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**„Effects of floodplain dynamics on richness,
abundance, composition and functional diversity of
grasshopper assemblages in the Donau-Auen
National Park (Austria)“**

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Effects of floodplain dynamics on richness, abundance, composition and functional diversity of grasshopper assemblages in the Donau-Auen National Park (Austria)

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Abstract

Flooding events are an important factor shaping arthropod communities on riverine meadows. We investigated to what extent species richness, abundance, species composition and functional diversity of grasshopper assemblages on meadows in the Donau-Auen National Park (Lower Austria) are affected by annual floods. Grasshoppers were sampled between June and September 2012 on 12 meadows prone to yearly summer inundations, and 13 meadows protected from such floods by a levee. All acoustically and visually detected individuals were counted. Excluding one stray species not associated to meadows and representatives of the genus *Tetrix*, which could not be recorded reliably with our sampling method, a total of 24 grasshopper species were recorded. Grasshopper abundance was negatively affected by flooding. Species richness was nearly identical on both meadow types. However, species composition differed prominently between regularly flooded and non-flooded meadows. While the relative abundance of xerophilous species was higher on non-flooded meadows, in hygrophilous species and grasshoppers with indifferent habitat preferences no significant differences were found. Further, flooding did not prove to affect functional diversity. This study shows that natural floodplain dynamics still have a high and significant impact on grasshopper assemblages of meadows in the Donau-Auen National Park. The perpetuation of high hydrological dynamics, like annual floodings, is a precondition to maintain the existing grasshopper fauna and to provide habitats for regionally threatened hygrophilous species.

Keywords: grasshoppers, Caelifera, Ensifera, species richness, abundance, species composition, habitat preferences, functional diversity, Donau-Auen National Park, floodplain meadows

Zusammenfassung

Überflutungen von an Flüssen gelegenen Wiesen sind ein wichtiger Faktor, der die Arthropoden-Gesellschaften formt beziehungsweise stark beeinflusst. Wir untersuchten in welchem Ausmaß Heuschrecken-Gesellschaften im Nationalpark Donau-Auen (Niederösterreich) durch jährliche Überschwemmungen, im Bezug auf Artenreichtum, Abundanz, Artenzusammensetzung und funktioneller Diversität beeinflusst werden. Heuschrecken wurden von Juni bis September 2012 auf 12 jährlich überfluteten und 13 vor Überflutungen durch einen Damm geschützten Wiesen untersucht. Alle akustisch und visuell bestimmten Individuen wurden gezählt. Ohne Berücksichtigung einer Heuschrecken-Art, die nicht typisch für Wiesenflächen ist und auch nur mit einem Individuum vertreten war und aller Individuen der Gattung *Tetrix*, die mit unserer Aufnahmemethode nicht ausreichend erfasst werden konnten, konnten 24 Heuschrecken-Arten nachgewiesen werden. Überflutung hatte einen negativen Einfluss auf die Abundanz von Heuschrecken. Der Artenreichtum war hingegen auf den beiden Wiesenflächentypen fast identisch. Die Artenzusammensetzung jedoch unterschied sich deutlich zwischen überfluteten und nicht-überfluteten Wiesenflächen. Während xerophile Arten signifikant höhere relative Abundanzen auf nicht-überfluteten Wiesenflächen zeigten, konnte für hygrophile Arten und Heuschrecken mit keinen deutlichen Habitatpräferenzen kein signifikanter Unterschied festgestellt werden. Weiterhin zeigten sich keine absicherbaren Auswirkungen von Überflutungen auf die funktionelle Diversität. Diese Untersuchung zeigt, dass die natürliche Überschwemmungsdynamik einen deutlichen Einfluss auf die Heuschrecken-Gesellschaften im Nationalpark Donau-Auen hat. Das Aufrechterhalten einer hohen hydrologischen Dynamik ist eine Voraussetzung dafür, dass die existierende Heuschrecken-Fauna und Habitate für regional bedrohte hygrophile Arten erhalten bleiben.

Schlüsselwörter: Heuschrecken, Caelifera, Ensifera, Artenreichtum, Abundanz, Artenzusammensetzung, Habitatpräferenzen, funktionelle Diversität, Nationalpark Donau-Auen, Überschwemmungswiesen

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Introduction

The community structure of aquatic and terrestrial plant and animal communities of floodplain ecosystems is shaped by hydrological dynamics (Ballinger et al. 2005, van Diggelen et al. 2006, Reckendorfer et al. 2006; but: Truxa & Fiedler 2012). In the present study, conducted in one of Europe's largest remaining floodplain ecosystems located in the Donau-Auen National Park (Lower Austria, east of Vienna), we analyzed to what extent grasshopper communities on meadows prone to summer inundations differ from those on meadows that are no longer subject to natural river dynamics. So far, effects of flood events on richness and composition of grasshopper communities have been only rarely investigated (Fischer & Witsack 2009, Dziock et al. 2011; cf. Demetz et al. 2013).

Grasshoppers have high conservation relevance because a substantial fraction of species is highly bonded to specific habitats and is reacting sensitively to environmental changes. Hence, they are frequently used as "bioindicators" (Reich 1991, Gerlach et al. 2013, Bazelet & Samways 2012). In this study, we addressed the following questions:

(1) *Is species richness of grasshopper assemblages on floodplain meadows shaped by vegetation structure and flooding events?*

We expect that regularly flooded meadows show a lower species richness than non-flooded meadows, because flooding events represent a severe disturbance negatively affecting a substantial fraction of grasshopper species. Species with lower active dispersal ability have a higher risk to drown in the flood and the moment of egg laying plays a major role in surviving flooding events too. Most eggs are highly resistant to flooding, even over longer periods (Ingrisch & Köhler 1998, Fischer & Witsack 2009). However, effects of flooding on species richness can vary depending on the studied taxonomic group. While richness of moth assemblages appears to remain unaffected by flooding (Truxa & Fiedler 2012), inundation events proved to have a strong negative impact on species richness of ants in floodplain forests (Ballinger et al. 2007) and leafhoppers on meadows (Rothenbücher & Schaefer 2005).

(2) *Is species composition of grasshopper assemblages on floodplain meadows shaped by vegetation structure and flooding events?*

We expect a different species composition of grasshopper assemblages at flooded meadows, because the plant species composition would be different on regularly flooded meadows.

Schaffers et al. (2008) discovered that local plant species composition is the most effective predictor of arthropod assemblage composition also investigating grasshoppers. Furthermore there is a filtering of species due to flooding events. Some species are more likely to survive floods because of higher active and/or passive (egg deposition in plants or under tree bark) dispersal ability. Species communities seem to have been filtered in two complimentary strategies: (1) the high active dispersal – low reproduction strategy in intensive land use situations and (2) the high passive dispersal – high reproduction strategy in areas with high flood disturbance. Passive dispersal implies a high reproduction rate, because many individuals could be transported by chance to unfavourable habitats. Species known to show passive dispersal are *Conocephalus* spp., *Metrioptera roeselii*, *Leptophyes albobittata*, *Chrysochraon dispar* and *Pholidoptera griseoaptera*. A high active dispersal ability to recolonise mown areas has been demonstrated for *Chorthippus parallelus* and *C. mollis* (Dziöck et al. 2011).

(3) *Are regularly flooded meadows characterized by hygrophilous and non-flooded meadows by xerophilous grasshopper species?*

We expect that there will be more hygrophilous species on regularly flooded meadows and more xerophilous species on non-flooded meadows. Lots of grasshopper species are highly bonded to specific habitats and are reacting sensitively to changes in their environment underlining their value as bioindicators. *Calliptamus italicus* for example is only found on very dry habitats, *Stethophyma grossum* in contrast is strictly bonded to wet habitats (Baur et al. 2006) and their eggs need “contact-water” to develop (Marzelli 1997).

