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The influence of spring floods on small mammal communities in the Nemunas River Delta, Lithuania

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Abstract: The influence of the annual spring floods on small mammal communities was studied in the Nemunas River Delta, SW Lithuania. The aim of the investigation was to compare the diversity of small mammals inhabiting spring-flooded meadows, meadows not subjected to flooding and spring-flooded forest in years characterized by differing heights and durations of spring flood. In the years of the high flood, the number of species and diversity index were higher, while index of dominance was less than in the years of low flood. Significantly, the highest proportions of *Apodemus agrarius* were recorded in spring-flooded meadows in years of high flood (41.7%), while *Microtus oeconomus* occurred in the highest proportions in spring-flooded meadows in years of low flood (66.8%) and in meadows not subjected to flooding (47.1%). In non-flooded areas, *M. oeconomus* is not expelled by the floods and outcompetes other species. After high levels of flooding, during the process of re-population, the voles may be outcompeted by *A. agrarius*. In the absence of dominant species, greater opportunities existed for the establishment of more species (13 species in flooded meadows). *Micromys minutus* accounted for up to 19.5–30.1% in the years of high flood. We concluded that the annual spring floods in the Nemunas Delta had no long-term negative effects, the number of small mammal species and their abundance had been restored in just a few months. The worst consequences of the high flood were recorded in forest habitat. Spring floods, and especially the higher floods, are natural environmental agents, maintaining the high diversity of small mammals in meadows and reed-beds.

Key words: small mammals; diversity; spring floods; Lithuania

Introduction

Flooding in the Nemunas Delta is caused by the seasonal rise of water in the rivers (the spring flood), or non-seasonal rise of water from the heavy rainfalls, which may occur more frequently along with climate change. Some predictions indicate that we can expect to see more extreme weather events such as flooding in the future (Climate 2009). Flooding of coastal and river areas affects mammals, amphibians and plants (Berry 2009). The influence of flooding on different species may be affected by its duration and coverage, as well as by the habitat structure of the area (Zhang et al. 2007). With the exclusion of arboreal species, flooding may become a lethal agent for most of the small mammals in the area (Andersen et al. 2000; Zhang et al. 2007) or significantly decrease their numbers (Chamberlain & Leopold 2003).

The Nemunas River Delta is the largest territory in Lithuania that is subjected to periodic flooding (Preliminary 2011). Most of the area's low-lying territory consists of summer polders (mainly meadows, protected only against autumn floods) and winter polders (agriculture lands and inhabited territories, protected against extremely high floods that can occur in spring). According to data from the National Land Service under the Ministry of Agriculture of the Republic of Lithuania, as well as from "Lietuvos Draudimas", the country's leading insurance company, the spring floods in 2010 and 2011 were particularly pronounced (lrytas.lt 2011). In 2004, the Habitat Directive designated the Nemunas River Delta as a Special Area for Conservation, and the Bird Directive designated the area as a Special Area for Bird Protection (Nemuno Delta 2012). In terms of biodiversity, the most important elements are the plant communities in the flooded meadows (Kriščiūnas et al. 1955) and the breeding and migratory populations of birds (Švažas et al. 2003; Raudonikis 2004).

Due to the regular spring flooding and specific habitats of the flooded meadows and reeds, the Nemunas River Delta offers unique opportunities for the study of small mammals. Here, a new mammal species for Lithuania, Mediterranean water shrew (*Neomys anomalus* Cabrera, 1907), was registered for the first time (Balčiauskas & Balčiauskienė 2012), and this territory was also the source for the spread of root vole *Microtus oeconomus* (Pallas, 1776) in Lithuania (Balčiauskas et al. 2010).

The main habitats of *M. oeconomus* are wet and regularly inundated areas of lakeshores, wet meadows and open bogs (Tast 1966; Mitchell-Jones et al. 1999; Linzey et al. 2008). These habitats are not the usual preferred habitat of striped field mouse *Apode-*

