

COMMUNITY-LEVEL RESPONSE TO DIFFERENT HUMAN DISTURBANCES AND LAND USE OF SMALL MAMMALS IN TWO MARSHLAND HABITAT PATCHES IN HUNGARY

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Abstract - Marshlands are important ecosystems that provide valuable habitats for wildlife communities. We investigated the small mammal community-level response to different human disturbances and land use in the Kis-Balaton Landscape Protection Area, which is an endangered marshland ecosystem of Hungary. Land use, conservation management and other human disturbances (burning, mowing) together with unfavorable weather conditions have caused the degradation of the original homogeneous sedgy marshland on both sampled areas. We measured the species turnover between the different periods separated by the habitat changes. Our results suggest that populations of the habitat-specialist species of marshland areas (e.g. endangered Hungarian subspecies of root vole) are sensitive to the negative effects of environment and human disturbances. The combined effect of human disturbances and the stochastic processes of the environment can cause the disappearance and substitution of character species stabilizing the communities, which in turn leads to the modification of species composition and structure of small mammal assemblages.

Key words: Human disturbance, small mammals, community, capture-mark-recapture, marshland, Hungary

INTRODUCTION

One of the main problems of biological conservation is the degradation of natural habitats, which is the most important factor in the local extinction of populations and decrease of biodiversity (Wilson, 1988, Diamond, 1989, Smith et al., 1993). The recognition and understanding of regional decline and the fragmentation of habitats is one of the basic ways of preserving the environment (Wilcove et al., 1986, Soulé and Khom, 1989). Habitat fragments are isolating, they compose habitat islands and plots, between which some of the species are able to move, whilst the migration of others does not exist (or occurs at a small rate). Isolated patches that evolve in the course of fragmentation are bordered by artificial areas, whose characteristics differ from the previous ones. Therefore, fragmentation is a great risk factor

to wild populations (Gilpin and Diamond, 1980, Ims and Stenseth, 1989). As soon as a given continuous habitat is divided up, the motion of animals becomes limited as a direct consequence (Fahrig and Merriam, 1985), which decreases the effective size and subsequently the viability of the population (Soule, 1986, Boyce, 1992).

Fragmentation processes are considerable in refugial, wet, marshy habitats as well, because of the dramatic changes in weather conditions, human land use (water management, marshland reconstruction, etc.) and other anthropogenic disturbances (Gibbs, 1993, 2000; Leibowitz, 2003). Wetlands are important ecosystems that provide valuable habitats for wildlife (Mitsch and Gosselink 2000) and these habitats are among the most threatened areas on Earth (Turner, 1991, Williams, 1993). Wetlands and marshlands

typically occur in discrete patches in the matrix of upland habitats, and the local populations of wetland species are small and isolated, and thus vulnerable to extinction (Gibbs, 1993, Gibbons, 2003, Dodd, 1990, Sjögren, 1991, Snodgrass et al., 2000).

Kis-Balaton is worth considering as one of these endangered areas of Hungary: it is the biggest near-natural wetland habitat in the country (14745 ha). The marshland area was drained in the 1920s and Kis-Balaton has been legally protected as a Landscape Protection Area since 1976. It has been part of the Balaton Uplands National Park since 1997 and has been under the protection of the Ramsar Convention since 1979. Nearly the whole area of Kis-Balaton has been part of the Natura 2000 Network since 1994, based on the Birds and Habitats Directives. For improving and broadening the natural filter-system of the marshlands, the Kis-Balaton wetlands have been under reconstruction since 1992. Because of flooding, wetland management has enlarged the range of the Kis-Balaton water-reserve system, and therefore the water level of reedy- and sedgy areas has grown, which is the most important abiotic constraint in these habitats with regard to the alteration of vegetation (van der Valk et al., 1994). Because of the relict characteristic of the Kis-Balaton marshlands, the water-reserve system-maintaining human interventions affect the biodiversity to a considerable degree: thus the hypothesis-testing control of these effects are highlighted projects in the Hungarian Biodiversity Monitoring System (HBMS).

