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ORIGINAL ARTICLE

Long-term changes in a small mammal community in a temperate zone meadow subject to seasonal floods and habitat transformation

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Abstract

We tested small mammal (SM) community response to the influence of seasonal floods and habitat transformation in a temporal zone meadow (west Lithuania). The habitat transitioned from a natural flooded meadow in 2008–2012 to a mowed and pastured area in 2020. SM were trapped in late summer to autumn using lines of 25 traps (145 in total), the number of trapping sessions being one or several per year. We tested the hypotheses that: (1) any reaction to the multiple disturbances is species-specific, that is, the relative abundance of SM species and their proportion in the community differs with respect to the flood magnitude and habitat transformation, and (2) at the guild level, disturbances favor habitat generalists, thereby changing the characteristics of SM community. The average relative density of SM was 20.25 individuals per 100 trap nights (range 7.56–40.67), with 4-year-long cyclical changes of density observed. In separate years, we recorded from 4 to 9 species; Shannon's diversity index varied from 0.46 to 2.19, with expressed change of the dominant species. Habitat generalist species were favored, while habitat specialists were disadvantaged. As the meadow transformation progressed, unfavored states in the SM community prevailed, with excessive numbers of granivore and herbivore species present. Our study suggests that multiple disturbances may lead to an increase in relative abundance, species richness, and diversity within the SM assemblages.

Key words: agricultural transformation, diversity, floods, small mammals, species richness

INTRODUCTION

Anthropogenic transformation of natural habitats often results in their fragmentation and destruction. As an outcome, local small mammal (SM) populations are subjected to changes or partial extinction (Schlinkert *et al.* 2016). Reaction to the change of habitat is, notably differing between habitat specialists and habitat generalists (Gentili *et al.* 2014). Recognizing that scale is an issue in the evaluation of changes in SM communities (Michel *et al.* 2007), investigations analyzing long-term changes within SM community patterns at the local scale are of interest. We therefore focused on the evolution of a SM community in a flooded meadow, this being an example of a terrestrial habitat related to the hydrosphere. Our previous insights (Balčiauskas *et al.* 2012, 2019a) are supplemented by analysis of impact of the recent anthropogenic changes, induced by the gradual converting of the semi-natural meadow to a seasonal pasture.

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Formation of the SM communities and maintaining their diversity is influenced by many interconnected factors: climate, habitat, and species biology (de la Sancha *et al*. 2020). Of these, human-induced landscape changes are recognized as being increasingly important (Zárybnická *et al*. 2017; Vigués *et al*. 2018). Some of the patterns, however, may be not observed in highly productive areas, for example, in the tropics (Hidasi-Neto *et al*. 2020) or habitats such as floodplain meadows (Balčiauskas *et al*. 2019a).

Seasonally flooded meadows are classical examples of the aquatic alteration of terrestrial ecosystems, where the terrestrial habitats receive far reaching inputs (Schulz *et al*. 2015). Floods create mosaic and temporal changes in terrestrial habitats (Larned *et al*. 2010), change food webs (Soykan & Sabo 2009), and change ecological processes (Opperman *et al*. 2017). The influence of floods is expressed in plants and invertebrates (i.e. Vanbergen *et al*. 2017), as well as in mammals, even registered in game animals (Wuczyński & Jakubiec 2013) and bats (Blakey *et al*. 2017). Obviously, the SM assemblage is the most flood-damaged group across different latitudes and various flooded habitats (Andersen *et al*. 2000; Williams *et al*. 2001; Klinger 2006; Zhang *et al*. 2014; Miklós *et al*. 2015; Suchomel & Hadaš 2017). However, the synergy of the impact of floods and human activity on SM has not been well analyzed (see Zhang *et al*. 2018).

Floods may result in a collapse of SM communities and populations not only in the meadows, but also in other habitats (Williams *et al*. 2001; Chamberlain & Leopold 2003; Brown & Fuller 2006; Kluever *et al*. 2016), suggesting animals migrate or die (Crespin *et al*. 2008). Recovery of the populations is possible from immigration, survivors in situ, or a combination of both (Golet *et al*. 2011; Hein & Jacob 2015).

Recovery and decline may be species specific (Balčiauskas *et al*. 2012) and dependent on the biology of species (Horváth & Herczeg 2013; Darinot & Favier 2014; Czabán *et al*. 2015; Hein & Jacob 2019). Knowledge of recovery patterns are of importance for pest management (Golet *et al*. 2011) and protection of species and biological diversity (Hein & Jacob 2015, 2019).

Finally, there could also be other factors involved, such as exposure of SM to heavy metals (Wijnhoven *et al*. 2008) or an increase of loads of pathogens in SM after floods (Wasinski & Dutkiewicz 2013; Markovych *et al*. 2019). In our study area for example, a novel virus strain was described in root voles [*Microtus oeconomus* (Pallas, 1776)]. However, as yet, the possibility of a virus influence on the decreasing abundances of this species is still unclear and has not been tested (Drewes *et al*. 2020).

We aimed to analyze changes in the SM community structure in a flooded meadow influenced by periodic flooding and increasing human-induced transformation. We tested the hypotheses that: (1) any reaction to the multiple disturbances is species-specific, that is, the relative abundance of SM species and their proportion in the community differs with respect to the flood magnitude and habitat transformation, and (2) at the guild level, disturbances favor habitat generalists, thereby changing the characteristics of SM community. At the species level, positive changes in the omnivore bank vole [*Clethrionomys glareolus* (Schreber, 1780)] and the habitat generalist granivore striped field mouse [*Apodemus agrarius* (Pallas, 1771)] were expected, while negative consequences were foreseen for herbivore *M. oeconomus* and granivore harvest mouse (*Micromys minutus* Pallas, 1771), both being habitat specialists.

MATERIAL AND METHODS

Study site

The SM community was studied in a spring-flooded meadow in the Nemunas River Delta (west Lithuania) (Fig. 1). The investigated meadow is 7.05 ha in size and flooded every year in spring (and sometimes in autumn). Depending on the flood height, the duration of submergence varies (Balčiauskas *et al*. 2012 and Table S1, Supporting Information). The site is located in a polder system, with its southern side bordering a raised embankment that stops water during flood periods. The investigated meadow is surrounded by ditches. An assessment of the habitat at all of the trapping locations in 2011–2016 confirmed its uniformity (Balčiauskas *et al*. 2019a). Later, habitat becomes increasingly transformed by human influence. Compared to other investigated sites in the Nemunas River Delta (see Balčiauskas *et al*. 2012), this was the only one subjected to the influence of both flooding and habitat transformation.