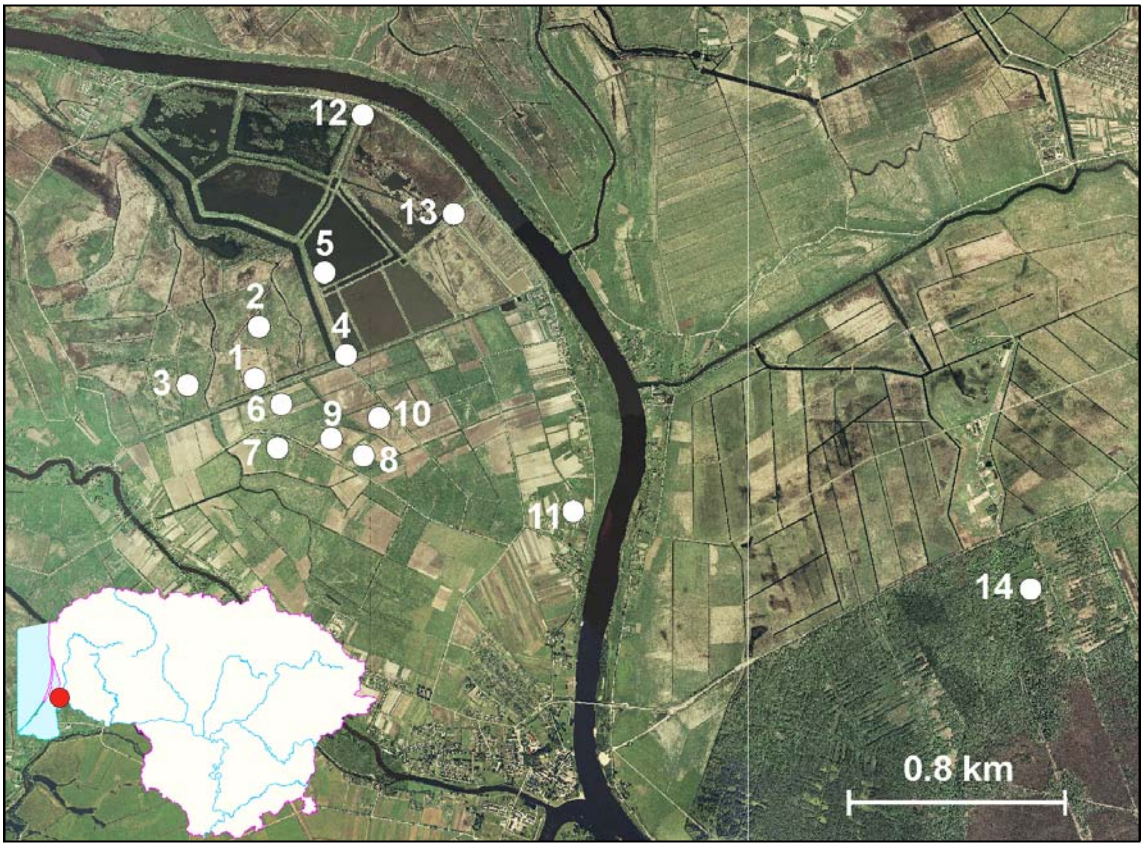

Fig. 1. Small mammal trapping sites in Nemunas River Delta, 2004–2011. 1–3: spring-flooded meadows; 4–11: non-flooded meadows and agriculture land; 12–14: spring-flooded forest habitats).

mus agrarius (Pallas, 1771) (Kaneko et al. 2008). In the Nemunas Delta area, however, *A. agrarius* were found inhabiting reed beds in high numbers, so we attempted to relate their dominance to the spring floods. As for harvest mouse *Micromys minutus* (Pallas, 1771), the preferred habitat is quite variable – ruderal succession habitat (Churchfield et al. 1997), reed-beds (Surmacki et al. 2005), fields of tall grass, and wetlands (Aplin et al. 2008). This small rodent is capable of competition with voles that are much bigger (Ylönen 1990).

The rationale of the study is to increase levels of knowledge of the impacts of spring floods on small mammal communities in Eastern Europe. Investigation into the impact of flooding may provide a deeper insight into the community structure of small mammals (Thibault & Brown 2008) and its dynamics under regular natural disturbance.

The aim of the study was to compare small mammal communities in the neighbouring spring-flooded and non-flooded habitats of the Nemunas Delta and discover how spring floods influenced their diversity. The duration of the flood period underpinned the working hypothesis – the higher the flood and the longer the duration, the more it expels species and the shorter is the period available for re-colonization, thus offering less opportunity for the dominant species (*M. oeconomus*) to survive and outcompete other species, thereby resulting in a higher diversity in the small mammal community.

Material and methods

The study area is located in the Nemunas River Delta, SW Lithuania (Fig. 1). Spring-flooded and non-flooded meadows and agricultural habitats near Rusnė settlement (55°20′10″ N; 21°18′54″ E) were investigated, as well as flooded forest habitat near Šyškrantė village (55°18′50″ N; 21°22′41″ E) and Žalgirių forest (55°18′40″ N; 21°26′10″ E).

Small mammals were trapped in the periods 2004–2006 and 2008–2011: June and August 2004 (2,485 trap-nights), September 2005 (460), June, August and October 2006 (2,710), October 2008 (1,650), July, September and October 2009 (4,200), August, September and October 2010 (2,100), and October 2011 (900 trap-nights). The total trapping effort amounted to 14,505 trap-nights. Snap trap lines consisting of 25 traps set at a distance of 5 m from each other (4 such lines for the habitat) were used. In meadows, most trap lines were close (2–10 m) to drainage ditches and adjacent reed belts. Traps were left in position for three days, checked once a day. Traps were baited with bread and sunflower oil (Balčiauskas 2004).

The low-lying flood meadows are vegetated by Poaceae and Cyperaceae plants and the area consists of a polder system with artificially-raised embankments to protect against high spring floods. All polders are surrounded by ditches, these with reeds on their margins, partially overgrown by shrubs. Meadows were not mowed. In spring, most of these areas are flooded.

In the areas of the territory not subject to spring flooding, non-mowed high grass meadows and ecotones of long laying fallow land were selected for study. In 2004–2011, no agricultural activity was registered in the trapping sites.

Table 1. Spring flood data in the Nemunas Delta, 2003–2011 (from Lithuanian Hydrometeorological Service under the Ministry of Environment).

