testing for differences in relative abundance and species richness of brachypterous bugs and mono-oligophagous species and relative abundance of feeding guilds (predators and herbivores) between meadows with different flooding regime. Results printed bold remained significant after controlled for false discovery rate (FDR) (Benjamini & Hochberg 1995).

Dependent variable	**One-way ANOVA**	**FDR-adjusted *p***
Brachypterous species		
Relative abundance[1]	$\mathbf{F_{3,24} = 7.67, p = 0.001}$	**0.003**
Relative richness[1]	$F_{3,24} = 0.60, p = 0.623$	0.692
Feeding guilds		
Relative abundance predators[2]	$\mathbf{F_{3,24} = 4.84, p = 0.009}$	**0.018**
Relative abundance herbivores[2]	$F_{3,24} = 0.30, p = 0.829$	0.829

Table 3 (cont.)

Dependent variable	One-way ANOVA	FDR-adjusted *p*
Feeding specificity of herbivorous species		
Relative abundance mono-oligophagous species[2]	$F_{3,24}$ **= 4.57,** p **= 0.011**	**0.018**
Relative richness mono-oligophagous species[2]	$F_{3,24}$ **= 7.74,** p **= 0.001**	**0.003**

[1] only adult specimens considered
[2] arcsin √x transformed

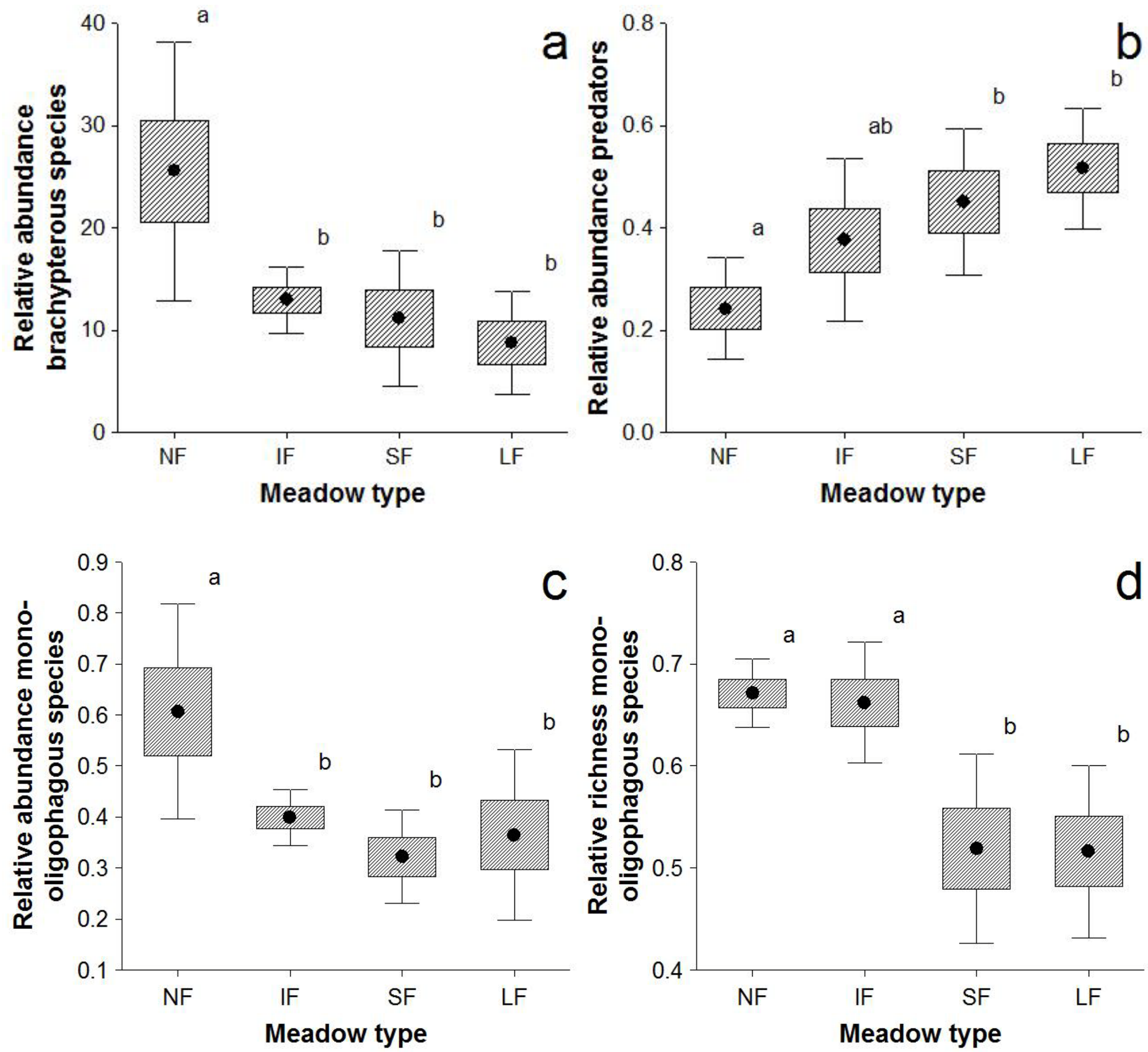

Figure 5. (a) Mean relative abundance ± SE (box) and 95% CI (whiskers) of brachypterous species (%), (b) predacious species (arcsin √x transformed), and (c) mono- and oligophagous species (arcsin √x transformed), and (d) mean relative richness ± SE (box) and 95% CI (whiskers) of mono- and oligophagous species (arcsin √x transformed) sampled on meadows with different flooding regime. Different letters indicate significant differences (LSD test). Meadow types: NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks.

Discussion

Total species richness and abundance

Disturbance caused by flood immediately reduces diversity, abundance, and biomass of the soil macrofauna. The effect becomes stronger with the duration of flooding (Plum 2005). The survival rate of species without special physiological adaptations, like certain annelids or insect larvae, is very low. For other groups the only way to respond to flooding is by active or passive movement, by re-colonization or reproduction from resistant stages (Plum 2005). Accordingly, also our study showed a negative impact of flooding events on bug communities. Both abundance and species richness on meadows decreased with increasing flooding intensity. The species accumulation curves calculated for the four meadow types indicate that also on a larger spatial scale non-flooded meadows were characterized by a higher richness. In addition, a reduced structural heterogeneity and diversity of the herb layer may have been contributed to this pattern (Morris 2000; Schwab et al. 2002). Although we did not conduct a vegetation mapping on the sampled meadows, we noticed, that NF and IF sites were characterized by a higher herb layer density and plant species richness, which should correspond to a higher plant biomass and