Marshlands are important habitats for small mammals (Martin et al., 1991; Krištofík, 2001; Bias and Morrison, 2006; Scott et al., 2008; Michelat and Giraudoux, 2006) and therefore small mammals are the typical subjects for the biodiversity monitoring of the relict Kis-Balaton marshlands. In terms of mammals, one of the main tasks of the project is connected to the critically endangered root vole, *Microtus oeconomus* (Pallas 1776). We are working on correcting the information about its distribution and we are mapping and monitoring its remaining populations. The spread of root vole was wider after the ice-age than it is nowadays, incorporating the

German coast of the North Sea, eastern and central Sweden and Great Britain (Tast, 1982, Mitchell-Jones et al., 1999, Yalden, 1999). The Hungarian subspecies of the root vole (*Microtus oeconomus mehelyi*), similarly to the root vole populations that have survived in other parts of Europe and which represent glacial and postglacial relicts (von Tast, 1982; Chaline, 1987, Leijs et al., 1999, Burnhoff et al., 2003), is particularly endangered as a result of human and natural disturbance. The strictly protected root vole, a species within the small mammal fauna of the Kis-Balaton area, is a relict species that has survived in refugial spots compared to the larger distribution range in earlier climatic periods. The other significant species of the fauna is the field vole, *Microtus agrestis* (Linnaeus, 1761). This rodent has Holarctic distribution, but has a more common and continuous Transdanubian range (Schmidt, 1974, Horváth et al., 2004). In addition to the species conservation and population biological approach, the other aims of monitoring programs are to examine if water-regulation processes and other marshland related human activities have measurable effects on the diversity of small mammal communities and their temporal changes (Lelkes and Horváth, 2000; Horváth, 2001, 2004).

In this study, we performed a community ecological analysis of data derived from the trapping that took place during the period 1999-2008 in two marshlands of Kis-Balaton, by comparing two neighboring marshland habitat patches. The two habitats are divided by a highway and differ in both their protection status and exposure to human disturbances and land use. Our basic question was the following: do the structure and content of the small mammal communities of the two habitats differ significantly between the macro-habitats that are very similar in the characteristics of vegetation but vary in land-use and disturbance effects? The aims of this study were (i) to compare the abundance relations of species in the small mammal community; (ii) to examine the alteration of community structure and species composition in comparison of the three sampled periods; (iii) to examine species substitution inside the community and evaluate the loss of species and recolonization.

MATERIALS AND METHODS

Study area

Two plots were selected for trapping in the Kis-Balaton area over a 10-year-long monitoring period. Of the two examined marshland patches, one was located on the northern side of Road 76, which connects Balatonszentgyörgy with Sármellék, and the other was situated on its western side (eastern-grove) (Fig. 1). The first sampling plot (SP_N) was on the northern part of the central cross-canal. It is a large, drying sedge-meadow that has a greater diversity of herbaceous plants compared to the other plots. This habitat appeared due to the filling up of the former freshwater marshland. The quadrat is an intensely degraded sedge habitat, where the high density of *Calamagrostis epigeios* indicates the negative effects of eutrophication (accumulation of nutrients). Altitudes are increasing uniformly from the reedy part towards the road, which is clearly shown by the gradual thinning and shrinkage of common reed stocks (*Phragmites australis*) so that only single and dwarf specimens are to be found. The second sampling plot (SP_S) was assigned on the southern side of the Road 76, characterized by homogeneous sedge beds with only a few non-continuous small reed patches. It is a low, rarely double-leveled reed-meadow where the dominant species of the vegetation is the lesser pond sedge (*Carex acutiformis*). Lower down, the area is characterized by higher water availability.

The two examined habitat patches differed in the manner of land-use and thereby by the conservation management, because Road 76 is the northern border of the Balaton Uplands National Park and Kis-Balaton as well. Therefore, the marshland area lying south of the road is under the management of the National Park as a protected area and has been part of the Natura 2000 network since 2004. The marshland, which is located north of the road, was protected as an “ex-lege” moorland until 2001, but almost the whole area was privatized in 2002.

The land use, conservation management and other human disturbances (burning, mowing and priva-

tization) with the unfavorable weather have caused the degradation of the original homogeneous sedge marshland in both of the sampled areas. The habitat alteration was the reason for separating the examined 10-year-long period into three terms/seasons in the community-level comparison of small mammals. *Period 1* (1999-2000): untouched, near-natural habitat; the root vole occurred in the area. *Period 2* (2002-2003): the combined effects of human activities (burning, mowing) and the dry weather caused considerable degradation of the vegetation, and the root vole disappeared from the two examined habitat patches. Burning was done only in the southern region, followed by regular mowing until 2004. There was no burning in the northern habitat: however, as part of private farming, the area was intensively mowed through the arid season until 2004. *Period 3*: because of the high level of rainwater, the owner was not able to use the field on the northern site, and therefore the anthropogenic effects ceased, which positively affected the quality of the habitat so that the root vole reappeared in the small mammal community of the examined habitat. We prepared the plans for management activities in the southern area in cooperation with the National Park. The discontinuation of mowing contributed to the regeneration of the vegetation in the patches with lower spatial altitude (i.e. our sampled sites). Mowing treatments concentrated only on the patches that are featured by higher spatial altitude and dominated by *Solidago gigantea* in order to stop the spreading of this invasive plant species.