Flood intensity and duration

Based on long-term data, spring floods normally start in the middle ten days of March and the average duration of the flood is 16 days (Direction of Nemunas Delta Regional Park 2011). The study site is situated in the area flooded nearly every year (Fig. 1c). The trapping site is totally flooded for only a short time each spring, but the SM communities are eradicated. In the years of very low flood, not reaching the datum-line, such as in 2009, 2014, and 2020 (Table S1, Supporting Information), some SM

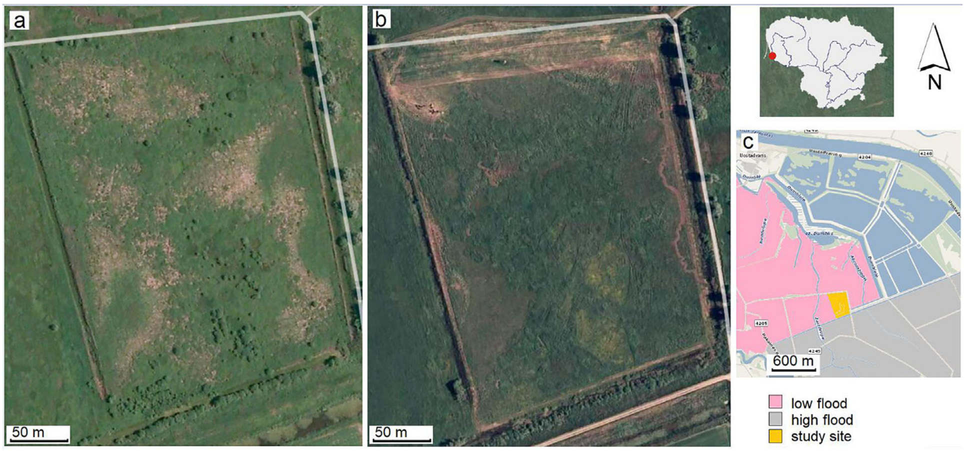

Figure 1 Study site in the Nemunas River Delta (central point 55°19’26.23"N, 21°20’24.15"E): (a) 2008–2012, before meadow mowing started; (b) 2017 after shrub removal, see machinery working in the northern part of the territory; (c) territory flooded in conditions of low flood and high flood (https://potvyniai.aplinka.lt/map), with the position in the country shown as an inset.

individuals may have survived in shrubs. The SM community is restored from nearest refugees, that is, surrounding levees (Balčiauskas *et al*. 2012).

In the last decade, floods have started earlier, reaching maximum water level even as early as January (Table S1, Supporting Information). We have therefore arbitrarily classified the onset as “late” if the maximum level was reached after February 14. Floods in 2008, 2010–2013, 2015, 2018, and 2019 were defined as high, while those in 2009, 2015, 2016, 2017, and 2020 as low. The onset of the flood in the years 2008, 2010–2012, and 2019 was late, while the onset in 2013, 2015–2018, and 2020 was early. 2009 and 2020 had no flood onset (Table S1, Supporting Information).

Development of the habitat transformation at the site

Prior to 2012, the meadow consisted mainly of Poaceae and Cyperaceae plants, partially overgrown by reeds and in several places by shrubs (Fig. 1a). Until 2012, it was not cut. In the summer of 2012 and 2013, the meadow was mowed once per year in the central part, leaving uncut reed belts along the side ditches. The width of the uncut belts was 5 to 25 m. By the time of SM trapping in autumn, areas that had been cut had regrown in full.

In 2014–2016, the meadow was not mowed; therefore, the growth of shrubs was intensive, reaching a maximum in 2016. In 2017, however, most of the shrubs were removed and the meadow was mowed again in the summer (Fig. 1b). The uncut belts of reeds on the sides were also narrower, 5–15 m wide. In 2018–2019, woody vegetation was minimal (stumps still present) and the reed belts narrow, up to 10 m wide. In 2020, meadow was transformed into a pasture (surrounded by electric fence), no woody vegetation was left at the site, stumps were removed, and the reed belts beyond the electric fence just 1–5 m wide. At the period of trapping, cattle were not present in the meadow, but kept in the neighboring territory.

Based on these data, habitat transformation in 2008–2011 was defined as low, in 2012–2016 as medium, and in 2017–2020 as high.

Small mammal trapping

We trapped SM in 2008–2020, using lines of 25 snap traps, each set 5 m apart. In 2011 and 2013–2020, we had one trapping session in the autumn, while in the other years, several sessions were used. Data from these sessions were pooled, as there were no shifts in the numbers of the most numerous SM species between the trapping sessions (Balčiauskas *et al*. 2019a). In total, 145 trap lines were used with a trapping effort of 9466 trap nights (Table 1).

Trap lines were positioned in the reed belts close to the drainage ditches at the perimeter of the site (Fig. 2). In 2009 and 2014, traps were also set diagonally (Fig. 2c,d). When the ground water was high, the configuration of the trap lines on the right side of the area was different: the lines were shorter (Fig. 2b,c) or positioned in a drier area (Fig. 2d,e). Traps were set for 3 days, checked once a day, and baited with bread crust and sunflower oil.

Table 1 Trapping time and trapping effort used in the study

Year	2008	2009	2010	2011	2012	2013	2014	2015, 2016, 2018, 2019	2017	2020
S	2	3	3	1	2	1	1	1	1	1
M	X	VII, IX, X	VIII, IX, X	X	IX, X	X	IX	IX or X	X	IX
TL	20	31	23	8	12	6	9	6	6	6

S, number of sessions; M, months; TL, number of trapping lines.

Figure 2 Design of the trapping: (a) 2008, August and September 2010, 2011–2013; (b) 2015–2020; (c) 2014; (d) 2009; (e) 2010 October.

Species were identified morphologically, with voles of the genus *Microtus* by their teeth. Skulls were deposited at the Laboratory of Mammalian Ecology of the Nature Research Centre (Vilnius, Lithuania).

The study was conducted in accordance with Lithuanian (the Republic of Lithuania Law on the Welfare and Protection of Animals No. XI-2271) and European legislation (Directive 2010/63/EU) on the protection of animals. Study was approved by the Animal Welfare Committee of the Nature Research Centre, protocol No GGY-7. In Lithuania, there is no need or obligation to obtain permission or approval to snap trap small mammals. Trapping was necessary, as we also collected material for pathogen evaluation and breeding parameters (not covered in the current paper). In less than 10 cases, trapped animals were killed by cervical dislocation.

Data processing

Relative abundance was evaluated as the number of trapped individuals per 100 trap nights and for every species (Table S2, Supporting Information). We used the Shannon–Wiener diversity index, H, on the base of $\log_2$ to express diversity, and Simpson's index, c, to express dominance within the SM community (Krebs 1999). In addition, species dominance was evaluated by the percentage of the total number of trapped individuals in a particular year.