a higher structural heterogeneity. Higher richness at non-flooded compared to flooded sites was also found for grasshoppers and spiders (Rothenbücher & Schaefer 2005; Katušić 2008). The latter group also showed a higher abundance in non-flooded grasslands (Katušić 2008). However, it appears that these patterns cannot be generalized. Remarkably, terrestrial beetles studied in a floodplain forest in south-eastern Australia showed an opposite response. Abundance, species richness and biomass were greatest at sites flooded for the longest period of about 4 months. Spiders maintained a similar abundance, species richness and biomass at flooded sites (Ballinger et al. 2005).

In our study, gradually increased disturbance due to increasing flooding duration did not have a prominent effect on the relative abundance of juvenile bugs. The relative abundance of juvenile stages was slightly higher at NF and IF sites, but this difference did not remain significant after correcting for FDR. This provides evidence that population cycles of bugs do not seem to be seriously disrupted by flooding, although it appears unlikely that terrestrial bugs of our study area evolved specific adaptations as it has been found, for instance, in Central Amazonian arthropods (Adis & Junk 2002). In grasshoppers, the chance to survive disturbing effects by flooding unscathed is higher for eggs than for larval stages and fully emerged adults (Fischer & Witsack 2009). It remains to be studied to what extent bug species with larva emerging from the eggs after the spring flooding are less affected by flooding than bugs with larva appearing earlier in spring.

Species composition

Our data show that the composition of bug species assemblages was significantly affected by flooding intensity. Similarly, differences in the inundation duration of riparian habitats are affecting species composition of spider and ground beetle assemblages (Bonn et al. 2002; Gerisch et al. 2006). In contrast, a high similarity of species composition between flooded and non-flooded sites was found in grasshoppers on floodplain meadows along the river Elbe (Germany), perhaps because most of the species survived the flooding period in the egg phase (Fischer & Witsack 2009). Also many planthopper and leafhopper species can tolerate flooding in the egg stage during winter (Rothenbücher & Schaefer 2006). A follow-up study has to identify which factors are responsible for the high sensitivity of bug assemblages against flooding in the Morava floodplains. Perhaps, the phenology of hydrological conditions plays an important role. Usually the Morava floodplains are flooded in spring, when the larva of the vast majority of bug species already emerged from the egg and are facing a high mortality due to flooding. So far, it is unknown to what extent the eggs or other stages of terrestrial bug species evolved submersion tolerating strategies.