Trapping method

The method applied in each of the sampling plots was the capture-mark-recapture (CMR) method with the same box-type live-traps (75x95x180 mm). We used the same 11 × 11 trap grid in both of the habitat patches, where traps were 5 m apart. Like the traps themselves, the trapping technique was also the same in all cases: bacon and cereals were mixed with aniseed extract and used with vegetable oil as bait. The traps were checked two times a day at 7 am and 7 pm, and the traps were triggered during the day. From the number of traps in the two sampling plots and the number of sampling nights in the three

monitoring periods, we counted the number of trap-occasions, which was 25,652 trapping-nights in the present study. The captured animals were marked individually and their sex was recorded (by females: gravidity or lactation), as well as their age and body mass. Animal age was estimated based on body mass and overall appearance.

Statistical methods

Our capture data were recorded in a Manly-Parr diary of captures and stored in a Microsoft Access database. The trap network used for all of the sampling plots was the same, but the number of the trapping nights in the three periods was different. We therefore had to standardize our data to 100 trap-nights for comparing the two sampled plots. The relative index of abundance (I) was calculated according to the following formula:

$$I = 100 \times n/P,$$

where n is the number of animals captured in the given trapping period and P is the number of trap-nights. We counted relative frequency values for every monitoring period from the summarized abundance data. Thus, we gave the species list of the three periods separately, the capture number and the relative index of abundance of species in every period, and finally we counted the relative proportion of the species in the community of the given period. We tested the distribution of character species between the periods by homogeneity testing (G-test) based on relative frequency data (Zar, 1996).

The structure and diversity of the small mammal community was described by four different indices: species richness (S), Shannon's index based on natural logarithms (H'), Shannon evenness ($E = H'/H_{max}$) and reciprocal Simpson's index ($1/D$) (Magurran, 1988). Values of Shannon's index were compared by the approximate t -test (Zar, 1996). Simpson's index is especially sensitive to the size of the population of different species and less sensitive to the number of species in a given community. Therefore, it is an adequate diversity index for characterizing small mammal

communities where the number of component species does not differ significantly, but there are great differences in the size of populations (Adamczewska-Andrzejewska et al., 1979). The use of reciprocal Simpson's index ensures the enlarging of diversity values so that we can get more expressive, descriptive numbers for typifying various communities by Simpson's diversity (Magurran, 1988, Heroldová et al., 2007). Additionally, we analyzed the dominance order within the community according to the relative frequency of the species.

We measured species turnover (β diversity) occurring between the different periods separated by habitat changes based on the Sørensen similarity index. The easiest way to measure the β diversity is by the use of similarity coefficients. This index is designed to equal 1 in cases of complete similarity and 0 if the sites are dissimilar and have no species in common (Magurran, 1988). As the two habitats differed in landscape usage and the effects of human disturbance (SP_N, SP_S), we classified the small mammal communities revealed in the three separate periods with the Sørensen binary and Bray-Curtis quantitative similarity index based on the usage of relative abundance data. The changes in the small mammal community structure were examined on the basis of the Bray-Curtis index. For hierarchic cluster analysis, we used the UPGMA fusion method in both cases: the calculations were carried out by the SYN-TAX 2000 program (Podani, 1997).

RESULTS

There were 16 small mammal species in the two examined marshland areas (SP_N; SP_S) in the 10-year-long monitoring period and the total number of captures was 1836. There were no significant differences between the two marshlands in the effectiveness of trapping summarized for the habitat patches of ($\chi^2 = 0.55$, n.s.). There was no significant difference either in the pairwise comparison of relative abundance values counted periodically from the summarized data on the marshlands lying north of the road ($\chi^2 = 0.08 - 2.53$, n.s.). Due to the joint effect of several disturbances (burning, mowing) characterizing the southern

Table 1. Capture parameters of small mammals in the two sampling plots and three sampling periods.