	2003	2004	2005	2006	2008	2009	2010	2011
Spring flooded area, ha	n/a[1]	11500	10780	7210	14700	n/a	23610	20500
Start of the spring flood	n/a	March 24	March 25	April 6	March 3	n/a	March 23	March 21
Duration of spring flood, days	n/a	14	24	7	10[2]	n/a	32	30[3]

Explanations: 1 – data not available (water level at the Rusnė watchpoint did not rise a critical flood level to trigger recording); 2 – 13,750 ha still flooded on 31 March; 3 – 20,500 ha still flooded on 20 April.

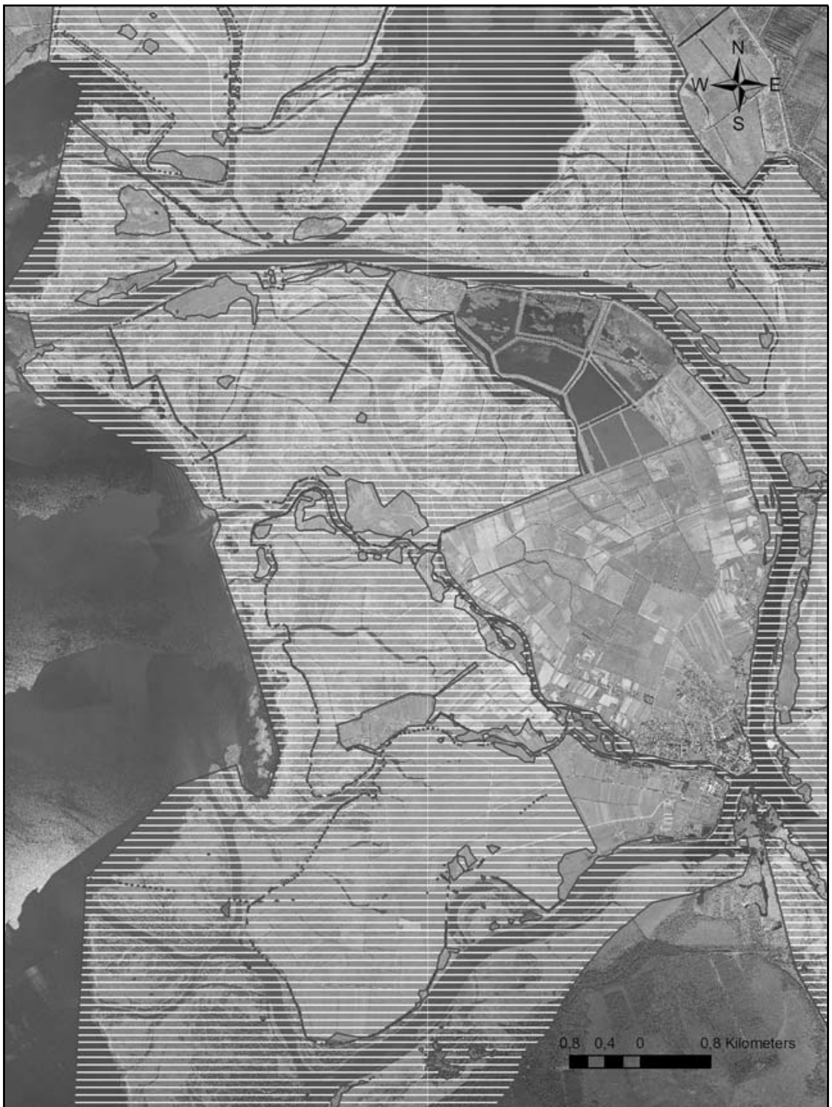

Fig. 2. Flooded territory in the Nemunas Delta in 2003, the year of low flood; stripped area was under water (2003 lidar data; National Land Service under the Ministry of Agriculture of the Republic of Lithuania).

Spring-flooded forest habitat is characterised as black alder stands, with a poor understorey. Bramble, willow, alder buckthorn, nettles and reedbeds are the main components of the understorey and grass layers.

The area flooded and duration of the spring floods were evaluated (Table 1). Water height in the lower reaches of the Nemunas River was measured in Rusnė, 5 to 10 km from the study sites. According to the Table 1, years 2004, 2005, 2008, 2010 and 2011 could be regarded as "high flood", while 2003, 2006 and 2009 as "low flood". At only 1–2 m above sea level, the meadows subject to flooding are low-lying and, as the average flood level at the Rusnė watchpoint is 1.3 m, these areas tend to be under water even in the years when floods are not recorded at Rusnė itself. The distribution of flooded areas in 2003, the year of low spring flood, is shown in the Fig. 2.

Table 2. Small mammal community structure in three types of habitats in the Nemunas River Delta, 2004–2011.