To discover the impact of floods and habitat transformation at different trophic guilds, we analyzed changes in favorable states. The favorability of the states of the community were defined by the equal representation of insectivore, granivore, herbivore, and omnivore species in the community (Fox 1987), the state being unfavorable if the difference between the numbers of species trapped between any of these 4 groups in a given year was greater than 1 (Balčiauskas *et al*. 2019a). With the pool of species as shown in Table 2, the probability of the presence of both insectivores and granivores was 0.273, that of herbivores 0.364 and omnivores 0.090. We also tested the favorability of states when attributing water vole to omnivores due to the considerable share of animal food in its diet (Bieberich 2007), the respective probabilities for insectivores, herbivores, and granivores then being 0.273 and omnivores 0.181.

All parameters (number of species, relative abundance, diversity, dominance, as well as proportions of the most abundant species) were expressed as yearly values. The normality of the analyzed parameters was tested using Kolmogorov–Smirnov D. All parameters were distributed normally (Table S3, Supporting Information). The impacts of the flood magnitude, flood onset, and habitat transformation, as categorical factors, on the various

Table 2 Numbers of trapped individuals and small mammal community parameters in the flooded meadow in the Nemunas River Delta, 2008–2020

														Total	
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	*N*	%
S. araneus[I]	35	42	31	2	44	9	14	9	7	8	7	11	7	226	11.8
S. minutus[I]	3	8	12		3	2		4	3			3		38	2.0
N. fodiens[I]	2													2	0.1
M. arvalis[H]		2					2					9		13	0.7
M. agrestis[H]			1				3	10	7	6	10	3		40	2.1
M. oeconomus[H]	46	102	30	14	67	5	7	37		7	3	10	1	329	17.2
A. amphibius[H/O]			1								1			2	0.1
M. glareolus[O]			13	2	2	1	10	13	3		1	3		48	2.5
A. agrarius[G]	22	60	193	124	57	17	55	53	63	29	141	139	143	1096	57.2
A. flavicollis[G]					3						4	2		9	0.5
M. minutus[G]	53		33		10		5	2	1	3	1	3	3	114	5.9
Number of individuals *N*	161	214	314	142	186	34	96	128	84	53	168	183	154	1917	100
Species richness, *S*	6	5	8	4	7	5	7	7	6	5	8	9	4	11	
Shannon's H	2.1	1.73	1.85	0.67	2.03	1.8	1.98	2.19	1.33	1.86	1.01	1.45	0.46	1.97	
Simpson's c	0.26	0.35	0.41	0.77	0.28	0.35	0.37	0.28	0.58	0.36	0.71	0.59	0.86	0.38	
TE	750	1995	1525	600	750	450	681	450	450	459	450	450	456	9466	
RA	21.47	10.73	20.59	23.67	24.80	7.56	14.10	28.44	18.67	11.55	37.33	40.67	33.77	20.25	

Diet preferences marked with superscripts: I, insectivores, H, herbivores; O, omnivores; G, granivores (according to Balčiauskas *et al.* 2019a; Bieberich 2007). TE, trapping effort (number of trap-nights); RA, relative abundance (number of individuals per 100 trap nights).

parameters of the SM species and community were analyzed using GLMM. These dependent parameters were: relative abundances of *S. araneus*, *M. agrestis*, *M. oeconomus*, *A. agrarius*, and *M. minutus* (expressed as the number of trapped individuals per 100 trap nights and for every species), share of these listed species in the community (in %), and parameters of the community—relative abundance, number of trapped individuals, species richness, diversity, and dominance indices. Temporal data variability in the model was controlled using time as continuous predictor. We numbered years according to the 4-year-long cyclic changes in relative abundance, 4 being the year of minimum abundance, then the next year again starting from 1.

Diversity and species richness comparisons (based on the number of specimens of each species and on the number of species respectively) were done using individual rarefaction and pairwise diversity i-tests in PAST, ver. 4.01 (Ø. Hammer, D.A.T. Harper, Oslo, Norway), other calculations in Statistica for Windows, ver. 6.0 (StatSoft, Inc., Tulsa, OK, USA). The minimum significance level was set at $P = 0.05$.

RESULTS

We trapped 1917 SM individuals, representing common shrews (*Sorex araneus* Linnaeus, 1758), pygmy shrews (*Sorex minutus* Linnaeus, 1766) and water shrews [*Neomys fodiens* (Pennant, 1771)], common voles [*Microtus arvalis* (Pallas, 1779)], short-tailed voles [*Microtus agrestis* (Linnaeus, 1761)] and water voles [*Arvicola amphibius* (Linnaeus, 1758)], *M. oeconomus*, *C. glareolus*, yellow-necked mouse [*Apodemus flavicollis* (Melchior, 1834)], *A. agrarius* and *M. minutus* (Table 2).

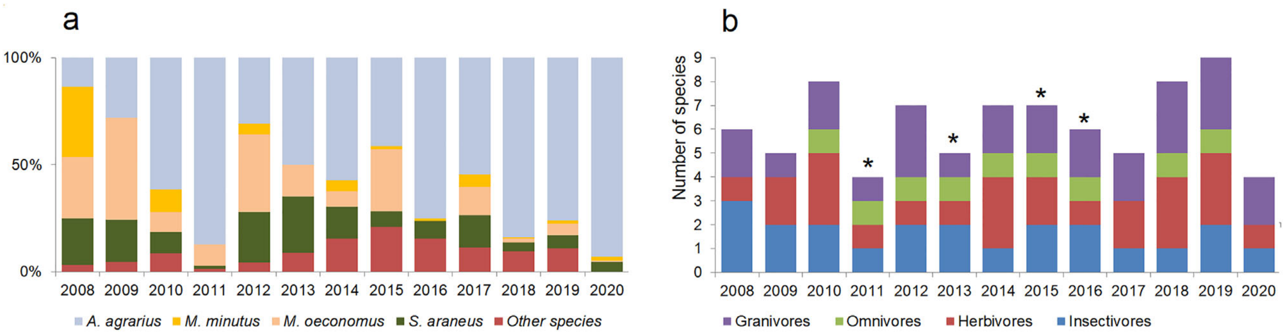

Figure 3 Proportions of the most abundant species (left) and trophic groups (right), 2008–2020a. Favorable states of the community are denoted with asterisks.