Biological traits

The lower relative abundance of brachypterous species on flooded meadows found in our study indicates that the mobility of terrestrial insects plays a crucial role for the survival of populations in floodplains, as emphasized by Zulka (1999a). Also assemblages of plant- and leafhoppers, ground beetles and spiders occurring in floodplain habitats along the river Lower Oder (Germany), with unpredictable, intense flooding events, are characterized by species with high dispersal capability (Rothenbücher & Schaefer 2006). As in bugs, flight ability appears to be also an important precondition in carabid beetles to deal successfully with environments characterized by a high hydrological dynamic (Bonn et al. 2002). Flightless species, which are not able to escape flooding, neither have a chance to survive rising water levels nor do they have the possibility to rapidly (re-)colonize newly emerged dry habitats.

In contrast to our hypothesis, the relative abundance of meadow-inhabiting predators increased with flooding intensity. A similar pattern was found for predacious beetles and spiders in Australian floodplain habitats (Ballinger et al. 2005). The time lag between the receding of floodwater and the regeneration of a dense vegetation cover, providing food sources for herbivorous insects, may be responsible for a higher relative abundance of predators on meadows affected by flooding events. Contrary to herbivores, the survival or successful (re-)colonization of meadows by predators after flooding might not strictly depend on vegetation succession. The vast majority of predators can be classified as generalists and, therefore, they do not particularly depend on herbivorous arthropods colonizing the herb layer. For example, individuals of the most abundant predacious genus *Nabis* even were recorded feeding on mosquitos (Culicidae; Gratzer, own observation), which appear in high densities in floodplains after flooding events.

Meadows with a lower frequency and intensity of disturbance should be characterized by a more predictable occurrence of certain plant species thereby favoring the colonization by host plant specialists. Indeed, the relative richness of mono- and oligophagous herbivores was higher at NF and IF sites than on meadows with a higher impact of flooding events. Also their mean relative abundance was highest in meadows not directly influenced by flooding. Studies on leafhoppers showed comparable results: the average host plant range of species was wider in ephemeral habitats, whereas specialists were prevalent in permanent habitats (Novotný 1994). A decline of specialized species in frequently disturbed grassland was also found for Auchenorrhyncha (Nickel & Hildebrandt 2003). On the contrary, in fallows of the Lower

Oder floodplain (Germany) most specialized leafhoppers occurred in habitats of medium flood disturbance (Rothenbücher & Schaefer 2005).

Conclusion

Our study proved that flooding does not only affect abundance, richness and species composition of bug assemblages but also has an impact on the relative importance of trophic guilds and negatively affects species with lower dispersal abilities. Therefore, river restoration measures changing the hydrological dynamics of adjacent floodplains do not only affect diversity of terrestrial arthropods but may have a significant ecological impact. It remains to be quantified by before-after impact studies to what extent such changes in the feeding guild composition and the trophic structure of arthropod communities are capable to affect ecosystem processes in the entire floodplain ecosystem.

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Appendix

Table A1. Sampled meadows.