(4) *Are there any effects according to the flooding regime on functional diversity?*

We expect that functional diversity declines from non-flooded towards flooded meadows as shown for ground beetle communities facing increasing disturbance intensities in periodically flooded grasslands along the Elbe River in Germany (Gerisch et al. 2012). Disturbance acts as a filter causing non-random local extinctions of species whose functional traits are not suitable to cope with inundations. Body size, overwintering strategy and wing morphology are critical for ground beetles to cope with floodplain dynamics, because these traits can serve as proxies for high mobility and rapid development and consequently favour population recovery after flood events. Ground beetle species showed relatively little functional differences on highly disturbed sites. Specialist species seem to be more affected by habitat disturbance than generalist species (Gerisch et al. 2012). According to grasshoppers, we can expect that

functional groups, like hygrophilous species, will be missing on non-flooded meadows and xerophilous species will be absent on regularly flooded meadows. The generalist species and species with high dispersal abilities should appear on both types of meadows.

Methods

Study area

The Donau-Auen National Park, a Riverine Wetlands National Park (IUCN Category II, 1997), ranges from the capitals Vienna to Bratislava and has a total area of 9,300 hectares. A total of 65% of the area is riparian forest, 15% are meadows and about 20% is covered by different water bodies. It represents the last remaining major floodplain ecosystem in Central Europe with the Danube still largely free flowing at a length of 36 km. The National Park is still influenced by the dynamics of the river Danube due to water level fluctuations of up to 7 m amplitude throughout the year, which cause periodic and stochastic overbank flows (water level fluctuations of the year 2012 can be seen in Annex 1). Due to the snowmelt in the Alps periodic floods occur from late spring to high summer. Aperiodic floods can be caused by heavy rainfall (Nationalpark Donau-Auen 2013). The river-floodplain system of the national park has been constrained due to major river regulation measures since 1875 (Reckendorfer et al. 2006).

This study was conducted in the Donau-Auen National Park north of the river Danube between the villages Mannsdorf an der Donau and Bad Deutsch Altenburg (Fig. 1).

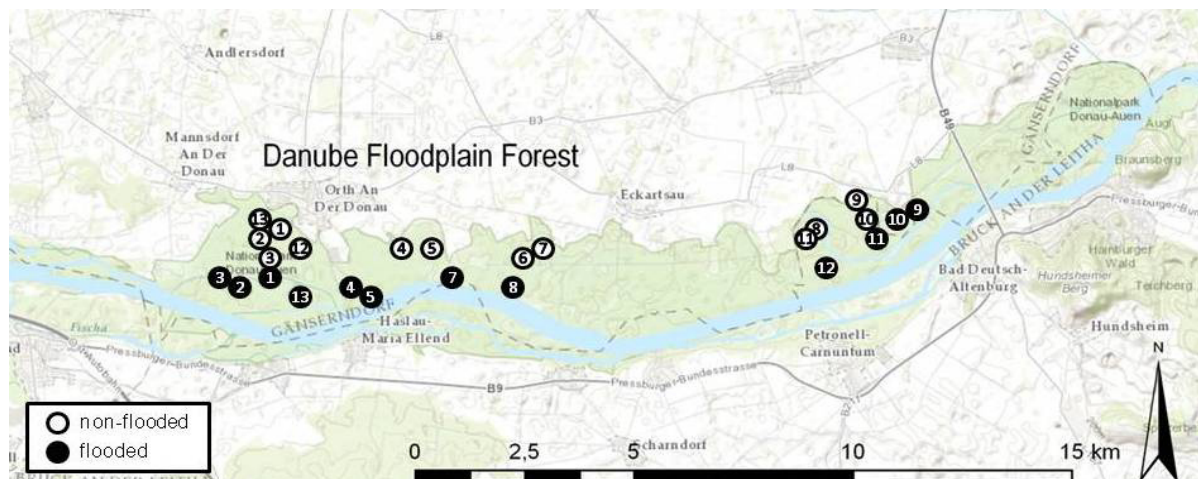


Figure 1. Map of the study area indicating sampled regularly flooded and non-flooded meadows.

The study area is divided by a levee (“Marchfeld-Schutzdamm”) which protects the area situated to the north against flooding during periods of high water level. In contrast, meadows south of the levee are still flooded almost every year. Twelve meadows were selected south of the levee, and 13 meadows north of it (Fig. 1). Mean size (\pm SD) of the selected meadows was 2.97 ± 1.54 ha (north of the levee) and 2.67 ± 1.61 ha (south), respectively, and did not differ significantly (t-test: $t = 0.46$, $p = 0.648$) between both groups of meadows (Tab. 1) (cf. Demetz et al. 2013).

Table 1. Data of selected meadows.

Flooding regime	Meadow code	Coordinates		Meadow size [ha]
		latitude	longitude	
non-flooded	1	48° 8.50'N	16° 41.47'E	1.29
	2	48° 8.37'N	16° 41.31'E	1.45
	3	48° 8.20'N	16° 41.39'E	2.04
	4	48° 8.17'N	16° 43.54'E	4.30
	5	48° 8.22'N	16° 44.23'E	4.14
	6	48° 8.13'N	16° 45.93'E	3.10
	7	48° 8.25'N	16° 46.21'E	5.04
	8	48° 8.54'N	16° 51.34'E	2.53
	9	48° 8.68'N	16° 52.05'E	3.80
	10	48° 8.54'N	16° 52.15'E	0.98
	11	48° 8.41'N	16° 51.02'E	5.74
	12	48° 8.28'N	16° 41.74'E	2.78
	13	48° 8.62'N	16° 41.15'E	1.37
flooded	1	48° 7.88'N	16° 41.33'E	1.09
	2	48° 7.79'N	16° 40.74'E	4.99
	3	48° 7.88'N	16° 40.48'E	4.78
	4	48° 7.77'N	16° 42.81'E	3.31
	5	48° 7.60'N	16° 43.06'E	1.58
	7	48° 7.80'N	16° 44.62'E	3.88
	8	48° 7.73'N	16° 45.82'E	5.08
	9	48° 8.68'N	16° 53.29'E	1.99
	10	48° 8.58'N	16° 53.02'E	1.50
	11	48° 8.34'N	16° 52.30'E	1.35
	12	48° 7.99'N	16° 51.71'E	1.28
	13	48° 7.67'N	16° 41.97'E	1.27

Grasshopper sampling

On each meadow grasshoppers were sampled once during each of the five sampling rounds: 18-22 June (sampling round A), 2-6 July (B), 23-27 July (C), 2-6 August (D) and 10-17 September 2012 (E). During sampling rounds A and C, grasshoppers were surveyed visually and acoustically for 15-30 minutes depending on meadow size by 4 recorders who walked the entire meadow area in a zig-zag like pattern. During the other three sampling rounds Agnes Demetz counted all visually and acoustically detected grasshoppers along transects (50 m transect length per ha meadow area). All visually detected grasshoppers were caught for identification with a sweep net. Identification was facilitated by available field guides (Bellmann 2006, Baur et al. 2006) and song recordings (Roesti & Keist 2009). In our analyses *Phaneroptera falcata* (one single recorded nymph), which is not associated with meadows (Zuna-Kratky et al. 2009), and all *Tetrix*-species which cannot be reliably surveyed with our sampling method because they are very small (mean body length between 8-15mm) and their mating sounds are very inconspicuous (Baur et al. 2006), were excluded (cf. Demetz et al. 2013).

Furthermore the following data was recorded for every meadow survey: beginning and ending time of the survey, cloudiness (eighth-scale), wind (Beaufort), maximum vegetation height (estimated in cm), dominance of grasses in comparison to herbs (1: only grasses to 5: only herbs) and mowing status (unmown, recently mown, mown a few days ago or mown a few weeks ago).

Data on plant species richness was provided for every investigated meadow by the ÖBf (“Österreichische Bundesforste”).

Data analysis

To compare species richness of grasshopper assemblages among flooded and non-flooded meadows randomized sample-based species accumulation curves were calculated and extrapolated to 30 samples using the software EstimateS (Colwell 2013). Furthermore a generalized linear model (GLM) testing for effects of flooding, mowing, dominance of grasses, vegetation height and plants species richness on species richness of grasshoppers and the abundance of grasshoppers per 10 m transect was calculated with the program STATISTICA vers. 7.1. Abundance of grasshoppers was calculated only with the data collected by Agnes Demetz, because of the different sampling methods.