Changes in small mammal abundance and community structure, 2008–2020

The relative abundance of SM showed a decrease every fourth year (2009, 2013, 2017), these years being approximately half of the long-term average, 20.25 individuals per 100 trap nights (Table 2). Only 3 species dominated, *M. minutus* in 2008 (comprising 32.9% of all trapped individuals), *M. oeconomus* in 2009 and 2012 (47.7% and 36.0%, respectively), and *A. agrarius* in the rest of the years (comprising 41.4–92.9% of all trapped individuals) (Fig. 3a). A non-interrupted presence of *M. agrestis* was recorded in 2014–2019, but the species was not numerous (Table 2) nor abundant (Table S2, Supporting Information).

With a few exceptions, the relative abundance of SM was dependent on the numbers of granivores, particularly *A. agrarius* (Table S2, Supporting Information). Herbivore numbers, particularly *M. oeconomus*, determined the general SM abundance in 2009, and significantly contributed to the general abundance in 2008, 2012, and 2015. The contribution of insectivores, particularly *S. araneus*, was significant in 2008 and 2012, but never decisive.

Proportions of the trophic groups and favored states

Favored states for the community composition were recorded only in four years, 2011, 2013, 2015, and 2016, all before the increase in the meadow transformation. Unfavored states were dependent on the absence of omnivores in 2008, 2009, 2012, and 2020, while excessive numbers of insectivores were responsible for the unfavored states in 2008 and 2009, excessive numbers of herbivores in 2009, 2010, 2014, and 2017–2019) and excessive numbers of granivores in 2012 and 2017–2020) (Fig. 3b). Thus, habitat transformation was positive for both herbivores and granivores.

Attributing *A. amphibius* to omnivores would change the community state to favored in 2010. However, the state would remain unfavored in 2018 due to the excess of granivore species.

Impact of flood and habitat transformation

The time-controlled GLMM model showed that habitat transformation had a higher impact on SM species and community parameters (Wilks $\lambda = 0.00006$, $F_{2,16} = 16.07$, $P = 0.06$) than flood magnitude did ($\lambda = 0.0067$, $F_{1,8} = 18.58$, $P = 0.18$), with the time factor having no significant influence ($\lambda = 0.0102$, $F_{1,8} = 12.18$, $P = 0.22$). The flood onset also had no significant influence ($\lambda = 0.0029$, $F_{2,14} = 2.50$, $P = 0.32$).

Early flood onset (a longer time of the investigated territory being under water compared to a late flood onset or absence of it) resulted in an increase in the relative abundance of the SM and an increase in dominance, as well as increase in the proportion of *M. agrestis* and *A. agrarius*. An early flood onset correlated with a decrease in the share of *S. araneus* and *M. oeconomus*, the number of species in the community and their diversity (Fig. 4).

Data on the share and relative abundance of the most abundant SM in relation to the flood magnitude and habitat transformation are presented in Table S4, Supporting Information; the influence of these factors on the parameters of the SM community are given in Fig. 5 and Table S5, Supporting Information.

At the species level, high habitat transformation coupled with high flood resulted in an increase in the relative abundance of *A. agrarius* ($F_{4,8} = 4.43$, $P < 0.05$) and the relative abundance of the SM ($F_{4,8} = 3.87$,

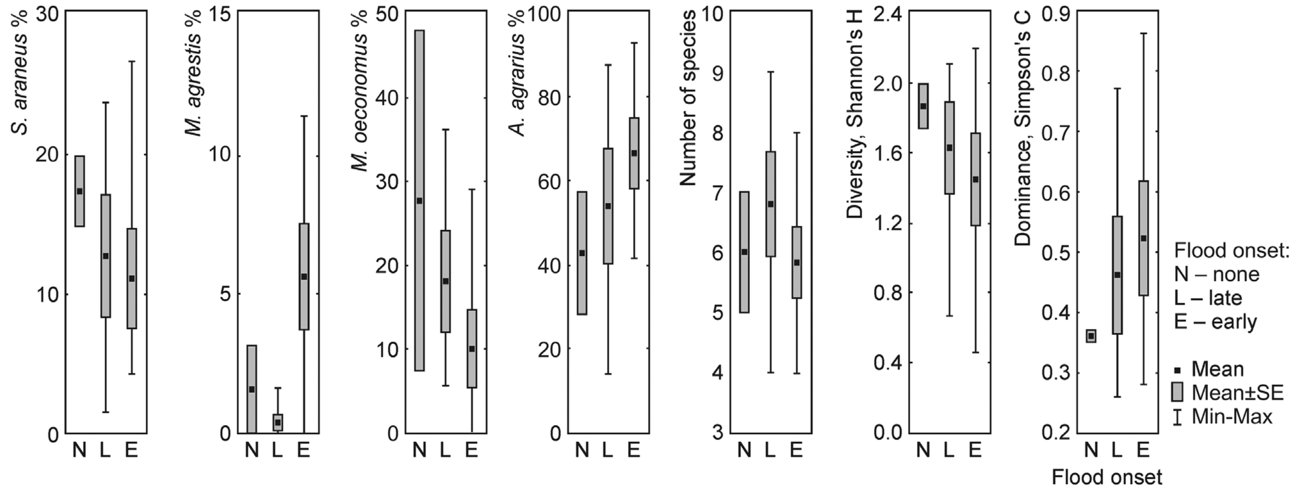

Figure 4 Best expressed influence of the onset of flood on small mammal species and community parameters.