Meadow #	Flooding intensity[1]	Coordinates	Sampling dates			
			July 2010	August 2010	May 2011	June 2011
1	NF	48° 16’ 45’’ N, 16° 53’ 44’’ E	14th	14th	20th	20th
2	NF	48° 16’ 07’’ N, 16° 53’ 40’’ E	12th	14th	20th	20th
7	NF	48° 16’ 40’’ N, 16° 53’ 40’’ E	12th	14th	20th	20th
8	NF	48° 19’ 50’’ N, 16° 51’ 53’’ E	14th	18th	6th	15th
9	NF	48° 17’ 41’’ N, 16° 53’ 05’’ E	18th	14th	11th	24th
10a	NF	48° 19’ 27’’ N, 16° 52’ 08’’ E	17th	18th	20th	15th
10b	NF	48° 19’ 35’’ N, 16° 51’ 51’’ E	17th	18th	6th	24th
12	IF	48° 20’ 04’’ N, 16° 52’ 24’’ E	12th	18th	11th	24th
13	IF	48° 20’ 24’’ N, 16° 51’ 58’’ E	17th	16th	6th	24th
14	IF	48° 20’ 46’’ N, 16° 52’ 22’’ E	17th	20th	6th	15th
15	IF	48° 18’ 08’’ N, 16° 53’ 39’’ E	18th	23rd	19th	21st
16	IF	48° 19’ 41’’ N, 16° 52’ 27’’ E	8th	23rd	6th	15th
17	IF	48° 17’ 37’’ N, 16° 53’ 22’’ E	18th	23rd	14th	21st
18	SF	48° 19’ 60’’ N, 16° 52’ 52’’ E	12th	18th	9th	16th
22	SF	48° 19’ 14’’ N, 16° 52’ 41’’ E	8th	14th	11th	16th
24	SF	48° 18’ 27’’ N, 16° 53’ 01’’ E	19th	23rd	19th	21st
26	SF	48° 19’ 45’’ N, 16° 53’ 14’’ E	19th	20th	9th	16th
27	SF	48° 17’ 11’’ N, 16° 53’ 29’’ E	14th	25th	14th	20th
29	SF	48° 19’ 48’’ N, 16° 52’ 44’’ E	19th	20th	9th	16th
32	SF	48° 20’ 08’’ N, 16° 52’ 13’’ E	17th	18th	11th	24th
35	SF	48° 17’ 48’’ N, 16° 53’ 31’’ E	18th	23rd	19th	21st
38	LF	48° 19’ 23’’ N, 16° 54’ 22’’ E	19th	20th	9th	16th
39	LF	48° 17’ 23’’ N, 16° 53’ 50’’ E	14th	25th	20th	20th
40	LF	48° 17’ 53’’ N, 16° 53’ 09’’ E	18th	25th	19th	21st
42	LF	48° 17’ 33’’ N, 16° 53’ 51’’ E	14th	25th	19th	20th
43	LF	48° 19’ 31’’ N, 16° 53’ 59’’ E	19th	20th	9th	16th
44	LF	48° 17’ 39’’ N, 16° 53’ 18’’ E	19th	25th	19th	21st
45	LF	48° 17’ 53’’ N, 16° 53’ 57’’ E	18th	23rd	19th	21st

[1] NF – non-flooded meadows, IF – infrequently (not annually) flooded meadows, SF – meadows annually flooded for a short period of some days, LF – meadows annually flooded for a longer period of some weeks

Table A2. List of recorded species and number of adults sampled on each meadow.

Family	Meadow #																												Σ
Species	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	
Anthocoridae																													
Anthocoris sp.																					1						1		**2**
Orius minutus																										1			**1**
Orius sp.						1			1					1			1		1							1			**6**
Indet.															1														**1**
Aradidae																													
Aneurus avenious															1														**1**
Berytidae																													
Berytinus clavipes	1							1																					**2**
Berytinus minor		10																											**10**
Coreidae																													
Ceraleptus gracilicornis						1																1							**2**
Coreus marginatus	2		5							2		4			1		2					2			1			1	**20**
Coriomeris denticulatus	1								1																				**2**
Gonocerus acuteangulatus														1															**1**
Syromastus rhombeus		1																											**1**
Cydnidae																													
Tritomegas sexmaculatus										1																			**1**
Lygaeidae																													
Cymus claviculus							1															1							**2**
Cymus glandicolor						1																		1					**2**
Cymus melanocephalus		15												1															**16**
Dimorphopterus spinolae		2			1	5					1							1				2							**12**
Ischnodemus sabuleti			1			1										1													**3**
Kleidocerys resedae									1					2					1			1							**5**
Megalonotus antennatus				1																									**1**
Ortholomus punctipennis							1																						**1**
Pachybrachius fracticollis[2]																										1			**1**

Table A2 (cont.)

Family / Species	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	∑
Family	Meadow #																												
Lygaeidae (cont.)																													
Peritrechus gracilicornis				1		1															1								**3**
Peritrechus nubilus		1				2																							**3**
Platyplax salviae	1					1																							**2**
Plinthisus brevipennis																				1									**1**
Rhyparochromus vulgaris				2																									**2**
Scolopostethus thomsoni		1	1																										**2**
Spilostethus saxatilis				21		1	5						1																**28**
Stygnocoris fuligineus									1																				**1**
Miridae																													
Acetropis carinata						8																							**8**
Acetropis longirostris			14		44	13				5				1		1					1				6		1		**86**
Adelphocoris lineolatus	6	5	2	2	3	9	13				1	6			2			1	1		1								**52**
Adelphocoris quadripunctatus				4						1																			**5**
Adelphocoris seticornis	1	23		19	6			1	2	4	2	2			5	2		8				1	7						**83**
Adelphocoris ticinensis		1	2		2			3	1	4	2	7			6	2		4	1				5	2			1	1	**44**
Agnocoris reclairei															1													1	**2**
Amblytylus nasutus										3		8		2			4												**17**
Apolygus lucorum								1			1				1													1	**4**
Apolygus spinolae			2							1		1	1										2		1			8	**16**
Capsodes gothicus						1																							**1**
Capsus ater	2		2	1							11					1						1		2					**20**
Charagochilus gyllenhalii				1		4			1		1				2														**9**
Charagochilus spiralifer																	1												**1**
Chlamydatus pulicarius	5	1					7																						**13**
Chlamydatus pullus	2			2			1				1	2					1												**9**
Closterotomus norwegicus																							1						**1**
Criocoris crassicornis						2																							**2**
Criocoris nigripes		1									1																		**2**

Table A2 (cont.)