To assess effects of flooding on species composition, abundance data from all five survey periods were pooled. Similarities between species assemblages were then quantified by Bray-Curtis similarities (calculated using square-root transformed abundances) for all combinations of meadows. Similarity relationships between grasshopper assemblages of sampled meadows were visualized in a non-metric dimensional scaling (NMDS) ordination (Clarke 1993). To test for differences in species composition of grasshopper assemblages between flooded and non-flooded meadows, an analysis of similarity (ANOSIM; with 999 permutations) was calculated with the program Primer (Clarke & Gorley 2001).

To test for effects of flooding on species groups with different habitat preferences, we calculated the relative abundance of hygrophilous, indifferent and xerophilous species on flooded and non-flooded meadows and applied tests using the software STATISTICA vers. 7.1..

Classification of species according to their habitat preferences was based on the information provided by Zuna-Kratky et al. (2009). The Red List status in Austria was extracted from Berg et al. (2005) (cf. Demetz et al. 2013) (Tab. 2).

Table 2. Classification of habitat preferences of recorded grasshopper species (according to Zuna-Kratky et al. 2009) and their Red List status in Austria (RL Austria) (Berg et al. 2005) (cf. Demetz et al. 2013).

Habitat preferences	Species	RL Austria
hygrophilous	<i>Chorthippus albomarginatus</i>	NT
	<i>Chrysochraon dispar</i>	NT
	<i>Mecostethus parapleurus</i>	NT
	<i>Ruspolia nitidula</i>	NT
	<i>Stethophyma grossum</i>	VU
xerophilous	<i>Calliptamus italicus</i>	VU
	<i>Chorthippus apricarius</i>	
	<i>Chorthippus biguttulus</i>	
	<i>Chorthippus brunneus</i>	
	<i>Euchorthippus declivus</i>	
	<i>Gryllus campestris</i>	
	<i>Leptophyes albobittata</i>	NT
	<i>Metrioptera bicolor</i>	NT
	<i>Omocestus haemorrhoidalis</i>	VU
	<i>Platycleis albopunctata grisea</i>	NT
	<i>Stenobothrus lineatus</i>	
indifferent	<i>Chorthippus dorsatus</i>	
	<i>Chorthippus mollis</i>	NT
	<i>Chorthippus parallelus</i>	
	<i>Conocephalus fuscus</i>	NT
	<i>Euthystira brachyptera</i>	
	<i>Metrioptera roeselii</i>	
	<i>Pholidoptera griseoaptera</i>	
	<i>Tettigonia viridissima</i>	

To evaluate if species respond differentially to the meadow parameters flooding, mowing status, plant species richness, maximum vegetation height and dominance of grasses, a canonical correspondence analysis was calculated with the program CANOCO. For this analysis, only the samplings by Agnes Demetz were used. Because of the different sampling methods, it was only possible to calculate the maximum abundance per 10 m transect using this data. The species *Leptophyes albobittata* and *Gryllus campestris* were excluded due to extremely low abundances.

To test for differences in abundance (maximum number of individuals per 10 m transect counted during one of the three transect surveys) and occurrence frequency of individual grasshopper species between flooded and non-flooded meadows Mann-Whitney U-tests and Fisher's exact tests were calculated, respectively, only including species which were recorded on at least three meadows.

Functional diversity (FD) measures were calculated in R and analyzed with the package "FD" (Laliberté & Legendre 2010). For this analysis the following functional traits were used: habitat preferences, feeding guilds, mean body length, dispersal ability, number of ovarioles and the location of oviposition (Annex 2). The habitat preferences were classified based on the information provided by Zuna-Kratky et al. (2009). The information on feeding guild affiliation, mean body length and used oviposition sites was extracted from Baur et al. (2006). Dispersal ability was classified as (1) low or moderate and (2) high according to Reinhardt et al. (2005). We considered *Euchorthippus declivus* and *Ruspolia nitidula* to have high dispersal ability. According to Baur et al. (2006) *Euchorthippus declivus* behaves equal to *Chorthippus* spp. and *Ruspolia nitidula* is a very agile species with the ability to fly. Numbers of ovarioles (provided in Reinhardt et al. 2005) were grouped into three classes: few (< 20 ovarioles), intermediate (21 - 35 ovarioles) and many (> 35 ovarioles).

We calculated the following FD measures: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). FRic estimates the dispersion of species in trait space by building a convex hull volume that includes all species, FEve measures the evenness of niche occupation or regularity of species abundances within the hull volume and FDiv describes the divergence of abundances of species within this volume (Laliberté & Legendre 2010).

Results

Species richness and abundance

A total of 24 grasshopper species (excluding *Phaneroptera falcata* and *Tetrix*-species) were recorded (Table 2): 22 species on flood-prone and non-flooded meadows, respectively. A GLM testing for effects of flooding, mowing, dominance of grasses, vegetation height and plants species richness on species richness of grasshoppers did not achieve a significant level ($r_{\text{multiple}} = 0.535$, $r^2_{\text{multiple}} = 0.286$, $F_{5,18} = 1.44$, $p = 0.2574$). In contrast, the GLM testing for effects on abundance achieved a significant level ($r_{\text{multiple}} = 0.727$, $r^2_{\text{multiple}} = 0.529$, $F_{5,18} = 4.04$, $p = 0.0124$). However, only flooding regime proved to significantly affect grasshopper abundance (Table 3). The abundance of grasshoppers per 10 m transect was higher on non-flooded, than flooded meadows (Fig. 2). Species accumulation curves calculated for regularly flooded and non-flooded meadows also indicate near identical species richness (Fig. 3) (cf. Demetz et al. 2013).

Table 3. Results of a GLM testing for effects of mowing, flooding regime, dominance of grasses, maximum vegetation height and plant species richness on grasshopper abundance. Only the flooding regime significantly affected grasshopper abundance.

Effect	SS	df	MQ	F	P
Constant	118.35	1	118.35	6.77	0.01806
Mowing	67.21	1	67.21	3.84	0.06565
Flooding regime	269.64	1	269.64	15.41	0.00099
Dominance grasses	0.51	1	0.51	0.03	0.86666
Max. vegetation height	21.45	1	21.45	1.23	0.28278
Plant species richness	4.54	1	4.54	0.26	0.61659
Error	314.89	18	17.49		

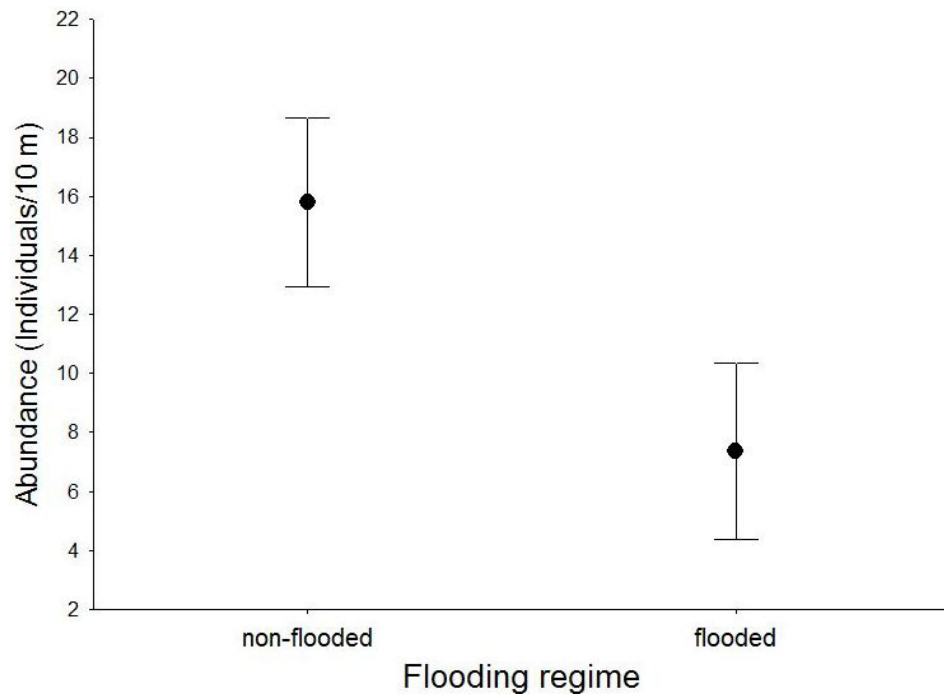


Figure 2. Mean abundance of grasshoppers on flooded and non-flooded meadows.