	Flooded meadows		Non-flooded meadows		Flooded forest	
	n	%	n	%	n	%
Sorex araneus	207	16.0	96	16.8	22	17.5
Sorex minutus	51	4.0	16	2.8	4	3.2
Neomys fodiens	1	0.1				
Neomys anomalus	1	0.1	1	0.2		
Myodes glareolus	19	1.5	12	2.1	9	7.1
Microtus arvalis	27	2.1	14	2.5		
Microtus agrestis	1	0.1			6	4.8
Microtus oeconomus	408	31.6	222	38.9	41	32.5
Arvicola terrestris	1	0.1			1	0.8
Apodemus agrarius	432	33.5	204	35.7	39	31.0
Apodemus flavicollis	4	0.3	1	0.2	3	2.4
Micromys minutus	137	10.6	4	0.7		
Mus musculus	1	0.1	1	0.2	1	0.8
Trap nights	8350		5205		1250	
Total species, s	13		10		9	
Total individuals, N	1290	100.0	571	100.0	126	100.0
Shannon's H	2.28		1.98		2.37	
Simpson's c	0.25		0.31		0.24	

The diversity of a small mammal community was expressed as Shannon–Wiener diversity index, H, on the base of log2; for expression of the dominance Simpson's index c was used, both according Krebs (1999). The similarity of small mammal communities in different habitats and in the years of high and low flood was compared according to Sørensen's index S, $S = 2c/(a+b)$, where a and b are numbers of species in compared communities, and c is number of species, present in both communities (Magurran 2004).

Differences in small mammal community diversity were tested using Rényi diversity numbers (Tóthmérész 1998). Diversity profiles were calculated using scale parameter α between 0 and 4. Calculations were performed in the freeware DOSBox ver. 0.74, running DivOrd program ver. 1.90 (Tóthmérész 1993). Differences in species composition of the communities were tested according chi-square test. All differences with $P > 0.05$ were considered non-significant. Calculations were done with Statistica for Windows, ver. 6.0 software (StatSoft 2004).

Results

In total, 1,987 individuals of 13 species of small mammals were trapped in 2004–2011. The dominant species were *Apodemus agrarius* (34.0% of the total catch) and *Microtus oeconomus* (33.8%), with common shrews (*Sorex araneus* L., 1758) accounting for 16.4% and *Micromys minutus* for 7.1%. Pygmy shrew (*Sorex minutus* L., 1758), bank vole *Myodes glareolus* (Schreber, 1780), common vole *Microtus arvalis* (Pallas, 1779) all occurred in small numbers, with water shrew *Neomys fodiens* (Pennant, 1771), *N. anomalus*, field vole *Microtus agrestis* (L., 1761), water vole *Arvicola terrestris* (L., 1758), yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) and house mouse *Mus musculus* L., 1758 also recorded rarely (a few individuals of each).

Comparing the habitats (Table 2), the small mammal communities in the spring-flooded meadows were characterized by the highest number of species and significantly higher proportion of *M. minutus* (compared to meadows not flooded in spring, chi-square 2×2 test with df = 1, $\chi^2 = 47.2$ and spring-flooded forest $\chi^2 = 12.8$, $P < 0.001$). In the meadows not subject to spring flooding, there were three species fewer (*N. fodiens*, *M. agrestis* and *A. terrestris* absent), with the proportion of *M. oeconomus* being significantly higher than in spring-flooded meadows ($\chi^2 = 9.29$, $P < 0.005$) and in spring-flooded forest ($\chi^2 = 29.26$, $P < 0.001$). In the spring-flooded forest, the number of species found was the smallest. This habitat was characterized by the highest proportions of *M. glareolus* (compared to meadows not subject to spring flooding, $\chi^2 = 9.0$, $P < 0.01$; compared to spring-flooded meadows, $\chi^2 = 18.8$, $P < 0.001$) and *M. agrestis* (respectively, $\chi^2 = 27.4$ and $\chi^2 = 51.2$, $P < 0.001$). The diversity of the small mammal community was higher in the spring-flooded meadows than the non-flooded ones, and there were no significant differences between these and the flooded forest (Fig. 3A).

The flood influence was tested for each of the investigated habitats. In the flooded meadows, the years of the high flood were characterized by the maximum number of small mammal species present (Table 3) and significantly higher diversity (Fig. 3B). In the years of low flood, the absolute dominant species was *M. oeconomus* ($\chi^2 = 312.3$, $P < 0.001$) and the proportions of *M. minutus*, *A. agrarius* and *M. arvalis* were significantly lower than in the years of high flood (respectively, $\chi^2 = 61.5$, 91.9 and 6.6, $P < 0.001$ and $P < 0.05$). In the years of low flood, four species (*N. fodiens, N. anomalus, M. glareolus* and *M. musculus*) were not trapped in the flooded meadows habitat.

Non-flooded meadows are quite close to the flooded area. In these meadows, the height of the flood had a less noticeable influence on the number of small mammal species present (Table 4), though the diversity index was still significantly higher in the years of high flood (Fig. 3C). Low flood years were characterized by a domination of *M. oeconomus* ($\chi^2 = 21.7$, $P < 0.001$),