Family														**Meadow #**														Σ
Species	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	
Miridae (cont.)																													
Criocoris sulcicornis		1				25																							**26**
Deraeocoris ruber		2	1	2	5					1	5	11	4				1		1	1		5		1					**40**
Dicyphus globulifer	1										5																		**6**
Europiella artemisiae							1																						**1**
Globiceps flavomaculatus						1						1																	**2**
Halticus apterus	4	5		60		11	5				19				1	1												1	**107**
Harpocera thoracica				1					1																				**2**
Isometopus intrusus[1]																							1						**1**
Leptopterna dolabrata	121	45	75	1	1	160	1			6	53	13		6	2	1	1	2				1							**489**
Liocoris tripustulatus					1				1		2																	15	**19**
Lygus pratensis	13	10	18	13	6		6	9	15	6	6	12	1	2	11	3	10	3	4	2	1	1	4	2	4	1	1	5	**169**
Lygus rugulipennis	9	3	16	7	6		4	23	32	6	1	10	1	7	18	5	3	20	5	6	14	1	2		5	4		8	**216**
Lygus sp.	1					1		2				1			1			1		3									**10**
Malacocoris chlorizans																								1					**1**
Megaloceroea recticornis		5	9	1		151				18	102	12		9			1	2											**310**
Mermitelocerus schmidtii				2									1																**3**
Notostira elongata	6	2	2	3	2		12				3	2	1		1							3							**37**
Notostira sp.	6	5		3	5	1	16	1		1	10		2											1					**51**
Orthocephalus vittipennis		1																											**1**
Orthops basalis	1	1	1																										**3**
Orthops sp.	1																												**1**
Orthotylus nassatus								1																					**1**
Orthotylus sp.																								1					**1**
Phytocoris populi															1														**1**
Phytocoris tiliae															1														**1**
Plagiognathus arbustorum		3	1								8												3	1	1			2	**19**
Plagiognathus chrysanthemi	3	2	15	4		7				2	14	2			1									1	2				**53**
Polymerus palustris	8		2	1	81	17		5				2			2			1											**119**
Polymerus sp.	11		3	18	62	37	4		3		2		2		10								1					1	**154**

Table A2 (cont.)

Family / Species	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	∑
	Meadow #																												
Miridae (cont.)																													
Polymerus unifasciatus	21	3		16		74	46					1	2																**163**
Polymerus vulneratus			1			4	6																						**11**
Psallus sp.		1		1					2																				**4**
Stenodema calcarata	4	5	11	8	1	2	24	4	3	21	2	16		30	11	10	20	5	15	1	2	17	7	5	2	1	12	4	**243**
Stenodema laevigata		1		11		1	1		1	1		2	1	1								6							**26**
Stenotus binotatus		8	1	1		14				1	414	2	8			2		2	1			2	1		1				**458**
Systellonotus triguttatus	1					4		1							1														**7**
Trigonotylus caelestialium	116	1	22	30	32	7	45	36	41	38	6	79	10	69	25	20	46	12	9	15	114	70	25	17	35	37	20	7	**984**
Tytthus pygmaeus												1																	**1**
Indet.	1	1		1						1					1			3						1					**9**
Nabidae																													
Himacerus apterus				4																		2							**6**
Himacerus mirmicoides		1																											**1**
Nabis ferus	2		1		2	2	1	3	2			1		7	4	3		5		1	3		4	2	1	1	1		**46**
Nabis pseudoferus	2	1	1	4		2	9	3	4	5	2	4	4	3	8		3			1		1	1		1		1		**60**
Nabis punctatus	6		9	5	3	3	1	7	19	10		14	1	10	10		3	21	1	4	3		5	3	3		4	6	**151**
Nabis rugosus				4																									**4**
Nabis sp.	21		20	15	4	10	14	16	25	20	10	20	3	20	13	4	5	24	7	9	6	4	14	7	28	5	6	4	**334**
Pentatomidae																													
Aelia acuminata	7	14	1	25		2	11	5	9	4	4	16		4	4				2		3	6	1						**118**
Carpocoris fuscispinus			1																										**1**
Carpocoris purpureipennis	2	7	5	1	1	3	1								1														**21**
Dolycoris baccarum	2	1				1						3	2		1		3												**13**
Eurydema oleracea			2	1	1		2			1	1	1			3					2		1							**15**
Eysarcoris aeneus	2		1								1	1						1											**6**
Eysarcoris ventralis											1																		**1**
Graphosoma lineatum		1				2																							**3**
Holcostethus vernalis		1					1															1							**3**
Neottiglossa leporina	2	4	2			1																							**9**
Neottiglossa pusilla	1																												**1**
Palomena prasina						1																							**1**

Table A2 (cont.)