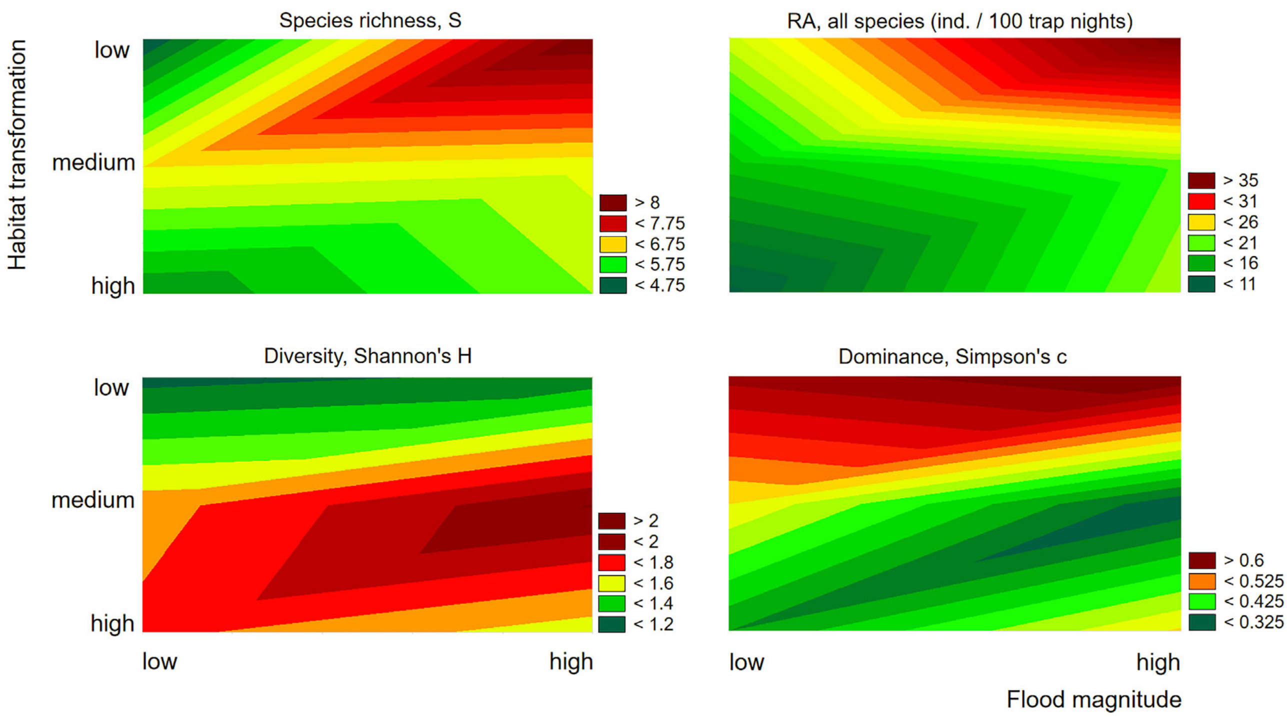

Figure 5 Impact of flood magnitude and habitat transformation on the community parameters. RA, relative abundance.

$P < 0.05$). Under such combination of factors, the maximum recorded share of *A. agrarius* in the community was registered, while the proportion of S. *araneus* was minimal (Fig. S1, Supporting Information). 53.3% of the variance of *A. agrarius* was explained by both factors, the RA of this species (25.0 ± 6.2 ind. per 100 trap nights) in the most transformed habitat significantly exceeding those in not transformed (9.8 ± 4.3, $P < 0.05$) and moderately transformed (9.0 ± 1.8, $P < 0.05$) habitats.

When high floods occurred in the medium transformed habitat, the relative abundance of *M. oeconomus* was at its highest. High floods in the years of low habitat transformation were positive to *M. minutus*, resulting in an increase in the proportion of this species in the community and resulting in its highest relative abundance (Table S4 and Fig. S1, Supporting Information).

Low floods occurring in the least transformed habitats resulted in the highest share of *M. oeconomus*. However, even in low flood levels, habitat transformation resulted in a decrease in the species share and its relative abundance (Fig. S1, Supporting Information).

Characteristics of the SM community were also influenced by flood magnitude and habitat transformation. We found that high floods resulted in an increase in the species richness in the natural and most transformed habitats, but no effect in the years when the meadow was medium transformed (Fig. 5). The poorest species richness was in the years after low floods (Fig. 6a; Table S5, Supporting Information).

In the years of high flood, the diversity of the SM community increased in natural (compared to the years of low flood, $t = 2.58$, $P = 0.01$), in medium transformed ($t = 3.00$, $P < 0.005$), and in transformed meadow ($t = 2.11$, $P < 0.05$). It was at its highest in the medium transformed meadow (compared to untransformed habitat, $t = 3.14$, $P < 0.005$; Fig. 6b; Table S5, Supporting Information).

In the years of low flood, the diversity of the SM community was at its poorest in the most transformed meadow (compared to natural, $t = 5.87$, $P < 0.001$ and to medium transformed habitat, $t = 5.79$, $P < 0.001$; Fig. 6b; Table S5, Supporting Information).

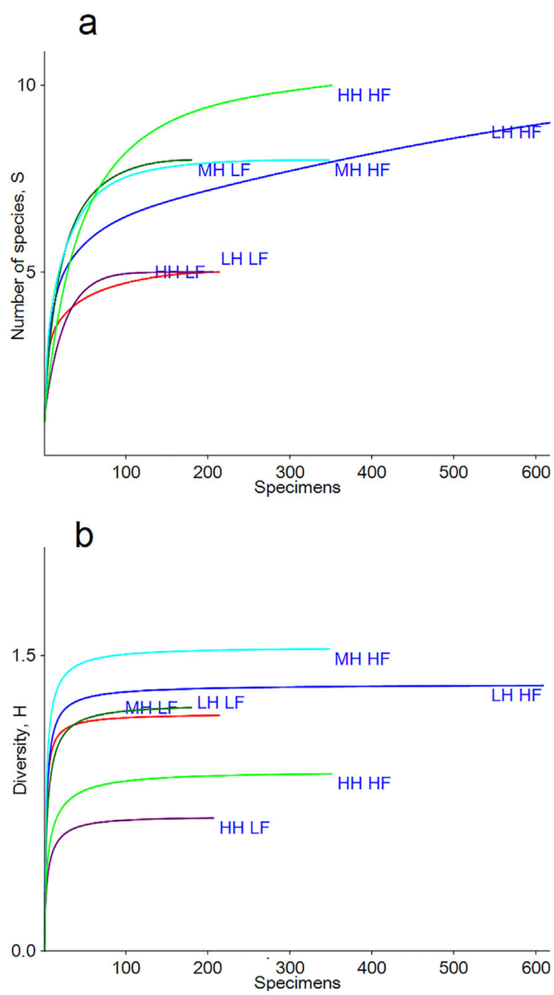

Figure 6 Differences in small mammal community characteristics depending on the flood magnitude and habitat transformation. LF, low; HF, high flood; LH, low; MH, medium; HH, high habitat transformation.

DISCUSSION

Correlating the patterns of the formation of animal communities to multiple disturbances, especially including species traits into the analysis, is a challenging task, but the results are valuable to ecology and conservation (Mouillot *et al*. 2013). Our results show that seasonal floods and habitat transformation work in synergy and have an effect on the SM community and their species.

Seasonal floods may be detrimental for small mammals

Seasonally flooded meadows are classical examples of an aquatic alteration of a terrestrial ecosystem which may be coupled with anthropogenic alteration (Schulz *et al*. 2015). Floods may be defined as catastrophic events, though flooding is expected to become more widespread and extreme (Datry *et al*. 2016). Flood impact is measurable to other extreme events, with their biological impact varying depending on the duration, severity and the timing of the flood, as well as being related to the biology and resilience of the affected organisms (Harris *et al*. 2018). In our study, the SM are most probably wiped out almost every spring (Balčiauskas *et al*. 2012), with only a small possibility of *M. minutus* surviving in the reedbeds during low, short-duration floods.