Sampling area/ period/capture values	Sampling Plot 1 (North)						Sampling Plot 2 (South)					
	Period 1 (1999-2000)		Period 2 (2002-2003)		Period 3 (2007-2008)		Period 1 (1999-2000)		Period 2 (2002-2003)		Period 3 (2007-2008)	
	C	I	C	I	C	I	C	I	C	I	C	I
<i>S. araneus</i>	102	2.91	41	1.06	82	1.51	155	4.42	23	1.12	61	1.74
<i>S. minutus</i>	15	0.43	6	0.15	1	0.02	26	0.74	0	0.00	3	0.09
<i>N. fodiens</i>	4	0.11	0	0.00	0	0.00	1	0.03	0	0.00	0	0.00
<i>N. anomalus</i>	3	0.09	0	0.00	0	0.00	1	0.03	0	0.00	0	0.00
<i>C. leucodon</i>	0	0.00	18	0.46	0	0.00	0	0.00	3	0.15	0	0.00
<i>C. glareolus</i>	3	0.09	0	0.00	0	0.00	7	0.20	0	0.00	0	0.00
<i>M. arvalis</i>	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.03
<i>M. subterraneus</i>	6	0.17	39	1.01	0	0.00	0	0.00	0	0.00	0	0.00
<i>M. agrestis</i>	17	0.48	3	0.08	42	0.77	17	0.48	0	0.00	123	3.51
<i>M. oeconomus</i>	54	1.54	0	0.00	182	3.34	129	3.68	0	0.00	8	0.23
<i>A. terrestris</i>	0	0.00	0	0.00	1	0.02	0	0.00	0	0.00	0	0.00
<i>A. agrarius</i>	62	1.77	23	0.59	197	3.62	78	2.22	33	1.60	113	3.22
<i>A. flavicollis</i>	10	0.28	1	0.03	1	0.02	0	0.00	0	0.00	6	0.17
<i>A. sylvaticus</i>	2	0.06	0	0.00	8	0.15	0	0.00	1	0.05	4	0.11
<i>M. minutus</i>	24	0.68	21	0.54	21	0.39	28	0.80	15	0.73	11	0.33
Total	302	8.61	152	3.93	535	9.83	442	12.6	75	3.65	330	9.40
Species richness (S)	12		8		9		9		5		9	
Shannon-diversity (H[S])	1.88		1.75		1.45		1.59		1.23		1.43	
Evenness (J)	0.76		0.84		0.66		0.73		0.77		0.65	
Simpson 1/D	1.25		0.58		0.69		1.33		1.47		1.41	

C: capture number of species

I: relative index of abundance (number of captures/100 trap night)

habitat patch, the effectiveness of capture decreased in the second period, and so the calculated relative abundance value significantly differed from the first undisturbed period ($\chi^2 = 4.93$, $P < 0.05$). Capture results of small mammals in the second period burdened with disturbances did not differ significantly from the third period ($\chi^2 = 2.53$, n.s.). The relative abundance value of this latter period that was characterized by regenerated habitat quality did not differ significantly from the first period either ($\chi^2 = 0.08$, n.s.). We evaluated the effectiveness of capture of both marshlands in the comparison of the same periods as well. There were no significant differences in the pairwise comparison of relative abundance values in any of the monitoring periods between the two marshlands separated by the road ($\chi^2 = 0.01 - 0.75$, n.s.).

The number of species was highest in the first period on the northern marshland: however, it decreased from 12 to 8 in the second period. We expected an increase in the number of species after the regeneration of the habitat, but in the third period, there were less species than in the first one. Species richness showed greater differences on the southern site. There were 9 species found in both the first and third periods: however, the number of species decreased to 5 in the second period. The species richness of the small mammal community was equal after the regeneration in both the northern and southern sampling areas in the third period (Table 1).