Family	**Meadow #**																												∑
Species	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	
Pentatomidae (cont.)																													
Podops inunctus		1																											**1**
Sciocoris distinctus						2		1																					**3**
Zicrona caerulea			1																										**1**
Piesmatidae																													
Piesma capitatum											1																		**1**
Reduviidae																													
Rhynocoris iracundus		1																											**1**
Rhopalidae																													
Corizus hyoscyami				1				1																					**2**
Myrmus miriformis	3									1	3			5															**12**
Rhopalus parumpunctatus	5	5		20		3	1	1	8	6	7	32	1	3	2	1		2	2		2	1	1					2	**105**
Rhopalus subrufus		3		1																									**4**
Stictopleurus punctatonervosus		6	3	2						1	7	1				1	1											1	**23**
Saldidae																													
Chartoscirta cincta																							1						**1**
Chartoscirta elegantula					1																								**1**
Saldula saltatoria																				4					1	1			**6**
Scutelleridae																													
Eurygaster maura	7	6	1	1		3		1			4										2					1			**26**
Eurygaster testudinaria								2		1			1	2		1	1	2				1	1						**12**
Tingidae																													
Acalypta carinata		1																											**1**
Agramma confusum		1																											**1**
Dictyla humuli			10		1			8	1			1	1		2	2	5	2		2		4	2			4		1	**46**
Oncochila simplex												5																	**5**
Tingis ampliata				1		2																							**3**
Tingis auriculata[2]		1																											**1**
Tingis reticulata						1																							**1**
Indet.							1																						**1**
∑	**411**	**221**	**265**	**323**	**271**	**606**	**241**	**136**	**175**	**172**	**714**	**296**	**48**	**186**	**155**	**61**	**112**	**122**	**51**	**52**	**154**	**136**	**89**	**48**	**92**	**58**	**48**	**69**	**5312**

[1] first evidence for Lower Austria

[2] classified as “vulnerable” in the Red List of Lower Austria (Rabitsch 2007)

Table A3. Number of juvenile bugs sampled per family and meadow.

Family	Meadow #																											∑
	1	2	7	8	9	10a	10b	12	13	14	15	16	17	18	22	24	26	27	29	32	35	38	39	40	42	43	44	45	
Berytidae						3																							**3**
Coreidae	4		2	4						5	4	13			3		10					14						1	**60**
Lygaeidae	2			6		2	4					1	1																**16**
Miridae	321	259	56	334	933	727	391	70	61	96	877	267	176	276	61	36	101	18	5	36	26	85	44	14	22	15	18	15	**5340**
Nabidae	51	3	30	27	36	7	6	17	22	24	4	64	9	18	50	5	3	35	1	11	7	7	24	13	13	11	8	10	**516**
Pentatomidae	16	83	23	48	5	17	7	5	6	34	15	45	4	27	5	1	9	8	5			32	3	4		1	5	1	**409**
Rhopalidae	5	6	1			6						57		3															**78**
Scutelleridae	2	6	6	5		10		3	2	8	28	4		33			1	2				3							**113**
Tingidae						1										2													**3**
Indet.	12	7		2	16	7	16	1	6	1	14	6	1					2	1		1		3		2	2			**100**
∑	**413**	**364**	**118**	**426**	**990**	**780**	**424**	**96**	**97**	**168**	**942**	**457**	**191**	**357**	**119**	**44**	**124**	**65**	**12**	**47**	**34**	**141**	**74**	**31**	**37**	**29**	**31**	**27**	**6638**

Table A4. Biological traits of recorded bug species.