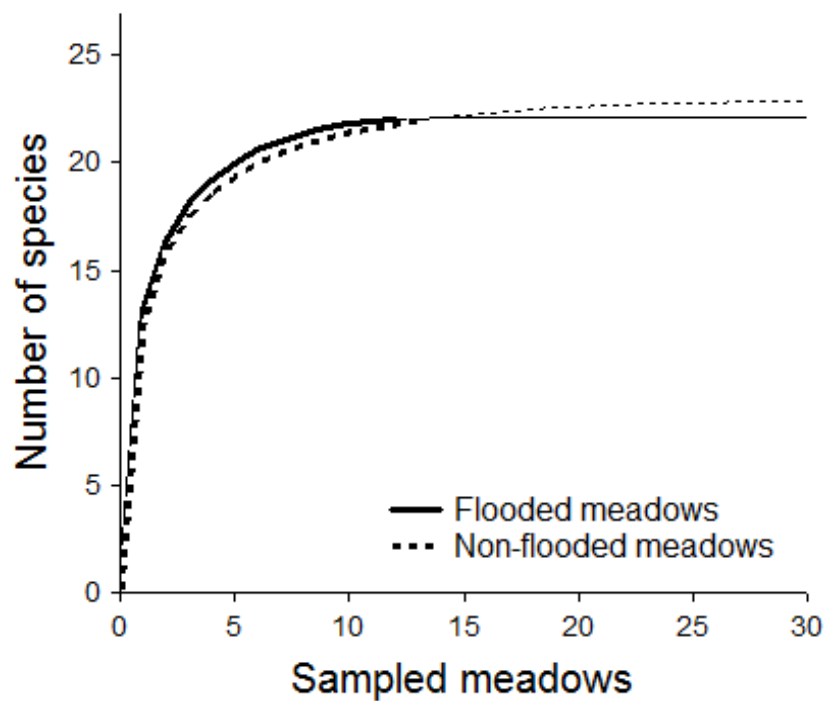


Figure 3. Species accumulation curves for grasshopper assemblages on flooded and non-flooded meadows extrapolated (thin lines) to 30 samples.

Species composition

A two-way analysis of similarity (ANOSIM) indicates a significant effect of flooding (Global $R = 0.251$, $p = 0.009$) but not of mowing (Global $R = -0.151$, $p = 0.951$) on species composition. Distinct grasshopper assemblages on meadow types with different flooding regime were also indicated by the NMDS (non-metric multidimensional scaling) ordination based on Bray-Curtis similarities. Grasshopper assemblages of flooded meadows aggregate in the left half, those of non-flooded meadows in the right half of the ordination plot (Fig. 4). Dimension 1 values correlated with plant species richness ($r = 0.62$, $p = 0.0014$). No significant correlations existed between the two dimensions and dominance of grasses and maximum vegetation height, respectively.

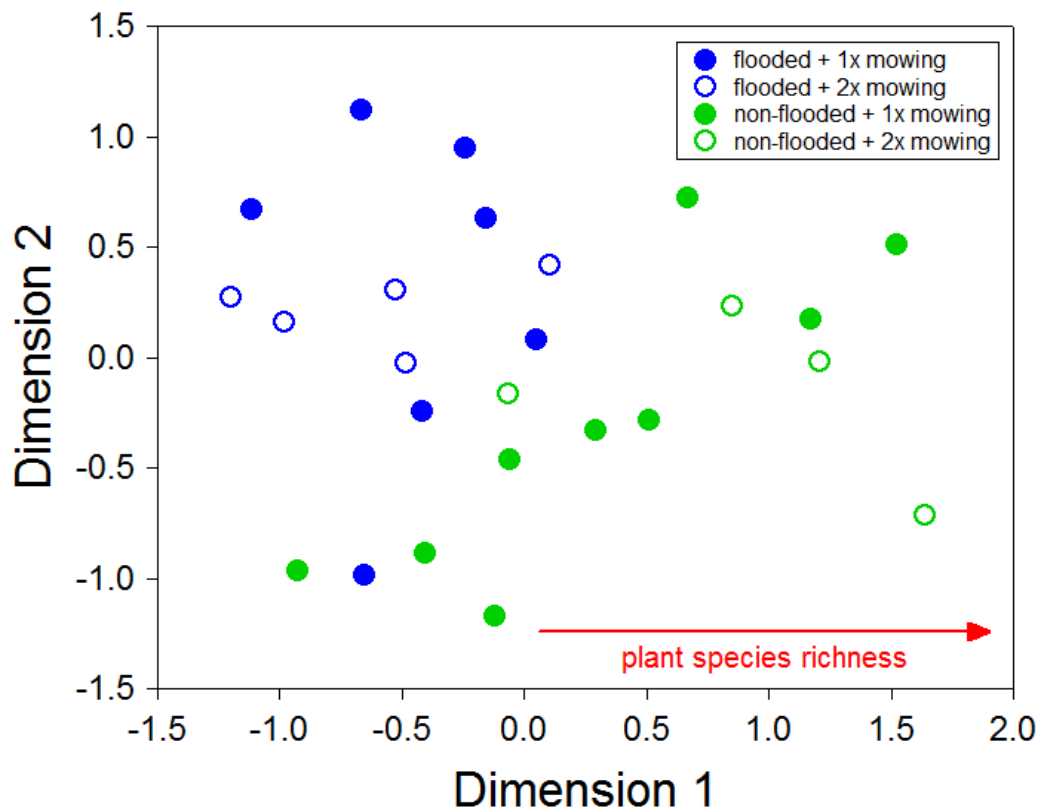


Figure 4. NMDS ordination (based on Bray-Curtis similarities) visualising similarity relationships of grasshopper assemblage composition recorded on flooded and non-flooded meadows with different mowing frequency. Dimension 1 values are correlated with plant species richness of meadows ($r = 0.62$, $p = 0.0014$) (cf. Demetz et al. 2013).

Effects on species with different habitat preferences

While relative abundances of hygrophilous and indifferent grasshopper species did not differ significantly between flooded and non-flooded meadows (Fig. 5a-b), the relative abundance of xerophilous species was higher on non-flooded meadows (Fig. 5c).

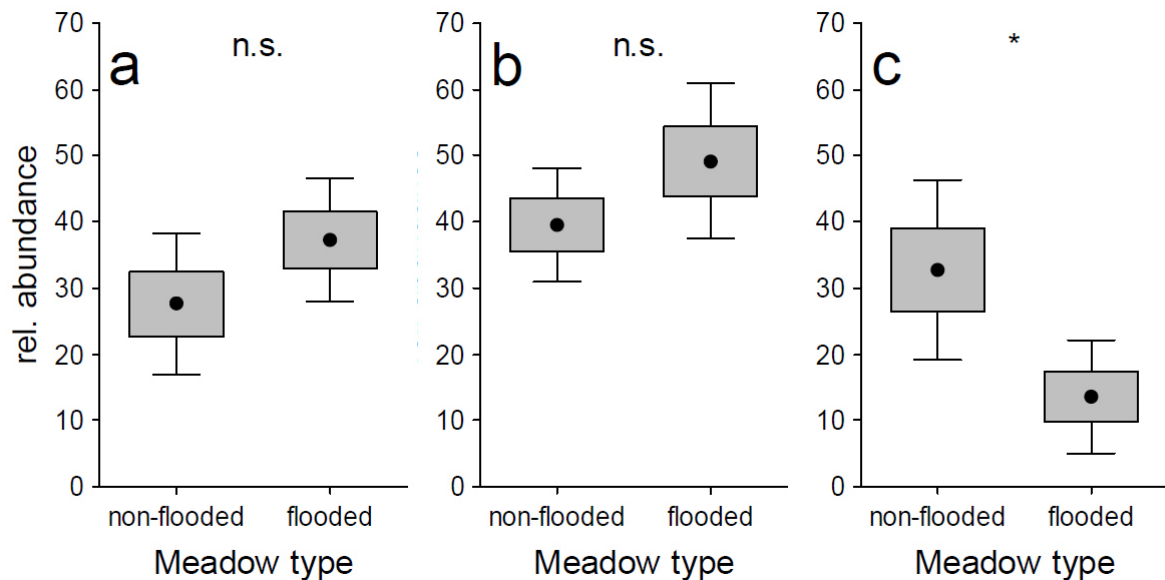


Figure 5. Mean relative abundance \pm SE (box) and 95% CI (whiskers) of (a) hygrophilous, (b) indifferent and (c) xerophilous species on flooded and non-flooded meadows. Results of t-tests: n.s. – non-significant, * – $p < 0.05$.