The value of Shannon-diversity did not show considerable decline because of disturbances in the northern site. The result of disturbance was a notable

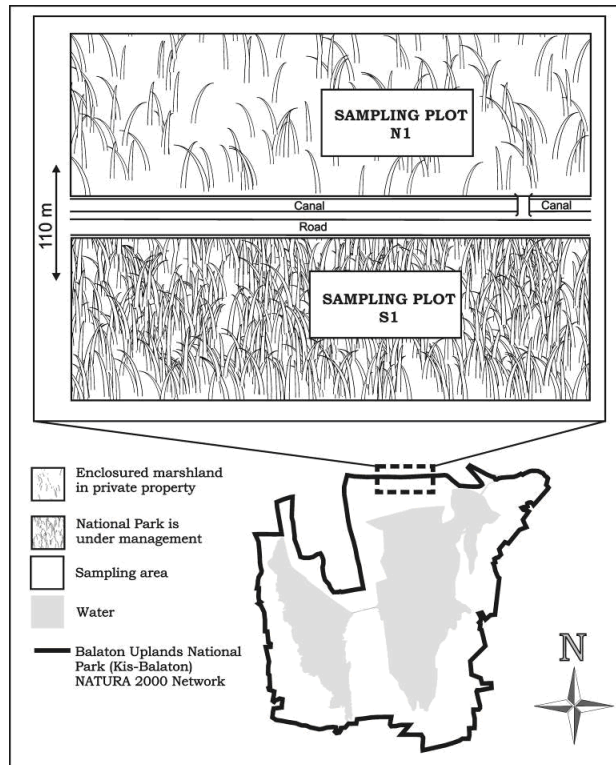


Fig. 1. The two examined marshland habitat patches in the Kis-Balaton Landscape Protection Area.

turnover, causing some species to disappear (e.g. *Neomys fodiens*, *Neomys anomalus*, *Microtus oeconomus*) and others to appear (e.g. *Crocidura leucodon*). Accordingly, we found significant differences between the Shannon-diversity values of the first and third, as well as between the second and third periods. Although species richness increased in the third period, α -diversity representing the species-abundance relationship continued to decline despite of the improvement in habitat quality. Values of Shannon-diversity showed different results in the southern area: we received significant differences between diversity values in the comparison of each season. The number of species and the value of Shannon-index approached the initial values of the monitoring in the regenerated habitat patch managed by the national park after the disturbing effects had ceased (Table 2). We tested the differences of Shannon-diversities of the small mammal community in the same period in the comparison of the northern (SP_N) and southern (SP_S)

Table 2. Statistical t -test of Shannon-diversity values.

	Period 1	Period 2	Period 3
Sampling Plot 1 (North)			
Period 1	-		
2	1.83	-	
3	7.00***	5.14***	-
Sampling Plot 2 (South)			
Period 1	-		
2	4.45***	-	
3	2.55*	2.37*	-

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

sampling areas as well. The Shannon-index values of the first and second periods were significantly higher for the community in the northern area than for the southern one ($t = 4.5 - 5.97$, $P < 0.001$). However, the diversities of the two communities equalized in the third period, with no significant differences found between the Shannon values ($t = 0.13$, n.s.).

Evenness values were the highest for the small mammal community of the second period in both examined marshlands. The local loss of two relict vole species played an important role in this result: the field vole, a typical character species of marshland habitats, disappeared from the southern marshland while the endangered root vole disappeared from both of the communities. The relative abundance values of the newly appearing species reached the values of typical species of the undisturbed marshlands remaining in the sampled habitat patch. Therefore, higher evenness values were typical within the community. Diversity decline caused by the negative effects of disturbances was reflected by Simpson 1/D values only in the case of the northern marshland. The Simpson-index, due to its sensitivity to species frequencies, showed a different diversity pattern than the Shannon-index regarding the dominance values of the communities of the consecutive periods (Table 1.).

We evaluated the order of species frequencies in both of the sampling sites, in all three periods, based on the relative abundance values of trapped small