Family / Species	Arboreal lifestyle	Feeding guild	Host plant specificity of herbivorous bugs[1]	Flight ability[2]
Anthocoridae				
Anthocoris sp.		predator	-	macropterous
Orius minutus		predator	-	macropterous
Orius sp.		-	-	macropterous
Aradidae				
Aneurus avenious	X	herbivore	unknown	macropterous
Berytidae				
Berytinus clavipes		herbivore	monophagous	brachypterous
Berytinus minor		herbivore	oligophagous	macropterous
Coreidae				
Ceraleptus gracilicornis		herbivore	oligophagous	macropterous
Coreus marginatus		herbivore	polyphagous	macropterous
Coriomeris denticulatus		herbivore	polyphagous	macropterous
Gonocerus acuteangulatus		herbivore	polyphagous	macropterous
Syromastus rhombeus		herbivore	polyphagous	macropterous
Cydnidae				
Tritomegas sexmaculatus		herbivore	polyphagous	macropterous
Lygaeidae				
Cymus claviculus		herbivore	polyphagous	macropterous
Cymus glandicolor		herbivore	polyphagous	macropterous
Cymus melanocephalus		herbivore	polyphagous	macropterous
Dimorphopterus spinolae		herbivore	polyphagous	brachypterous
Ischnodemus sabuleti		herbivore	polyphagous	brachypterous
Kleidocerys resedae	X	omnivore	-	macropterous
Megalonotus antennatus		unknown	unknown	brachypterous
Ortholomus punctipennis		unknown	unknown	macropterous
Pachybrachius fracticollis		herbivore	oligophagous	macropterous
Peritrechus gracilicornis		herbivore	polyphagous	macropterous
Peritrechus nubilus		herbivore	polyphagous	macropterous
Platyplax salviae		herbivore	monophagous	macropterous
Plinthisus brevipennis		unknown	unknown	brachypterous
Rhyparochromus vulgaris		herbivore	polyphagous	macropterous
Scolopostethus thomsoni		herbivore	monophagous	brachypterous
Spilostethus saxatilis		herbivore	polyphagous	macropterous
Stygnocoris fuligineus		unknown	unknown	macropterous
Miridae				
Acetropis carinata		herbivore	polyphagous	brachypterous
Acetropis longirostris		herbivore	monophagous	brachypterous
Adelphocoris lineolatus		herbivore	polyphagous	macropterous
Adelphocoris quadripunctatus		herbivore	monophagous	macropterous
Adelphocoris seticornis		herbivore	oligophagous	macropterous
Adelphocoris ticinensis		herbivore	polyphagous	macropterous
Agnocoris reclairei	X	herbivore	monophagous	macropterous
Amblytylus nasutus		herbivore	oligophagous	macropterous
Apolygus lucorum		herbivore	polyphagous	macropterous

Table A4 (cont.)

Family Species	**Arboreal lifestyle**	**Feeding guild**	**Host plant specificity of herbivorous bugs**[1]	**Flight ability**[2]
Miridae (cont.)				
Apolygus spinolae		herbivore	monophagous	macropterous
Capsodes gothicus		herbivore	polyphagous	brachypterous
Capsus ater		herbivore	oligophagous	macropterous
Charagochilus gyllenhalii		herbivore	monophagous	macropterous
Charagochilus spiralifer		herbivore	unknown	macropterous
Chlamydatus pulicarius		herbivore	polyphagous	macropterous
Chlamydatus pullus		herbivore	polyphagous	macropterous
Closterotomus norwegicus		herbivore	polyphagous	macropterous
Criocoris crassicornis		herbivore	monophagous	macropterous
Criocoris nigripes		herbivore	monophagous	macropterous
Criocoris sulcicornis		herbivore	monophagous	macropterous
Deraeocoris ruber		predator	-	macropterous
Dicyphus globulifer		herbivore	oligophagous	macropterous
Europiella artemisiae		herbivore	monophagous	macropterous
Globiceps flavomaculatus		omnivore	-	brachypterous
Halticus apterus		herbivore	oligophagous	brachypterous
Harpocera thoracica	X	omnivore	monophagous	macropterous
Isometopus intrusus	X	predator	-	macropterous
Leptopterna dolabrata		herbivore	polyphagous	brachypterous
Liocoris tripustulatus		herbivore	monophagous	macropterous
Lygus pratensis		herbivore	polyphagous	macropterous
Lygus rugulipennis		herbivore	polyphagous	macropterous
Lygus sp.		herbivore	polyphagous	macropterous
Malacocoris chlorizans	X	omnivore	-	macropterous
Megaloceroea recticornis		unknown	unknown	macropterous
Mermitelocerus schmidtii		omnivore	-	macropterous
Notostira elongata		herbivore	polyphagous	macropterous
Notostira sp.		herbivore	polyphagous	macropterous
Orthocephalus vittipennis		herbivore	oligophagous	brachypterous
Orthops basalis		herbivore	oligophagous	macropterous
Orthops sp.		herbivore	oligophagous	macropterous
Orthotylus nassatus	X	omnivore	-	macropterous
Orthotylus sp.		-	-	macropterous
Phytocoris populi	X	predator	-	macropterous
Phytocoris tiliae	X	omnivore	-	macropterous
Plagiognathus arbustorum		herbivore	polyphagous	macropterous
Plagiognathus chrysanthemi		herbivore	polyphagous	macropterous
Polymerus palustris		herbivore	monophagous	macropterous
Polymerus sp.		herbivore	monophagous	macropterous
Polymerus unifasciatus		herbivore	monophagous	macropterous
Polymerus vulneratus		herbivore	monophagous	macropterous
Psallus sp.		-	-	-
Stenodema calcarata		herbivore	polyphagous	macropterous
Stenodema laevigata		herbivore	oligophagous	macropterous
Stenotus binotatus		herbivore	polyphagous	macropterous