Comparison with the intermediate disturbance hypothesis

Notwithstanding that the intermediate disturbance approach was criticized (see Fox 2013), it has largely been assumed until recently that species diversity reaches its maximum at intermediate levels of disturbance (Shea *et al*. 2004; Mouillot *et al*. 2013). According to Crandall *et al*. (2003), the intermediate disturbance approach may not work for mobile vertebrates, as they can avoid flood and survive. If they do not survive however, the SM diversity after a flood will be facilitated by a recovery mechanism, which depends on the flood intensity and duration, the presence and distance of refuge areas, species composition and their biology (Hein & Jacob 2015), and predators (Sundell *et al*. 2012).

We found several SM community parameters having a distinct pattern in the multiscale disturbance space. The diversity of the SM community was highest in the moderately transformed habitat and after high flood (Figs 5 and 6), while other parameters (species richness, dominance, and relative abundance of SM) were at their highest in transformed habitat and after high flood. Therefore, our data only partially support the intermediate disturbance hypothesis. We interpret the general pattern as a successional response of SM, being in accordance with classic theory (see Shafi & Yaranton 1973; Kirkland 1990; Swihart & Slade 1990). The multi-disturbance effect on the flooded meadow is most probably close to the nonequilibrium state-and-transition model proposed by Letnic *et al*. (2004), though our time period is too short to test it.

Disturbance effects on small mammal species

Two generalist SM species, *M. agrestis* and *A. agrarius*, reacted positively to multi-disturbance: their relative abundance and share in the community were highest after high floods and in transformed habitat (see Fig. S1, Supporting Information). *M. agrestis* is "an unspecialized opportunist living in a variety of habitat types" (Hansson 1977); therefore, we may expect different species reactions in various ecosystems. The preferred habitats are open grasslands (Sundell *et al*. 2012), wet meadows, and forests with lush herbaceous vegetation (Mathias *et al*. 2017). The main competitors of *M agrestis* are other vole species (Myllymäki 1977). The reaction of *M. agrestis* to agricultural changes in the landscape is not well expressed (Yletyinen & Norrdahl 2008), but it is clearly negative to sheep grazing (Wheeler 2008). In our study site, grazing started in 2020, but *M. agrestis* was absent, thus we need more time to confirm any negative impact.

A. agrarius is considered as habitat generalist (Schlinkert *et al*. 2016). Though it was reported as being abundant in crops and fallow land, but not in mowed meadow and pastures (Benedek & Sîrbu 2018), recently observed species expansion in Slovakia (Miklós *et al*. 2015; Tulis *et al*. 2016; Kalivodová *et al*. 2018) allows us to expect this process being characteristic to other countries. In Lithuania, *A. agarius* is very abundant in commercial orchards (Balčiauskas *et al*. 2019b), expanding to forest (Balčiauskas *et al*. 2017) and already present in commensal habitats (Balčiauskas & Balčiauskienė 2020).

The reaction of the specialist species to multi-disturbance was negative. We found *M. minutus* to be most abundant in not transformed habitat and in the years of high flood (Table 2; Fig. S1, Supporting Information). This species of SM is particularly related to reedbeds (Kiviat 2019) and other tall-grass and shrub habitats (Kuroe *et al*. 2007; Hata *et al*. 2009), unmowed areas being very important for *M. minutus* wintering (Vecsernyés 2020). During the habitat transformation, the reedbed area was notably lessened at the site. In our interpretation, high floods are advantageous to this species lessening concurrence with other granivore SM species (Balčiauskas *et al*. 2012, 2019a). Therefore, our data refute the position of Darinot and Favier (2014) that the impact of floods on this species and SM communities is unknown—it is positive, at least in fine-grained habitat to be re-colonized by SM in the several months following a flood.

In the studied meadow, the share of *M. oeconomus* in the SM community was largest in 2008 and 2009, these being the years with no human disturbance of the habitat (see Fig. S1, Supporting Information). Relative abundance increased in the years after high floods. This is in accordance with Tast (1966), who reported that flooded meadows and thickets are the most suitable habitats for the species. An intolerance of disturbance, especially mowing, has also been shown to be characteristic of *M. oeconomus* in other countries (Horváth & Herczeg 2013), while floods and impoundments are important in maintaining marshy habitats (van Laar 2018). We may therefore expect a further decrease of *M. oeconomus* numbers at the studied site. Although a novel virus strain specific to *M. oeconomus* was present in 2015–2017 samples (Drewes *et al*. 2020), we have no data if it affects species numbers or animal viability.

Finally, *S. araneus* manifested as a SM species whose response to multiple disturbances was closest fit to the intermediate disturbance hypothesis (see Fig. S1, Supporting Information). As shown by Czabán *et al*. (2015), dry areas are required by *S. araneus*; thus, they must leave during flood periods and re-colonize territory later. According to Schmidt *et al*. (2009), low grazing intensity (equaling medium transformation in our case) however results in a higher abundance of these shrews and has no negative effects on other parameters (body mass, reproduction, and sex ratio). We noted a trend of decrease of *S. araneus* abundance after the maximum habitat transformation in the years after 2017 (see Table S2, Supporting Information).

Small mammal communities subject to flooding and habitat transformation

Extreme climatic events, including floods, are becoming more frequent and intense (Diez *et al*. 2012), and they might add to the anthropogenic transformation of floodplain habitats. We agree with Gentili *et al*. (2014) that such transformed habitats will be dominated by a few generalist species (in our case, *A. agrarius*), while the abundance of habitat specialists will decrease, and shifts in life histories may occur (Brown & Fuller 2006). Therefore, we might prognose that a transformation of flooded meadows by agricultural activities will result in a decrease in SM diversity.

Generalizing, our study suggests that synergic disturbances (seasonal floods and habitat transformation) in a flooded meadow may lead to a loss of diversity and complexity of the SM assemblages, but not necessarily to a loss of the overall abundance of individuals. The impact of habitat transformation was higher than the impact of the flood magnitude, and the date of flood onset had no significant influence. Habitat generalist species (such as *A. agrarius*) were favored, while habitat specialists (*M. minutus* or *M. oeconomus*) were disadvantaged. After an increase in the meadow transformation due to mowing and grazing, unfavored states in the SM community prevailed, with excessive numbers of herbivore and granivore species present. At the species level, the variability of responses depended on their life histories and biology traits.

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REFERENCES

Andersen DC, Wilson KR, Miller MS, Falck M (2000). Movement patterns of riparian small mammals during predictable floodplain inundation. *Journal of Mammalogy* **81**, 1087–99.