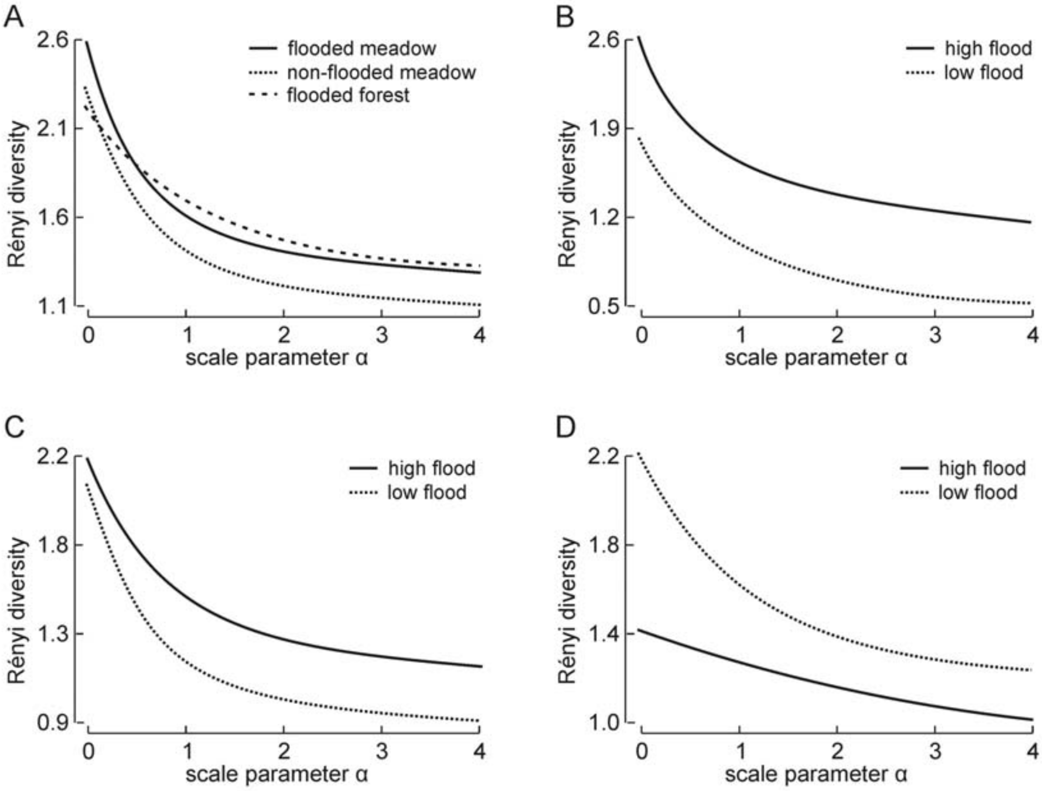

Fig. 3. Comparison of the small mammal community diversity: A – comparison between habitats; B – high flood versus low flood in the flooded meadows habitat; C – high flood versus low flood in the non-flooded meadows habitat; D – high flood versus low flood in the flooded forest habitat. Statistically significant differences in diversity are shown by non-intersecting curves.

Table 3. Small mammal community structure in the spring-flooded meadows of the Nemunas River Delta, 2004–2011.

	High flood							Low flood			
	2004	2005	2008	2010	2011	Σ	%	2006	2009	Σ	%
Sorex araneus	65	6	38	37	2	148	16.3	23	36	59	15.4
Sorex minutus	17	1	4	18		40	4.4	5	6	11	2.9
Neomys fodiens			1			1	0.1				
Neomys anomalus			1			1	0.1				
Myodes glareolus	4			13	2	19	2.1				
Microtus arvalis	19		6			25	2.8	1	1	2	0.5
Microtus agrestis				1		1	0.1				
Microtus oeconomus	49	1	46	42	14	152	16.8	167	89	256	66.8
Arvicola terrestris				1		1	0.1				
Apodemus agrarius	3	12	31	208	124	378	41.7	15	39	54	14.1
Apodemus flavicollis	1		3			4	0.4				
Micromys minutus			58	78		136	15.0	1		1	0.3
Mus musculus				1		1	0.1				
Trap nights	1550	200	900	2100	600	5350		1100	1900	3000	
Total species, s	7	4	9	9	4	13		6	5	6	
Total individuals, N	158	20	188	399	142	907	100.0	212	171	383	100.0
Shannon's H	2.05	1.40	2.37	2.04	0.67	2.34		1.09	1.66	1.41	
Simpson's c	0.29	0.46	0.22	0.33	0.77	0.25		0.64	0.37	0.49	

while in the years of high flood, the small mammal community had significantly higher proportions of *M. glareolus* ($\chi^2 = 8.3$, $P < 0.005$), *M. arvalis* ($\chi^2 = 10.8$, $P = 0.001$), and slightly higher proportions of *S. araneus* ($\chi^2 = 3.3$, $P < 0.1$). *A. flavicollis* and *M. musculus* were not trapped in the years of low flood.

By contrast however, the small mammal communities in the spring-flooded forest were devastated in the years of the high flood (Table 5). In total, only five small mammal species were registered in the years of high flood as compared to nine species after low flood; the diversity index was also significantly higher after low flood (Fig. 3D). After high flood, the small mammal community was characterized by a higher proportion of insectivores, *S. araneus* ($\chi^2 = 8.8$, $P < 0.005$) and *S. minutus* ($\chi^2 = 5.2$, $P < 0.05$). Due to small sample size,

Table 4. Small mammal community structure in the non-flooded meadows of the Nemunas River Delta, 2004–2011.