Table A4 (cont.)

Family Species	**Arboreal lifestyle**	**Feeding guild**	**Host plant specificity of herbivorous bugs**[1]	**Flight ability**[2]
Miridae (cont.)				
Systellonotus triguttatus		omnivore	-	brachypterous
Trigonotylus caelestialium		herbivore	polyphagous	macropterous
Tytthus pygmaeus		predator	-	macropterous
Nabidae				
Himacerus apterus		predator	-	brachypterous
Himacerus mirmicoides		predator	-	brachypterous
Nabis ferus		predator	-	macropterous
Nabis pseudoferus		predator	-	brachypterous
Nabis punctatus		predator	-	brachypterous
Nabis rugosus		predator	-	brachypterous
Nabis sp.		predator	-	-
Pentatomidae				
Aelia acuminata		herbivore	oligophagous	macropterous
Carpocoris fuscispinus		herbivore	polyphagous	macropterous
Carpocoris purpureipennis		herbivore	polyphagous	macropterous
Dolycoris baccarum		herbivore	polyphagous	macropterous
Eurydema oleracea		herbivore	oligophagous	macropterous
Eysarcoris aeneus		herbivore	polyphagous	macropterous
Eysarcoris ventralis		herbivore	polyphagous	macropterous
Graphosoma lineatum		herbivore	oligophagous	macropterous
Holcostethus vernalis		herbivore	polyphagous	macropterous
Neottiglossa leporina		herbivore	oligophagous	macropterous
Neottiglossa pusilla		herbivore	polyphagous	macropterous
Palomena prasina		herbivore	polyphagous	macropterous
Podops inunctus		herbivore	oligophagous	macropterous
Sciocoris distinctus		herbivore	oligophagous	macropterous
Zicrona caerulea		predator	-	macropterous
Piesmatidae				
Piesma capitatum		herbivore	polyphagous	brachypterous
Reduviidae				
Rhynocoris iracundus		predator	-	macropterous
Rhopalidae				
Corizus hyoscyami		herbivore	polyphagous	macropterous
Myrmus miriformis		herbivore	oligophagous	brachypterous
Rhopalus parumpunctatus		herbivore	polyphagous	macropterous
Rhopalus subrufus		herbivore	polyphagous	macropterous
Stictopleurus punctatonervosus		herbivore	polyphagous	macropterous
Saldidae				
Chartoscirta cincta		predator	-	macropterous
Chartoscirta elegantula		predator	-	macropterous
Saldula saltatoria		predator	-	macropterous
Scutelleridae				
Eurygaster maura		herbivore	polyphagous	macropterous
Eurygaster testudinaria		herbivore	polyphagous	macropterous

Table A4 (cont.)

Family Species	**Arboreal lifestyle**	**Feeding guild**	**Host plant specificity of herbivorous bugs**[1]	**Flight ability**[2]
Tingidae				
Acalypta carinata		herbivore	unknown	macropterous
Agramma confusum		herbivore	oligophagous	macropterous
Dictyla humuli		herbivore	oligophagous	macropterous
Oncochila simplex		herbivore	monophagous	macropterous
Tingis ampliata		herbivore	monophagous	macropterous
Tingis auriculata		herbivore	oligophagous	macropterous
Tingis reticulata		Herbivore	polyphagous	macropterous

[1] Herbivorous bugs were classified as monophagous (feeding on only one plant genus), oligophagous (feeding on only one plant family) or polyphagous (sources: Wagner 1952, 1966, 1967; Bantock & Botting 2010; Strauß 2011)
[2] Species which are generally flightless or have morphs with partly reduced wings, which were recorded during our surveys, were defined as brachypterous

Lebenslauf

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