Balčiauskas L, Balčiauskienė L, Janonytė A (2012). The influence of spring floods on small mammal communities in the Nemunas River Delta, Lithuania. *Biologia* **67**, 1220–9.

Balčiauskas L, Čepukienė A, Balčiauskienė L (2017). Small mammal community response to early meadow–forest succession. *Forest Ecosystems* **4**, 11.

Balčiauskas L, Skipitytė R, Balčiauskienė L, Jasiulionis M (2019a). Resource partitioning confirmed by isotopic signatures allows small mammals to share seasonally flooded meadows. *Ecology and Evolution* **9**, 5479–89.

Balčiauskas L, Balčiauskienė L, Stirkė V (2019b). Mow the grass at the mouse's peril: Diversity of small mammals in commercial fruit farms. *Animals* **9**, 334.

Balčiauskas L, Balčiauskienė L (2020). On the doorstep, rodents in homesteads and kitchen gardens. *Animals* **10**, 856.

Benedek AM, Sîrbu I (2018). Responses of small mammal communities to environment and agriculture in a rural mosaic landscape. *Mammalian Biology* **90**, 55–65.

Bieberich C (2007). *Microtus oeconomus* (on-line), Animal Diversity Web. [Cited 10 Dec 2020.] Available from URL: https://animaldiversity.org/accounts/Microtus_oeconomus/

Blakey RV, Kingsford RT, Law BS, Stoklosa J (2017). Floodplain habitat is disproportionately important for bats in a large river basin. *Biological Conservation* **215**, 1–10.

Brown TT, Fuller CA (2006). Stress and parasitism of white-footed mice (*Peromyscus leucopus*) in dry and floodplain environments. *Canadian Journal of Zoology* **84**, 1833–9.

Chamberlain MJ, Leopold BD (2003). Effects of a flood on relative abundance and diversity of small mammals in a regenerating bottomland hardwood forest. *Southwestern Naturalist* **48**, 306–9.

Crandall RM, Hayes CR, Ackland EN (2003). Application of the intermediate disturbance hypothesis to flooding. *Community Ecology* **4**, 225–32.

Crespin L, Papillon Y, Abdoulaye D, Granjon L, Sicard B (2008). Annual flooding, survival and recruitment in a rodent population from the Niger River plain in Mali. *Journal of Tropical Ecology* **24**, 375–86.

Czabán D, Zsebok S, Cserkész T, Farkas J (2015). Impact of changing water level on shrew populations in the kis-balaton wetlands, Western Hungary. *Applied Ecology and Environmental Research* **13**, 349–60.

Darinot F, Favier C (2014). Inondation hivernale et mouvements migratoires au sein d'une population de rat des moissons, *Micromys minutus* (Pallas, 1771). *Publications de la Société Linnéenne de Lyon* **83**, 235–44.

Datry T, Fritz K, Leigh C (2016). Challenges, developments and perspectives in intermittent river ecology. *Freshwater Biology* **61**, 1171–80.

Diez JM, D'Antonio CM, Dukes JS *et al*. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment* **10**, 249–57.

Direction of Nemunas Delta Regional Park (2011). *Floods*. [Cited 15 Nov 2020.] Available from URL: http://www.nemunodelta.lt/16976/gamta/potvyniai.html

Drewes S, Jeske K, Straková P *et al*. (2020). Identification of a novel hantavirus strain in the root vole (*Microtus oeconomus*) in Lithuania, Eastern Europe. *Infection, Genetics and Evolution* **90**, 104520.

Fox BJ (1987). Species assembly and the evolution of community structure. *Ecology and Evolution* **1**, 201–13.

Fox JW (2013). The intermediate disturbance hypothesis should be abandoned. *Trends Ecology and Evolution* **28**, 86–92.

Gentili S, Sigura M, Bonesi L (2014). Decreased small mammals species diversity and increased population abundance along a gradient of agricultural intensification. *Hystrix* **25**, 39–44.

Golet GH, Hunt JW, Koenig D (2011). Decline and recovery of small mammals after flooding: Implications for pest management and floodplain community dynamics. *River Research and Applications* **29**, 183–94.

Hansson L (1977). Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. *Oikos* **29**, 539–44.

Harris RMB, Beaumont LJ, Vance TR *et al*. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* **8**, 579–87.

Hata S, Sawabe K, Natuhara Y (2009). A suitable embankment mowing strategy for habitat conservation of the harvest mouse. *Landscape and Ecological Engineering* **61**, 133–42.

Hein S, Jacob J (2015). Recovery of small rodent populations after population collapse. *Wildlife Research* **42**, 108–18.

Hein S, Jacob J (2019). Population recovery of a common vole population (*Microtus arvalis*) after population collapse. *Pest Management Science* **754**, 908–14.

Hidasi-Neto J, Bini LM, Siqueira T, Cianciaruso MV (2020). Ecological similarity explains species abundance distribution of small mammal communities. *Acta Oecologica* **102**, 103502.

Horváth GF, Herczeg R (2013). Site occupancy response to natural and anthropogenic disturbances of root vole: conservation problem of a vulnerable relict subspecies. *Journal for Nature Conservation* **21**, 350–8.

Kalivodová M, Kanka R, Miklós P, Sládkovičová VH, Žiak D (2018). Importance of wetland refugia in agricultural landscape provided based on the community characteristics of small terrestrial mammals. *Ekológia (Bratislava)* **37**, 358–68.

Kirkland GL Jr (1990). Patterns of initial small mammal community change after clearcutting of temperate North American forests. *Oikos* **59**, 313–20.

Kiviat E (2019). Organisms using *Phragmites australis* are diverse and similar on three continents. *Journal of Natural History* **53**, 1975–2010.

Klinger R (2006). The interaction of disturbances and small mammal community dynamics in a lowland forest in Belize. *Journal of Animal Ecology* **75**, 1227–38.

Kluever BM, Gese EM, Dempsey SJ (2016). The influence of wildlife water developments and vegetation on rodent abundance in the Great Basin Desert. *Journal of Mammalogy* **97**, 1209–18.

Krebs CJ (1999). *Ecological Methodology*, 2nd edn. Addison-Wesley Educational Publishers, Inc., Menlo Park, CA.

Kuroe M, Ohori S, Takatsuki S, Miyashita T (2007). Nest-site selection by the harvest mouse *Micromys minutus* in seasonally changing environments. *Acta Theriologica* **52**, 355–60.

Larned ST, Datry T, Arscott DB, Tockner K (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology* **55**, 717–38.

Letnic M, Dickman CR, Tischler MK, Tamayo B, Beh CL (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114.