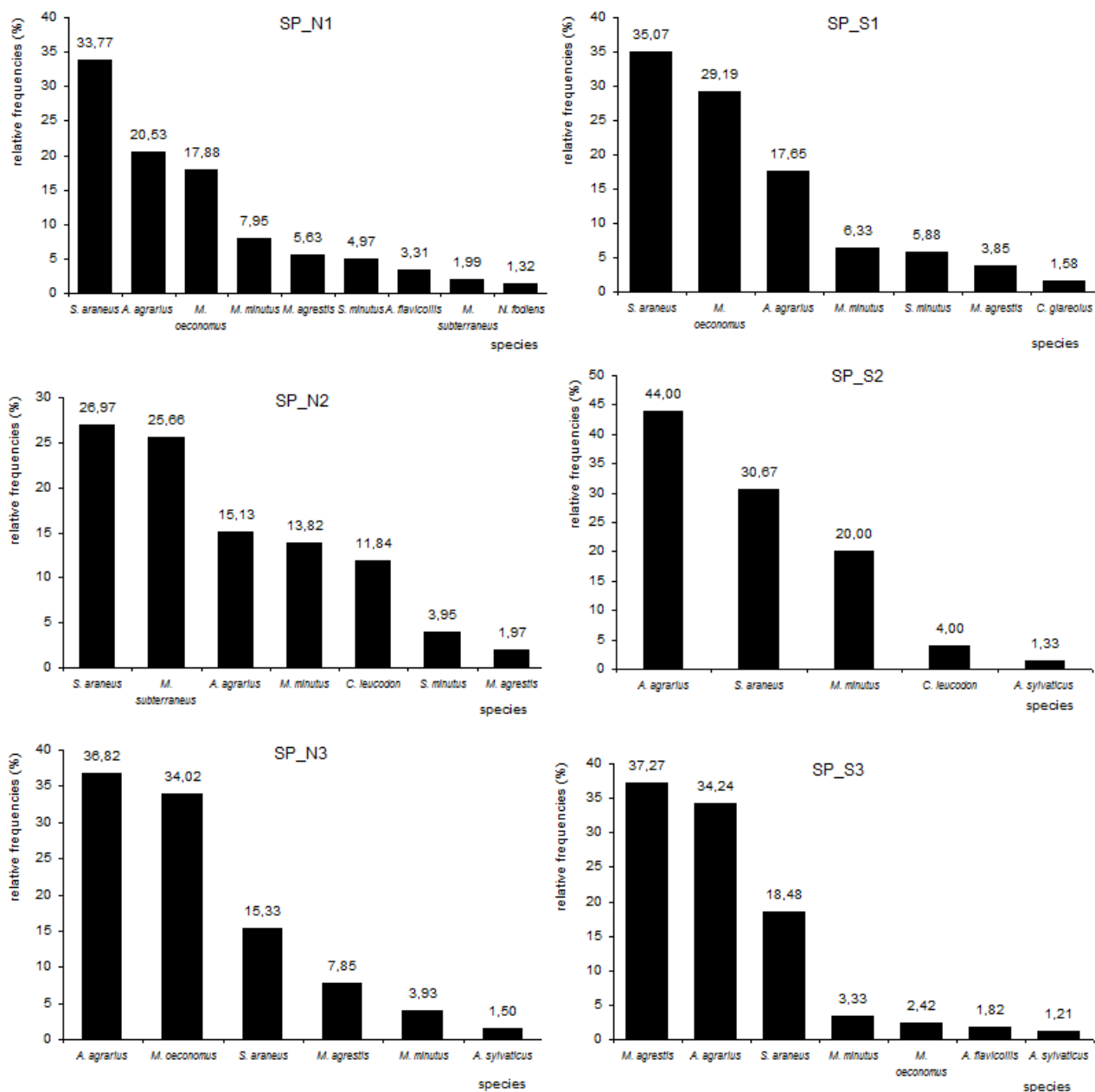


Fig. 2. Relative abundance of small mammals in both investigated habitat patches in the three sampling periods.

mammals (Fig. 2). The frequency values were greater than 1% for 9 species in the first, undisturbed period, the common shrew, *Sorex araneus* (Linnaeus, 1758) being the most frequent small mammal. The next species in the order was the striped field mouse, *Apodemus agrarius* (Pallas, 1771), with a 10% lower

frequency value, while the root vole appeared to be the third most frequent species.

The remaining species in the dominance order occurred with lower than 10% frequency values. It is typical in the northern marshland during this pe-

riod that besides the critically endangered root vole there is another glacial relict vole present in the small mammal community, namely the field vole that has a larger distribution area, and thus in this period in the northern marshland we proved their co-occurrence (Fig. 2). Both the relative abundance values and the order of species frequency changed in the second period because of anthropogenic disturbances. The wetland-loving common shrew proved to be the most frequent species with its higher than 25% abundance value in this period as well. Due to disturbances, the root vole disappeared locally from the community. We therefore obtained significantly higher G values for homogeneity testing in the comparison of the first two periods (Table 3). Although the frequency of the field vole decreased considerably in the disturbed period, the distribution of its relative abundance did not show a significant difference.