	High flood						Low flood			
	2004	2005	2008	2011	Σ	%	2006	2009	Σ	%
Sorex araneus	3	2	44		49	20.1	16	31	47	14.4
Sorex minutus		1	7		8	3.3	3	5	8	2.4
Neomys anomalus								1	1	0.3
Myodes glareolus	8			2	10	4.1		2	2	0.6
Microtus arvalis	12				12	4.9		2	2	0.6
Microtus oeconomus	4	1	63		68	27.9	112	42	154	47.1
Apodemus agrarius	10	8	34	41	93	38.1	12	99	111	33.9
Apodemus flavicollis				1	1	0.4				
Micromys minutus			2		2	0.8	1	1	2	0.6
Mus musculus				1	1	0.4				
Trap nights	585	210	750	300	1845		1360	1700	3060	
Total species, *s*	5	4	5	4	9		5	8	8	
Total individuals, *N*	37	12	150	45	244	100.0	144	183	327	100.0
Shannon's *H*	2.16	1.42	1.82	0.57	2.20		1.10	1.77	1.73	
Simpson's c	0.24	0.49	0.32	0.83	0.27		0.62	0.38	0.36	

Table 5. Small mammal community structure in the flooded forests of the Nemunas River Delta, 2004–2011 (na – not applicable).

	High flood				Low flood			
	2004	2005	Σ	%	2006	2009	Σ	%
Sorex araneus	7		7	43.8	1	14	15	13.6
Sorex minutus	2		2	12.5		2	2	1.8
Myodes glareolus					4	5	9	8.2
Microtus agrestis	1		1	6.3		5	5	4.5
Microtus oeconomus	2		2	12.5	5	34	39	35.5
Arvicola terrestris					1		1	0.9
Apodemus agrarius	3	1	4	25.0	11	24	35	31.8
Apodemus flavicollis						3	3	2.7
Mus musculus						1	1	0.9
Trap nights	350	50	400		250	600	850	
Total species, *s*	5	1	5		5	8	9	
Total individuals, *N*	15	1	16	100.0	22	88	110	100.0
Shannon's *H*	2.01	na	2.02		1.84	2.30	2.32	
Simpson's *c*	0.30	na	0.29		0.34	0.26	0.26	

the difference in the proportion of *M. oeconomus*, high in percentage, was not significant ($\chi^2 = 3.35$, $P < 0.1$). Even characteristic forest dwellers, *M. glareolus* and *A. flavicollis* were not trapped in the forest following high spring floods.

In general, increased trapping effort was related to bigger number of small mammal species trapped (Pearson's $r = 0.64$, $P < 0.05$) but not related to diversity ($r = 0.25$, NS). In the flooded meadow habitat there was no relation between trapping effort and number of trapped species or Shannon's index (both correlations not significant). In non-flooded meadow habitat increased trapping effort yielded bigger number of trapped species ($r = 0.86$, $P < 0.05$). As for flooded forest, sample size is insufficient for similar conclusion.

Only six small mammal species (*S. araneus*, *S. minutus*, *M. glareolus*, *M. oeconomus*, *A. agrarius* and *M. musculus*) were common for all habitats, irrespective of the flood height. According to the values of Sorensen's index, small mammal communities were quite similar across the habitats. Between spring-flooded and non-flooded meadows, ten small mammal species were the same, $S = 0.87$, and between flooded meadow and flooded forest, nine species, $S = 0.82$. Non-flooded meadows and spring-flooded forests had seven species in common (10 and 9 in the compared habitats, $S = 0.74$).

Less similarity in small mammal communities was found in comparing years of high and low spring flood in the same habitat: in the flooded meadows $S = 0.63$, flooded forest $S = 0.71$, just in non-flooded meadows $S = 0.82$. Thus, the similarity of small mammal communities was more dependent on the flood regime than on the habitat type.

Discussion

Flooding induces changes in the community structure of different groups of organisms, generally benefiting the biological diversity by initiating a post-flood succession (Berry 2009). The abundance and diversity of terrestrial soil macrofauna is reduced in the immediate aftermath of grassland flooding, and the effect of regular winter floods is pronounced. The resultant changed structure of the community reflects an increased abundance of well-adapted, widespread and opportunistic species (Plum 2005). In the case of ground-dwelling beetles, post-flood species richness and biomass was greatest in the sites flooded for the longest period, while species richness and biomass for spiders were also not reduced (Ballinger et al. 2005). For rodents, it has been shown that flooding induces mortality, changes of dominant species, trends of populations and community, thus reorganizes the community structure and metapopulation dynamics (Thibault & Brown 2008).

Our data confirm Klinger's (2006) conclusion that the duration and intensity of flood determine the effect on the small mammal community, but this effect lasts less than one year. Even in the years of highest flood, the number of small mammal species and their abundance was already high by summer to autumn (see Tables 3 and 4), thus restoration was occurring in just a few months in the territory of our study. Time available for re-colonization of the territory is shorter after high floods, thus less advantageous to the dominant species *M. oeconomus*. We found that there was a positive correlation between the number of species found and the amount of time from the end of flood to our small mammal trapping. This could, however, explain only about 25% of the registered diversity. Habitat type and the capabilities of the species to spread should also be influencing factors.