The canonical correspondence analysis (Fig. 6) with the dependent variable maximum abundance per 10 m transect and the independent variables maximum vegetation height, flooding regime, mowing regime, dominance of grasses and plant species richness as vectors indicate a particularly strong effect of flooding. While abundances of several species such as *Metrioptera roeselii*, *Tettigonia viridissima* and *Ruspolia nitidula* were positively influenced by flooding, others such several *Chorthippus*-species and *Calliptamus italicus* appeared to respond negatively. For other species the ordination provides evidence for an impact of mowing on abundances. For example, *Stethophyma grossum* appeared to respond positively to an increased mowing frequency, *Mecostethus parapleurus* and *Chorthippus mollis* were negatively affected. The dominance of grasses seemed to be an important factor for predicting the abundance of *Omocestus haemorrhoidalis*.

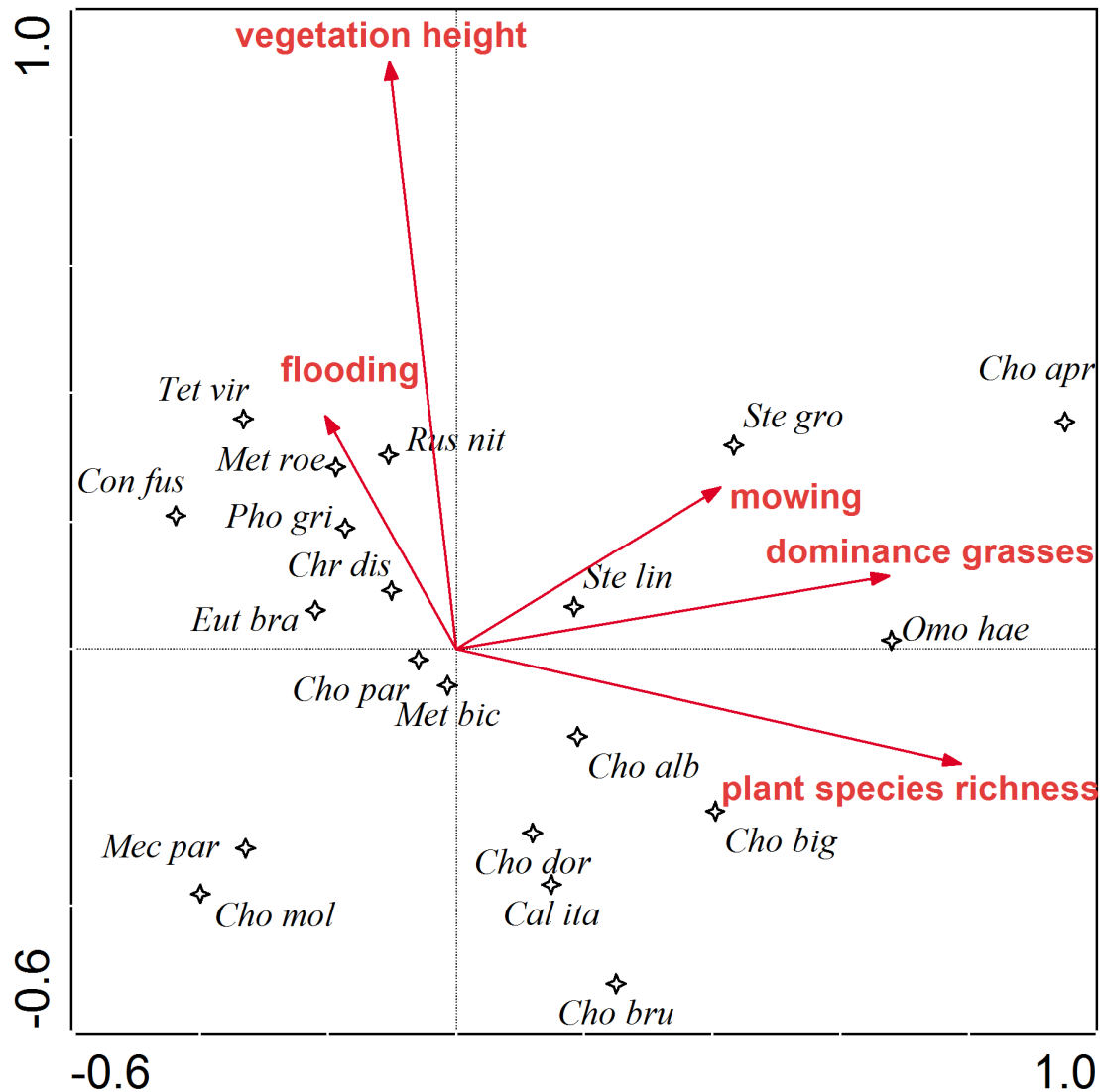


Figure 6. CCA ordination with habitat variables (maximum vegetation height, flooding regime, mowing regime, dominance of grasses and plant species richness) as vectors and all grasshopper species recorded by Agnes Demetz (excluding the rare species *Leptophyes albobittata* and *Gryllus campestris*) as points. The dependent variable was the maximum abundance per 10m transect of the grasshopper species. (*Cal ita* = *Calliptamus italicus*, *Cho alb* = *Chorthippus albomarginatus*, *Cho apr* = *Chorthippus apricarius*, *Cho big* = *Chorthippus biguttulus*, *Cho bru* = *Chorthippus brunneus*, *Cho dor* = *Chorthippus dorsatus*, *Cho mol* = *Chorthippus mollis*, *Cho par* = *Chorthippus parallelus*, *Chr dis* = *Chrysochraon dispar*, *Con fus* = *Conocephalus fuscus*, *Eut bra* = *Euthystira brachyptera*, *Mec par* = *Mecostethus parapleurus*, *Met bic* = *Metrioptera bicolor*, *Met roe* = *Metrioptera roeselii*, *Omo hae* = *Omocestus haemorrhoidalis*, *Pho gri* = *Pholidoptera griseoptera*, *Rus nit* = *Ruspolia nitidula*, *Ste gro* = *Stethophyma grossum*, *Ste lin* = *Stenobothrus lineatus*, *Tet vir* = *Tettigonia viridissima*)

Abundances of individual grasshopper species differed significantly between flooded and non-flooded meadows only in *Chorthippus dorsatus*, *Metrioptera bicolor* and *Stenobothrus lineatus*. All three species proved to have higher abundances on non-flooded meadows. Occurrence frequency of *Metrioptera bicolor* was significantly higher at non-flooded meadows. Only two species, *Conocephalus fuscus* and *Stethophyma grossum*, appeared to

occur with higher abundances and higher occurrence frequency at flooded meadows. However, differences did not achieve a significant level (Tab. 4).

Table 4. Differences in abundance (maximum number of individuals per 10 m transect) and occurrence frequency of different grasshopper species between flooded and non-flooded meadows, tested with Mann-Whitney U-test and Fisher's exact test, respectively. Species found on less than three meadows were excluded. * indicates significant differences.