The previously dominant position of the two relict vole species was taken over by the common pine vole, *Microtus subterraneus* (de Sélys Longchamps, 1836), which appeared due to the structural changes of vegetation caused by anthropogenic disturbances. Therefore, differences between the two periods were confirmed by the significantly high G values in case of this species as well (Table 3). The appearance of the bicolored white-toothed shrew, *Crocidura leucodon* (Hermann, 1780), also proved the changes in habitat quality. The result of the homogeneity test was significant for this species as well, based on the relative abundance values of the second period. The spreading of the common pine vole changed even the relative abundance of the habitat generalist striped field mouse too, so that the striped field mouse was ranked third in the frequency ordering for the northern habitat patch (SP_N2) (Fig. 2).

The species composition of the small mammal community changed again in the third period in the northern habitat patch through the regenerating effect of wetter weather and the ending of anthropogenic disturbances. We manifested the recolonizing stock of root vole, its relative abundance value approaching the abundance value of the generally prevailing striped field mouse in the northern

site. Therefore, these two species were the first two members of the frequency ranking (Fig. 2). The bicolored white-toothed shrew and the common pine shrew disappeared from the community with the qualitative improvement of the sedgy marshland habitat, so that there was significant inhomogeneity in many comparisons of abundance values between the second and third periods due to species turnover (Table 3.). We found significant differences between the frequency distribution of three species in the comparison of the first undisturbed and the third, disturbance-representing period. The common shrew was present with significantly lower frequency in the community forming in the regenerated habitat than in the first period. Striped field mouse and root vole became the dominant, decisive species of the community until the third period (Table 3).

The relative abundance values of seven small mammal species exceeded 1% in the initial disturbance-free period of the sampling in the southern examined marshland (Fig. 2). The three most frequent species were common shrew, root vole and striped field mouse. Data confirmed the presence of a stable stock of the relict root vole in the first period in this area. Co-occurrence of the glacial relict root vole and field vole was shown in the southern marshland in the first period, but like the northern sampling site, field vole occurred with a lower frequency value in the southern area. Since the area was burned before the mowing on the southern habitat patch, the species loss, changes of relative abundance of species and changes in community structure were more drastic due to the effect of consecutive human disturbances than in the northern area. Three from the remaining 5 species were dominant (*A. agrarius*, *S. araneus*, *M. minutus*) (Fig. 2).

The combined effect of human disturbances and a drier weather period caused changes in the vegetation structure that clearly favored the spread of striped field mice so that there was a significant increase in their relative abundance (Table 4.). Turnover caused significantly high G-values in the case of the locally extinct root vole, field vole and bicolored

Table 3. Homogeneity (*G*) test of relative abundance of species between sampling periods in the northern habitat patch.

Sampling period/Species	SP_N1 ^(99-'00) vs SP_N2 ^(02-'03)			SP_N1 ^(99-'00) vs SP_N3 ^(07-'08)			SP_N2 ^(02-'03) vs SP_N3 ^(07-'08)		
	P _i ^(99-'00)	P _i ^(02-'03)	<i>G</i>	P _i ^(99-'00)	P _i ^(07-'08)	<i>G</i>	P _i ^(02-'03)	P _i ^(07-'08)	<i>G</i>
<i>S. araneus</i>	33.77	26.97	0.76	33.77	15.36	7.08**	26.97	15.36	3.23
<i>C. leucodon</i>	0.00	11.84	16.42***	0.00	0.00	0.00	11.84	0.00	16.42***
<i>M. agrestis</i>	5.63	1.97	1.83	5.63	7.68	0.32	1.97	7.68	3.60
<i>M. oeconomus</i>	17.88	0.00	24.79***	17.88	34.08	5.14*	0.00	34.08	47.25***
<i>M. subterraneus</i>	1.99	25.66	24.03***	1.99	0.00	2.75	25.66	0.00	35.57***
<i>A. agrarius</i>	20.53	15.13	0.82	20.53	36.89	4.73*	15.13	36.89	9.39**
<i>M. minutus</i>	7.95	13.82	1.60	7.95	3.93	1.38	13.82	3.93	5.83*

*: $P < 0.05$. **: $P < 0.01$. ***: $P < 0.001$ Table 4. Homogeneity (*G*) test of relative abundance of species between sampling periods in the southern habitat patch.