For Lithuania it was shown that threshold of the trapping effort yielding sufficient diversity estimates in the homogenous habitat is 300–500 trap days; effort less than 300 trap days yields under-trapping and insufficient list of determined species, even if diversity estimation did not suffer (Balčiauskas & Juškaitis 1997). In most years of our investigation number of traps was above threshold, and there was no correlation between trapping effort and diversity estimate.

Different small mammal species react to floods in different ways; while some die out, others remain (Jacob 2003). Arboreal species are at an advantage, experiencing less decline after floods in the forest (Golet et al. 2011). Best known in this respect is white-footed mouse *Peromyscus leucopus* (Rafinesque, 1818), a species which seems to be not affected by floods (Ruffer 1961; Blem & Blem 1975; Williams et al. 2001). *Myodes glareolus* and *A. flavicollis* may survive even major floods, while *M. arvalis* tends to be the most affected (Jacob 2003). Re-colonization abilities also differ: *M. arvalis*, *S. araneus* and *M. glareolus* appear in the area immediately after the flood, but *M. glareolus* manages to re-colonize only about 120 m in the first year after the flood, while *M. minutus* restore their densities in autumn (Wijnhoven et al. 2006). *Microtus oeconomus* does not immediately reappear in areas after flood, but does so much later in the summer (Tast 1966). By contrast, *A. agrarius* exhibit an extremely good capability for spreading, covering distances of several hundred meters in a few days (Szacki & Liro 1987).

In the Nemunas Delta, we found that small mammal populations were almost decimated after high spring floods in the investigated forest, but the number of species and diversity remained high when low floods occurred. Conditions did not prove advantageous to *A. flavicollis* or *M. minutus*. After high flood levels, the dominant species in the forest was *S. araneus*, this conforming to rapid re-populating abilities of the species found by Wijnhoven et al. (2006).

We conclude that the small mammal community structure and diversity in the spring-flooded and non-flooded meadows was different in the years with different levels of the spring flood. In the years of the high flood, the number of species and diversity were higher, while index of dominance was less than in the years of low flood. These differences are related to small mammal extirpation of the flooded areas and later re-colonization. The absence of dominant species in the area gave rise to opportunities for chances more species to establish due to reduced competition. As a natural disturbance process, flooding leads to a decline in small mammal populations (Golet et al. 2011) and a later restoration of communities, though it was shown that in areas where flooding exceeding one kilometer, not all the area might be re-colonized in the same year (Wijnhoven et al. 2006).

A very important feature of spring-flooded and non-flooded meadows in the Nemunas River Delta is presence of reeds. Some reed-beds are adjacent to the tall grass meadows and are characteristic to drainage ditches, present in all the surveyed territory (see Fig. 1). In Estonian coastal wetlands, the highest diversities of small mammals were recorded in reed-beds, a total of only six species, dominated by *A. agrarius* (Scott et al. 2008). In eastern part of Slovakia, *A. agrarius* may become the dominating species in reed habitats (Stanko et al. 2008), while in the Slovakian Danube area, a total of 16 species were registered in reed habitat with *S. araneus*, *M. glareolus*, and *A. sylvaticus* dominating. The absence of *A. agrarius* here has different reasons (Krištofík 2001).

Comparing the habitats of Nemunas River Delta (see Table 2), it was found that spring-flooded and non-flooded meadows are both dominated by *A. agrarius* and *M. oeconomus*. The main difference between these habitats was that there was a significantly higher proportion of *M. oeconomus* in non-flooded meadows, while spring-flooded meadows were characterized by higher proportions of *A. agrarius* and *M. minutus*. In the non-flooded areas, *M. oeconomus* is not expelled by floods, thus maintains high numbers and outcompetes other species. In spring-flooded areas however, the species can only remain present in the years of low flood (see Table 3). In the years of high flood, post-flood competition amongst small mammals is high, and voles may be outcompeted by *A. agrarius*.

Spring-flooded tall grass meadows and reed-beds are suitable habitats for all of these three species. *Microtus oeconomus* is known as an inhabitant of wet and flooded habitats (Mitchell-Jones et al. 1999; Linzey et al. 2008), preferring high vegetation and dense cover, such as reed-beds, sedge meadows and willow thickets

(Tast 1966). From the northern part of Fennoscandia, it is known that *M. oeconomus* outcompetes *M. agrestis* (Tast 1966). In the Nemunas Delta, *M. agrestis* was almost absent, with just a few individuals being caught in the spring-flooded forest (see Table 1). As for the much smaller *M. minutus*, its semi-arboreal way of life lessens its competition with other small mammal species in vegetative period (Ylönen 1990). High densities of *M. minutus* in the reeds have been registered in Austria and Poland, suggesting reed-beds as primary habitat of the species (Haberl & Kryštufek 2003) (Surmacki et al. 2005). Spring-flooded meadows, especially those after high spring floods, were the most suitable habitat of *M. minutus* in the Nemunas Delta. The species accounted for an average of 15.0% of the small mammals present, a proportion rising to 30.1% in 2008 and 19.5% in 2010, both years of high flood (see Table 3). These are much higher figures than anywhere in Lithuania (Juškaitis 2002; Juškaitis & Ulevičius 2002; Ulevičius et al. 2002; Baranauskas et al. 2003; Ulevičius & Juškaitis 2003; Pakeltytė & Andriuškevičius 2004; Jasiulionis et al. 2011).