Species	Results of U-tests		Higher abundance at	Fisher's exact <i>p</i>	Higher occurrence frequency at
	<i>U</i>	<i>P</i>			
<i>Chorthippus albomarginatus</i>	61	0.3338	-	0.4296	-
<i>Chorthippus biguttulus</i>	66.5	0.5072	-	0.5821	-
<i>Chorthippus brunneus</i>	77	0.951	-	0.5959	-
<i>Chorthippus dorsatus</i>	41	0.0353 *	non-flooded	0.1628	-
<i>Chorthippus mollis</i>	64.5	0.3752	-	0.3867	-
<i>Chorthippus parallelus</i>	43	0.0567	-	0.48	-
<i>Chrysochraon dispar</i>	63.5	0.4301	-	1	-
<i>Conocephalus fuscus</i>	50	0.0659	(flooded)	0.0766	(flooded)
<i>Euthystira brachyptera</i>	77	0.9321	-	0.6722	-
<i>Mecostethus parapleurus</i>	74.5	0.8454	-	0.56	-
<i>Metrioptera bicolor</i>	17	0.0007 *	non-flooded	0.0005 *	non-flooded
<i>Metrioptera roeselii</i>	75	0.8703	-	0.5313	-
<i>Omocestus haemorrhoidalis</i>	68.5	0.5141	-	0.5503	-
<i>Pholidoptera griseoaptera</i>	72	0.5633	-	0.4687	-
<i>Ruspolia nitidula</i>	50.5	0.1283	-	0.3867	-
<i>Stenobothrus lineatus</i>	29.5	0.0083 *	non-flooded	0.74	-
<i>Stethophyma grossum</i>	58.5	0.0603	(flooded)	0.0957	(flooded)
<i>Tettigonia viridissima</i>	64	0.3742	-	0.1628	-

Functional diversity

GLMs testing for effects of meadow variables on functional diversity measures did not indicate any significant effects (FRic: $r_{\text{mult.}} = 0.41$, $r^2_{\text{mult.}} = 0.17$, $F = 0.76$, $p = 0.5867$; FEve: $r_{\text{mult.}} = 0.54$, $r^2_{\text{mult.}} = 0.29$, $F = 1.58$, $p = 0.2136$; FDiv: $r_{\text{mult.}} = 0.53$, $r^2_{\text{mult.}} = 0.28$, $F = 1.51$, $p = 0.2329$).

Discussion

Species richness and abundance

Regular flood events did not prove to affect species richness of grasshopper assemblages on meadows in the Donau-Auen National Park. The high active or passive dispersal ability of 50% of all recorded grasshopper species may be one important reason. Only *Chorthippus apricarius* and *Platycleis albopunctata grisea* appeared exclusively on non-flooded meadows, *Euchorthippus declivus* and *Stethophyma grossum* exclusively on flooded meadows (Annex 3). However, these four species were very rare in our survey. They appeared only at one to four different meadows and the total number of individuals of each species ranged from two to eight. They were found on five flooded and non-flooded meadows respectively (cf. Demetz et al. 2013).

Fischer & Witsack (2009) also showed that there are high similarities between grasshopper assemblages on flooded and non-flooded meadows of the Elbe floodplains (Germany) according to dominance and abundance of species (cf. Demetz et al. 2013). Gratzner et al. (2013) discovered a decline in bug species (Heteroptera) richness with increasing inundation period on the Morava River floodplains. In the Donau-Auen National Park a study on butterflies showed higher species richness on non-flooded meadows (Fies 2014). In contradiction, moth assemblages sampled at floodplain forest sites appeared to be relative resistant to flooding (Truxa & Fiedler 2012). A negative effect of flooding was found on species richness of ants (Ballinger et al. 2007) and most leafhopper species were observed by Rothenbücher and Schaefer (2005) in sites that were not flooded; sites with medium flood intensities had the lowest species richness.

A slightly positive effect of flooding on species richness was found by Truxa & Fiedler (2012), but the inundations had negative impacts on ground-layer species. Arboreal moths

were less affected. Species richness of terrestrial beetles increased with duration of inundation in floodplain forests in south-eastern Australia (Ballinger et al. 2005).

To summarize, flooding has a high impact on the species richness of predominantly ground-dwelling insects (e.g. ants) and insects of the herb layer (e.g. bugs, butterflies, leafhoppers, grasshoppers). The species richness normally tends to be lower on flooded sites than on non-flooded.

The abundance of grasshoppers per 10 m transect was higher on non-flooded than flooded meadows. Considering that vegetation variables (dominance of grasses, plant species richness and vegetation height) were not related to abundance difference between our surveyed meadows, flooding appeared to have the major impact on grasshopper abundance. Most likely, a large number of grasshoppers drown in the flood. The only way to survive a flooding event is in the egg-phase or by flying away (macropterous species). Although macropterous species can repopulate areas after a flood event, this apparently cannot compensate for the increased mortality during flooding events. Overlapping egg-generations are necessary for grasshopper populations to survive (Fischer & Witsack 2009). In 2012 there was a flooding event in the middle of June (Annex 1), which could have had a big influence on the grasshopper species, because most of the species are in the last larval stage at this time. Grasshopper larvae have the least chance of surviving a flood, because they are not able to escape the inundation by flight. Also a study on bugs recorded a negative effect of flooding on abundance (Gratzer et al. 2013).

Species composition

While inundation did not prove to affect species richness in our study, it had a strong effect on the composition of grasshopper species assemblages. While several hygrophilous species achieved a higher abundance or were even exclusively recorded on regularly flooded meadows, some xerophilous species showed a reverse response to flooding. Fischer & Witsack (2009) didn't find differences in species composition of grasshoppers between flooded and non-flooded meadows in the Elbe floodplains. In contrast to our study area, where flood events typically occur in early summer, the Elbe floodplains are usually flooded in spring, when the majority of grasshopper larvae still have not hatched from the eggs. The egg phase is the only life-history stage for most grasshoppers to survive flood events (Fischer

& Witsack 2009). Hence, summer floods as typical for the Danube floodplains have a much higher potential in shaping the composition of grasshopper assemblages, resulting in a higher prevalence of hygrophilous species on flooded meadows (cf. Demetz et al. 2013).

Also Truxa & Fiedler (2012) and Fies (2014) found different species compositions in moths and butterflies on the floodplain forest sites (Truxa & Fiedler 2012) and meadows (Fies 2014) of the Donau-Auen National Park respectively. Gratzner (2013) found the species composition of bugs in the Morawa floodplains significantly affected by flooding too.

Thus, flooding (summer inundations) seems to have a high impact on species composition of different insect groups.

Habitat preferences of species

While the relative abundance of hygrophilous grasshoppers and species without pronounced habitat preferences did not prove to differ between flooded and non-flooded meadows, xerophilous species were negatively affected by inundation.

That might be, because flooded meadows cannot be dry enough for these xerophilous species. Van Wingerden et al. (1991) found differences in the duration of postdiapause development (PDD) of grasshoppers, which takes place in spring until hatch, according to the temperature and humidity of the habitats. In humid habitats the PDD was shorter and in dry habitats longer. The microclimate differed between wet and dry sites. Wet sites were colder than dry ones and xerophilous species showed longer PDDs than hygrophilous species. The maximum temperature in the egg environment is a selective factor in habitat determination (van Wingerden et al. 1991). Hygrophilous species were found more often at flooded meadows, but the result was not significant. That leads us back to Fischer & Witsack (2009), who found out, that grasshopper species were more connected to the type of meadow, than to the flooding regime. In our study the flooding regime seems to play a role according to habitat preferences of grasshoppers, although some non-flooded meadows can be affected by rising ground water and wet and dry habitats can be found on both types of meadows.

Chorthippus dorsatus, *Metrioptera bicolor* and *Stenobothrus lineatus* were more abundant on non-flooded meadows, *Conocephalus fuscus* and *Stethophyma grossum* achieved higher

abundances on flooded meadows. According to Zuna-Kratky et al. (2009) *Chorthippus dorsatus* is an indifferent species, which can be found nearly everywhere on extensively used meadows. Hence, the lower abundance on meadows south of the levee is most likely caused by the regular inundation events. *Metrioptera bicolor* and *Stenobothrus lineatus* are classified as xerophilous species and *Stethophyma grossum* is a hygrophilous species. The higher abundances found on non-flooded and flooded meadows, respectively, fit to that. *Conocephalus fuscus* is a species which needs meadows with a well-developed vertical structure. On two meadows south of the levee (flooded) the mean maximum vegetation height was more than 1.2 m. The mean maximum vegetation height of all meadows was about 54 cm north of the levee and about 65 cm south of it. So the higher abundance of *Conocephalus fuscus* on flooded meadows fits to that. Although abundance differences between meadow types in thermophilous and hygrophilous species reflect their preferences for dry and wet habitats, respectively, both of them can appear on both types of meadows. For example the xerothermophilous species *Calliptamus italicus* was found 22 times on non-flooded meadows and 9 times on flooded meadows. From the end of July the first adult individuals were detected on flooded meadows, while before (in June) larvae were only recorded on non-flooded meadows. *C. italicus* is classified as very good flyer and can fly over distances up to 6 km (Brose 1997). However, according to Reinhardt et al. (2005) the species' dispersal ability is classified as moderate (also see Annex 2). Reinhardt et al. (2005) referred to a previously list of dispersal estimations by Bruckhaus & Detzel (1997) modified with wing morphology, results from individual movement in population studies and long-term observations of local and regional colonization dynamics. Hence, most likely adult individuals dispersed from over the levee to regularly flooded meadows.