Markovych O, Tymchyk V, Kolesnikova I (2019). Leptospirosis in Zakarpattia Oblast (2005–2015). *Vector-Borne and Zoonotic Diseases* **19**, 333–40.

Mathias ML, Hart EB, Ramalhinho MG, Jaarola M (2017). *Microtus agrestis* (Rodentia: Cricetidae). *Mammalian Species* **49**, 23–39.

Michel N, Burel F, Legendre P, Butet A (2007). Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France. *Landscape Ecology* **228**, 1241–53.

Miklós P, Žiak D, Hulejová Sládkovičová V (2015). Community of small terrestrial mammals in Danubian inundation area in autumn 2013. *Folia Faunistica Slovaca* **20**, 105–11.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* **28**, 167–77.

Myllymäki A (1977). Interactions between the field vole *Microtus agrestis* and its microtine competitors in Central-Scandinavian populations. *Oikos* **29**, 570–80.

Opperman JJ, Moyle PB, Larsen EW, Florsheim JL, Manfree AD (2017). *Floodplains: Processes and Management for Ecosystem Services*. University of California Press, Oakland, CA.

de la Sancha NU, Maestri R, Bovendorp RS, Higgins CL (2020). Disentangling drivers of small mammal diversity in a highly fragmented forest system. *Biotropica* **52**, 182–95.

Schlinkert H, Ludwig M, Batáry P *et al*. (2016). Forest specialist and generalist small mammals in forest edges and hedges. *Wildlife Biology* **22**, 86–94.

Schmidt NM, Olsen H, Leirs H (2009). Livestock grazing intensity affects abundance of Common shrews (*Sorex araneus*) in two meadows in Denmark. *BMC Ecology* **9**, 2.

Schulz R, Bundschuh M, Gergs R *et al*. (2015). Review on environmental alterations propagating from aquatic to terrestrial ecosystems. *Science of the Total Environment* **538**, 246–61.

Shafi MI, Yarranton GA (1973). Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* **54**, 897–902.

Shea K, Roxburgh SH, Rauschert ESJ (2004). Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* **7**, 491–508.

Soykan CU, Sabo JL (2009). Spatiotemporal food web dynamics along a desert riparian–upland transition. *Ecography* **32**, 354–68.

Suchomel J, Hadaš P (2017). Effects of moisture conditions on the small mammal communities of floodplain forests in south Moravia (Czech Republic). *Šumarski List* **141**, 557–62.

Sundell J, Church C, Ovaskainen O (2012). Spatio-temporal patterns of habitat use in voles and shrews modified by density, season and predators. *Journal of Animal Ecology* **81**, 747–55.

Swihart RK, Slade NA (1990). Long-term dynamics of an early successional small mammal community. *The American Midland Naturalist* **123**, 372–82.

Tast J (1966). The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. *Annales Zoologici Fennici* **3**, 127–71.

Tulis F, Ambros M, Baláž I *et al*. (2016). Expansion of the Striped field mouse (*Apodemus agrarius*) in the south-western Slovakia during 2010–2015. *Folia Oecologica* **43**, 64–73.

van Laar V (2018). Herkomst en verspreidingsgeschiedenis van de noordse woelmuis (*Microtus oeconomus* (Pallas, 1776)) in West-Europa, in het bijzonder in Nederland. *Lutra* **61**, 219–67.

Vanbergen AJ, Woodcock BA, Gray A *et al*. (2017). Dispersal capacity shapes responses of river island invertebrate assemblages to vegetation structure, island area, and flooding. *Insect Conservation and Diversity* **10**, 341–53.

Vecsernyés F (2020). Autumn habitat selection of the harvest mouse (*Micromys minutus* Pallas, 1771) in a rural and fragmented landscape. *Revue Suisse de Zoologie* **126**, 111–25.

Vigués J, Grajera J, Arrizabalaga A, Torre I (2018). Long-term human-induced landscape changes and small mammal communities in a Mediterranean place. *Galemys* **30**, 37–47.

Wasinski B, Dutkiewicz J (2013). Leptospirosis-current risk factors connected with human activity and the environment. *Annals of Agricultural and Environmental Medicine* **20**, 239–44.

Wheeler P (2008). Effects of sheep grazing on abundance and predators of field vole (*Microtus agrestis*) in upland Britain. *Agriculture, Ecosystems & Environment* **123**, 49–55.

Wijnhoven S, Leuven RS, van der Velde G, Eijsackers HJ (2008). Toxicological risks for small mammals in a diffusely and moderately polluted floodplain. *Science of the Total Environment* **406**, 401–6.

Williams AK, Ratnaswamy MJ, Renken RB (2001). Impacts of a flood on small mammal populations of lower Missouri River floodplain forests. *The American Midland Naturalist* **146**, 217–21.

Wuczyński A, Jakubiec Z (2013). Mortality of game mammals caused by an extreme flooding event in south-western Poland. *Natural Hazards* **69**, 85–97.

Yletyinen S, Norrdahl K (2008). Habitat use of field voles (*Microtus agrestis*) in wide and narrow buffer zones. *Agriculture, Ecosystems & Environment* **123**, 194–200.

Zárybnická M, Riegert J, Bejček V *et al*. (2017). Long-term changes of small mammal communities in heterogenous landscapes of Central Europe. *European Journal of Wildlife Research* **63**, 89.

Zhang M, Wang Y, Li B *et al*. (2014). Small mammal community succession on the beach of Dongting Lake, China after the Three Gorges Project. *Integrative Zoology* **9**, 294–308.

Zhang M, Wang Y, Li B, Feng Z, Zhao Y, Xu Z (2018). Synergistic succession of the small mammal community and herbaceous vegetation after reconverting farmland to seasonally flooded wetlands in the Dongting Lake Region, China. *Mammal Study* **43**, 229–43.

SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Data on floods in the Nemunas River Delta, representing influence upon the study site

Table S2 Relative abundance (individuals per 100 trap nights) of small mammals in the flooded meadow in the Nemunas River Delta, 2008–2020

Table S3 Results of normality test for analyzed parameters (expressed as yearly averages), based on Kolmogorov-Smirnov D. Distributions of all parameters are perfectly normal

Table S4 Impact of the flood magnitude and habitat transformation on the proportion of the most abundant small mammal species (in % of all trapped individuals) and their relative abundance (individuals per 100 trap nights) in the flooded meadow in the Nemunas River Delta

Table S5 Impact of the flood magnitude and habitat transformation on small mammal community parameters in the flooded meadow in the Nemunas River Delta

Figure S1 Impact of the flood magnitude and habitat transformation on the most abundant small mammal species. RA – relative abundance, individuals per 100 trap nights.

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