The influence of flooding on small mammal communities had not previously been investigated in Lithuania. To answer whether these meadows were of special note for the small mammal communities, data were utilized from investigations in meadows elsewhere in Lithuania for comparison. In central Lithuania, the natural meadows and boggy ox-bows of the Nevėžis river floodplain are largely similar from a habitat perspective to the flooded meadow in the Nemunas Delta. This area was dominated by *A. agrarius* (in the meadows and ox-bows, respectively, 47.1% and 61.3% of the total catch), *S. araneus* being sub-dominant species (Pakeltytė & Andriuškevičius 2004). In the Curonian Spit National Park, a narrow belt of land between the Baltic Sea and Curonian and at a distance of 20 to 40 km from the Nemunas Delta, wide and partially flooded reed-beds are a characteristic feature. The dominant species of small mammal here was *M. oeconomus*, particularly abundant in the coastal reed-beds and wet meadows. *M. minutus* was rarely trapped in wet habitats with high vegetation, such as sedge meadows and reed-beds (Juškaitis & Ulevičius 2002).

We can thus confirm that the community structures of small mammals in wet natural meadows not subjected to flooding in other parts of Lithuania differ from structures recorded in our study area, in particular by generally lower proportions of *M. oeconomus* and *M. minutus* in these non-flooded areas. While both have been trapped in wet habitats (lakeshore meadows, reed-beds and high sedge meadows) in Žemaitija National Park, NW Lithuania, (Ulevičius et al. 2002) and Verkiai Regional Park, SE Lithuania, (Baranauskas et al. 2003), neither is very abundant. In S Lithuania *M. oeconomus* was not common, inhabiting wet meadows and reed-beds (Balčiauskas et al. 2010).

The dominance of *A. agrarius* in meadows of the Nemunas Delta was much more expressed than in other parts of Lithuania. This species was characteristic to anthropogenic habitats in NW (Ulevičius et al. 2002), SE (Baranauskas et al. 2003) and S Lithuania (Juškaitis 2002). For three consecutive years, *A. agrarius* was not trapped in the floodplains of four rivers in S Lithuania (Ulevičius & Juškaitis 2003). In C Lithuania, the abundance of *A. agrarius* in cultivated meadows was exceptionally high after the sowing of cereals (Maldžiūnaitė et al. 1981). Under meadow-forest succession, the proportion of *A. agrarius* in overgrown meadows was just a few percent (Jasiulionis et al. 2011).

Bias problems in the trapping of rodents and insectivores related to the trapping method (live traps, pitfalls, snap traps) are well documented (e.g., Williams & Braun 1983; Stanko et al. 1999). In our case, there were very limited possibilities for pitfall trapping in the spring-flooded meadows due to the floods themselves and, later in the season, the excessive wetness of some of the habitat in autumn and after rainfall. Pitfalls may also yield even less species than registered by live traps (Lešo & Kropil 2010) as well as creating a bias amongst shrews, voles and mice trapped (Torre et al. 2010). We rely on the presumption that any possible bias of snap trapping against insectivores and *M. minutus* was comparable between investigated habitats. The same method of snap trap lines was used throughout 2004–2011. It should be noted that shrews and *M. minutus* were quite abundantly trapped, so we expect bias was minimal.

Long duration heavy flooding has more detrimental consequences to small mammals, though this may be buffered by the presence of refuges and the mobility of organisms (Zhang et al. 2007). The disruptive consequences of a flood depend on the water level, the duration of a flood and the speed of water rise (Andersen et al. 2000). On average, spring floods in the Nemunas River Delta start on about the 19th of March and lasts 16 days (maximum 51 days). Summer polders are usually completely flooded, with winter polders flooding only a few times a century (Preliminary 2011). We presume that in the years of the high spring flood, the small mammals in the flooded areas were drowned. Due to the low altitude, there are no escape areas in the flooded territory other than the polder embankments. Small mammals with an arboreal way of life may have had some refuges only in the flooded forest.

In our case, the flooded areas provide virtually no escape or refuges, thus after high spring flood, all areas need to be re-colonised. Small mammals have to repopulate from adjacent sites (Ellis et al. 1997), and the flood consequences on rodent communities are short-term (Zhang et al. 2007). In the case of *M. oeconomus*, it is known that the re-population of formerly flooded areas occurs along linear structures of the landscape, such as roads, channels and rivers (Tast 1966). In our investigation, such structures are reclamation ditches, roads and polder embankments.

We conclude that annual spring floods in Nemunas Delta had no long-term negative effects on the small mammal community. The re-colonization of previously flooded land has already started in May and the number of small mammal species and their abundance is restored in just a few months. Removing the dominant small mammal species, high floods created favourable conditions for other species. The worst consequences of the high flood were recorded amongst the small mammal communities in flooded forests. In the spring-flooded meadows, the spring floods, and especially the high floods, are natural environmental agents, maintaining high diversities within the small mammal communities.

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