The canonical correspondence analysis showed a positive influence of flooding on the species *Metrioptera roeselii*, *Ruspolia nitidula* and *Tettigonia viridissima*. *Tettigonia viridissima* and *Metrioptera roeselii* are meant to be indifferent species. *Tettigonia viridissima* prefers vegetation structures of a medium height and has a high ability to fly. Maybe they can find food easier after flooding events because they are nearly exclusively feeding on other insects. *Metrioptera roeselii* has a predisposition to wet habitats and *Ruspolia nitidula* is a hygrophilous species.

Flooding appeared to negatively affect *Calliptamus italicus*, which is a xerophilous species and several *Chorthippus*-species, which are all indifferent or xerophilous, except of *Chorthippus albomarginatus*.

The vegetation height affected *Calliptamus italicus* and *Chorthippus brunneus*, like flooding, negatively. *Calliptamus italicus* prefers open dry grassland and rocky substrate, *Chorthippus brunneus* needs uncovered soil for its egg deposition and prefers open vegetation and dry and warm sites (Baur et al. 2006). It seems to be the combination of dry sites and short vegetation that attracts these species most.

The mowing regime seemed to have the strongest positive effect on *Stethophyma grossum*. This species was very seldom and only found on three meadows, with a total of eight individuals. In our surveys *Stethophyma grossum* was only found on meadows before mowing. During the surveys, who took place directly after disturbance by mowing, no individuals were found. According to Marzelli (1997) the moment of mowing is of high importance for the population development of *Stethophyma grossum*. Mowing should take place twice a year; the first time should be at the beginning of June (before the appearance of larvae and adults) and the second time in the middle of September (after oviposition). The mowing supports the egg development by increasing the soil temperature, which is important, because the temperature is minor in wet habitats.

Mecostethus parapleurus and *Chorthippus mollis* were negatively affected by mowing. *Mecostethus parapleurus* prefers high grasses and *Chorthippus mollis*-populations can be delicately disturbed by mowing (Baur et al. 2006).

The dominance of grasses is apparently an important factor for *Omocestus haemorrhoidalis*, which is strictly feeding on grasses.

Effects of flooding on functional diversity

Our study did not provide any evidence that functional diversity of grasshopper assemblages was affected by disturbance caused by flooding events. Gerisch et al. (2012) found a decline in functional diversity from non-flooded to flooded meadows for ground beetle communities on periodically flooded grasslands along the Elbe River in Germany. They emphasized body

size, overwintering strategy and wing morphology as being critical for ground beetles to cope with floodplain dynamics. These traits were highlighted as proxies for high mobility and rapid development favouring population recovery after flood events. Habitat disturbance seems to have a higher impact on specialist species than on generalist species, because generalist species can easier cope with changes in the environment (Gerisch et al. 2012).

In our study the ecological niches seemed to be similarly filled and a rapid reoccupation after the flooding appears to prevent a decline in functional diversity. The species temporarily extinct by inundations recolonise the meadows through active and or passive dispersal. Because of that we couldn't find any decline in functional diversity.

Conservation relevance and conclusions

In our study a large number of recorded species are classified as near threatened (9 species) or vulnerable (3 species) according to the Red List for grasshoppers in Austria (Berg et al. 2005). This shows the high conservation value of meadows in the Donau-Auen National Park.

All of the five recorded hygrophilous species are near threatened or vulnerable on a national scale. *Stethophyma grossum* is the only hygrophilous species classified as vulnerable (Tab. 2). This species is strictly bonded to wetlands (Baur et al. 2006). It needs high humidity near the ground and in the soil and a heterogeneous vertical vegetation structure (Sonneck et al. 2008). The eggs are laid near the ground and require high soil humidity and so-called “contact-water” to develop (Ingrisch 1983, Marzelli 1997). The hatching of the larvae happens from June until September in the following year and the first adults can be found at the end of June (Ingrisch & Köhler 1998). According to Bönsel & Sonneck (2011) the species has a very low median active dispersal ability of 37 m (males) and 27 m (females) (Bönsel & Sonneck 2011). During our survey, we recorded a total of only eight individuals of *S. grossum* on three annually flooded meadows. That could indicate a relatively low habitat quality for this threatened species. Perhaps large numbers of individuals will die during the summer inundations and the population is only saved by late hatching larvae, which have survived the flood in their egg stage (cf. Demetz et al. 2013).

This study emphasizes that natural floodplain dynamics still have a high and significant impact on grasshopper assemblages of meadows in the Donau-Auen National Park. The

perpetuation of high hydrological dynamics causing annual flooding is a precondition for maintaining the current grasshopper fauna and the area's high conservation value for regionally threatened hygrophilous species (cf. Demetz et al. 2013).

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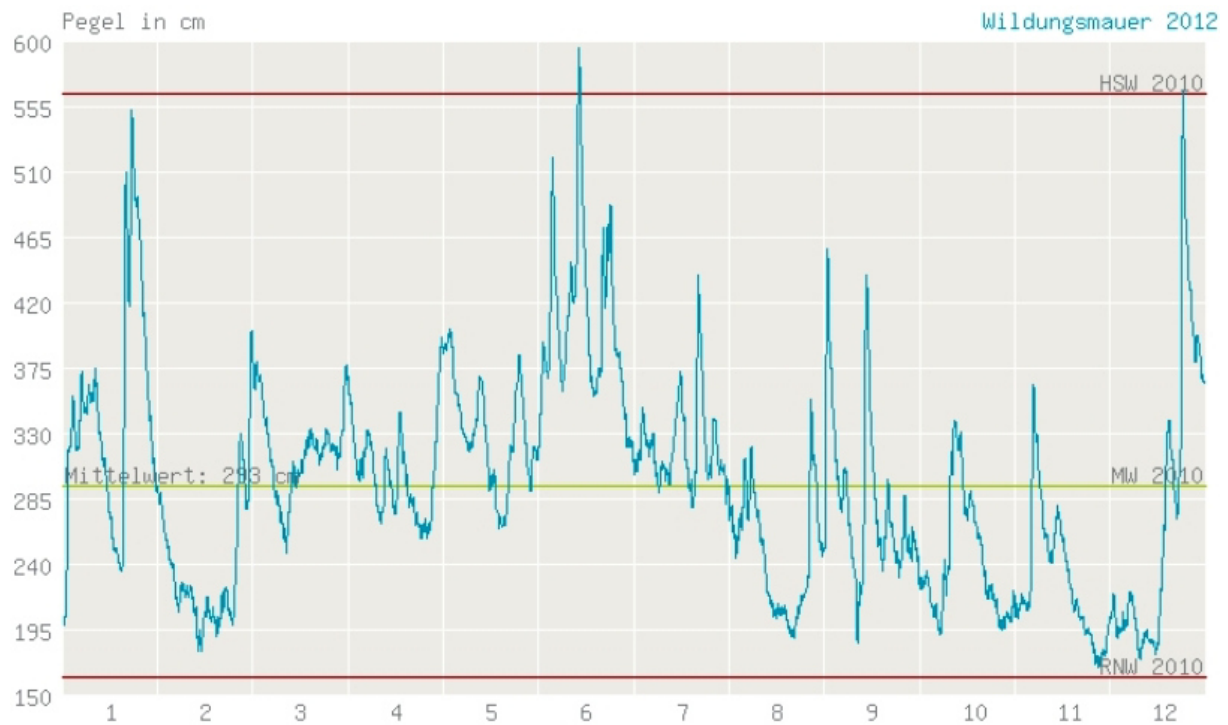
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Appendices



Annex 1. Water level fluctuations of the Danube in the year 2012 at test point Wildungsmauer showing the maxima of water level at each day (http://www.doris.bmvit.gv.at/pegel_und_seichtstellen/jahresverlauf/, 01.04.2015).

Annex 2. Functional traits matrix of all detected grasshoppers used for calculating functional diversity measures.

Species	wet habitats	dry habitats	herbivorous (non-grass feeder)	grass feeders	carnivores	mean body length [mm]	dispersal ability (moderate/low 1-2 high)	number of ovarioles (1-3)	oviposition in plants	oviposition at ground
<i>Calliptamus italicus</i>	0	1	1	0	0	23.75	1	3	0	1
<i>Chorthippus albomarginatus</i>	1	0	1	1	0	17.25	2	1	0	1
<i>Chorthippus apricarius</i>	0	1	1	1	0	16.5	1	1	0	1
<i>Chorthippus biguttulus</i>	0	1	1	1	0	16.5	2	1	0	1
<i>Chorthippus brunneus</i>	0	1	1	1	0	18.25	2	1	0	1
<i>Chorthippus dorsatus</i>	1	1	1	1	0	19	2	1	1	0
<i>Chorthippus mollis</i>	1	1	1	1	0	17.25	2	1	0	1
<i>Chorthippus parallelus</i>	1	1	1	1	0	17.25	2	1	0	1
<i>Chrysochraon dispar</i>	1	0	1	1	0	21.25	1	2	1	0
<i>Conocephalus fuscus</i>	1	1	0	0	1	15.25	2	3	1	0
<i>Euchorthippus declivus</i>	0	1	1	1	0	20.75	2	no data	0	1
<i>Euthystira brachyptera</i>	1	1	0	1	0	18	1	1	1	0
<i>Gryllus campestris</i>	0	1	1	1	1	22.5	1	3	0	1
<i>Leptophyes albobittata</i>	0	1	1	0	0	13	2	2	1	0
<i>Mecostethus parapleurus</i>	1	0	0	1	0	22.75	1	2	0	1
<i>Metrioptera bicolor</i>	0	1	1	1	1	16	2	2	1	0
<i>Metrioptera roeselii</i>	1	1	1	1	1	17.25	1	3	1	0
<i>Omocestus haemorrhoidalis</i>	0	1	0	1	0	15	1	1	0	1
<i>Pholidoptera griseoaptera</i>	1	1	1	1	1	17.75	1	2	1	1
<i>Platycleis albopunctata grisea</i>	0	1	1	1	1	20.25	1	3	1	0
<i>Ruspolia nitidula</i>	1	0	1	1	1	26.75	2	no data	1	1
<i>Stenobothrus lineatus</i>	0	1	0	1	0	20.5	1	1	1	1
<i>Stethophyma grossum</i>	1	0	0	1	0	22.25	1	2	1	1
<i>Tettigonia viridissima</i>	1	1	1	1	1	34.5	2	3	0	1

Annex 3. List of all recorded species (in alphabetic order) including the total numbers of counted individuals at flooded and non-flooded meadows. The number of meadows, on which they were found, is provided in brackets.

Species	flooded	non-flooded	sum total
<i>Calliptamus italicus</i>	9 (4)	22 (2)	31 (6)
<i>Chorthippus albomarginatus</i>	26 (6)	121 (10)	147 (16)
<i>Chorthippus apricarius</i>	-	5 (1)	5 (1)
<i>Chorthippus biguttulus</i>	35 (8)	131 (8)	166 (16)
<i>Chorthippus brunneus</i>	34 (8)	91 (6)	125 (14)
<i>Chorthippus dorsatus</i>	56 (10)	256 (10)	312 (20)
<i>Chorthippus mollis</i>	19 (4)	45 (7)	64 (11)
<i>Chorthippus parallelus</i>	603 (12)	1136 (13)	1739 (25)
<i>Chrysochaon dispar</i>	500 (12)	1017 (13)	1517 (25)
<i>Conocephalus fuscus</i>	96 (9)	13 (3)	109 (12)
<i>Euchorthippus declivus</i>	2 (2)	-	2 (2)
<i>Euthystira brachyptera</i>	4 (2)	167 (3)	171 (5)
<i>Gryllus campestris</i>	1 (1)	16 (2)	17 (3)
<i>Leptophyes albovittata</i>	4 (2)	1 (1)	5 (3)
<i>Mecostethus parapleurus</i>	360 (10)	640 (9)	1000 (19)
<i>Metrioptera bicolor</i>	39 (6)	378 (13)	417 (19)
<i>Metrioptera roeselii</i>	604 (12)	867 (12)	1471 (24)
<i>Omocestus haemorrhoidalis</i>	13 (3)	114 (4)	127 (7)
<i>Phaneroptera falcata</i>	-	1 (1)	1 (1)
<i>Pholidoptera griseoaptera</i>	27 (10)	55 (11)	82 (21)
<i>Platycleis albopunctata grisea</i>	-	7 (4)	7 (4)
<i>Ruspolia nitidula</i>	229 (11)	27 (10)	256 (21)
<i>Stenobothrus lineatus</i>	188 (12)	1329 (13)	1517 (25)
<i>Stethophyma grossum</i>	8 (3)	-	8 (3)
<i>Tetrix bipunctata or kraussii</i>	-	3 (2)	3 (2)
<i>Tetrix sp.</i>	1 (1)	10 (1)	11 (2)
<i>Tetrix subulata</i>	-	5 (1)	5 (1)
<i>Tetrix tenuicornis</i>	2 (2)	5 (3)	7 (5)
<i>Tetrix undulata</i>	1 (1)	1 (1)	2 (2)
<i>Tettigonia viridissima</i>	57 (11)	22 (8)	79 (19)
sum total	2918	6485	9403

Curriculum vitae

Persönliche Daten

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Bildungsweg

1995 – 2003

Bundesgymnasium und
Bundesrealgymnasium Lilienfeld, Matura

WS 2003 – SS 2005

Studium der Biologie an der Universität Wien

WS 2005 – SS 2008

Studium der Zoologie/Evolutionsbiologie/Entomologie an der
Universität Wien

Juni 2008 – September 2010

Diplomarbeit: „Die nachtaktive Fluginsektenfauna in den
Grünanlagen des Regierungsviertels St. Pölten“

14. Oktober 2010

Diplomprüfung über Entomologie und Evolutionsbiologie mit
Auszeichnung abgelegt

WS 2010 – SS 2011

Lehramtsstudium Biologie und Umweltkunde und Mathematik an der
Universität Wien

WS 2011 – SS 2015

Masterstudium Naturschutz und Biodiversitätsmanagement an der
Universität Wien

Juli 2012 – März 2015

Masterarbeit: „Effects of floodplain dynamics on richness, abundance,
composition and functional diversity of grasshopper assemblages in
the Donau-Auen National Park (Austria)“

Beruflicher Werdegang

Sommersemester 2008, 2009, 2010

Tutorin bei den zoologischen Bestimmungsübungen an der Universität
Wien

Frühjahr 2013 und 2014

Mitarbeit bei Amphibienerhebung des Forschungsvereins LANIUS im
Stadtgebiet St. Pölten

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Berufspraktikum in der Naturschutzabteilung des
Landes NÖ

Projektpraktika und Exkursionen

Tropenbiologisches PP in Costa Rica (2007) - *Heliconius*-Falter

PP in den Hohen Tauern (2007) –Bestäuber an *Thymus* sp.

Bestäubungsbiologisches PP Mittelgriechenland (2008) – *Ophrys* spp.

Exkursion Mallorca (2009) – *Ophrys* spp.

Publikationen

Demetz, A., K. Fiedler, T. Dreschke & C.H. Schulze 2013. Natural
floodplain dynamics shape grasshopper assemblages of meadows in
the Donau-Auen National Park (Austria). Conference Volume. 5th
Symposium for Research in Protected Areas 10 to 12 June 2013,
Mittersill. p. 125 – 130.