Sampling period/Species	SP_S1 ^(99-'00) vs SP_S2 ^(02-'03)			SP_S1 ^(99-'00) vs SP_S3 ^(07-'08)			SP_S2 ^(02-'03) vs SP_S3 ^(07-'08)		
	P _i ^(99-'00)	P _i ^(02-'03)	<i>G</i>	P _i ^(99-'00)	P _i ^(07-'08)	<i>G</i>	P _i ^(02-'03)	P _i ^(07-'08)	<i>G</i>
<i>S. araneus</i>	35.07	30.67	0.29	35.07	18.48	5.22*	30.67	18.48	3.05
<i>C. leucodon</i>	0.00	4.00	5.55*	0.00	0.00	0.00	4.00	0.00	5.55*
<i>M. agrestis</i>	3.85	0.00	5.33*	3.85	37.27	31.46***	0.00	37.27	51.67***
<i>M. oeconomus</i>	29.19	0.00	40.46***	29.19	2.42	26.71***	0.00	2.42	3.36
<i>A. agrarius</i>	17.65	44.00	11.64***	17.65	1.82	26.71***	44.00	1.82	48.22***
<i>M. minutus</i>	6.33	20.00	7.45	6.33	0.00	8.78**	20.00	3.33	13.22***

*: $P < 0.05$. **: $P < 0.01$. ***: $P < 0.001$

Table 5. Values of Sørensen similarity index between species composition of different sampling plots and periods.

	SP_N1	SP_S1	SP_N3	SP_S3	SP_N2	SP_S2
SP_N1	1					
SP_S1	0.857	1				
SP_N3	0.700	0.588	1			
SP_S3	0.556	0.533	0.714	1		
SP_N2	0.762	0.667	0.706	0.667	1	
SP_S2	0.667	0.556	0.588	0.533	0.889	1

white-toothed shrew, appearing due to the structural changes of habitat (Table 4).

Field vole appeared with the largest relative proportion in the third period, which indicated the qualitative improvement of the sedgy marshland habitat. The striped field mouse was the second species in dominance ranking with a quite similar relative abundance value, while the third species proved to be the common shrew, which had the lowest frequency values in the southern habitat

patch also in the third period (Fig. 2). Due to habitat regeneration, field vole appeared initially, then colonizing individuals of root vole turned up, but the relative abundance values of the third period did not reach the values of the first, undisturbed sampling period. There were significant differences between the relative proportions of species in four cases in the comparison of the second and third periods (Table 4). There were significant differences in the case of 5 species when testing the homogeneity of abundance values in the comparison of the first,

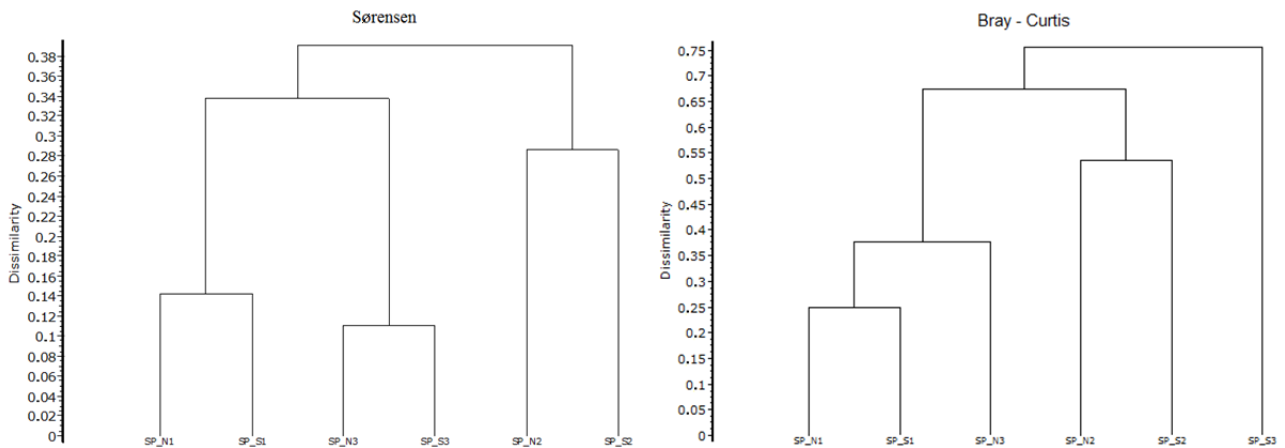


Fig. 3. Classification of 6 small mammal communities recorded in the two marshland habitats during three sampling periods.

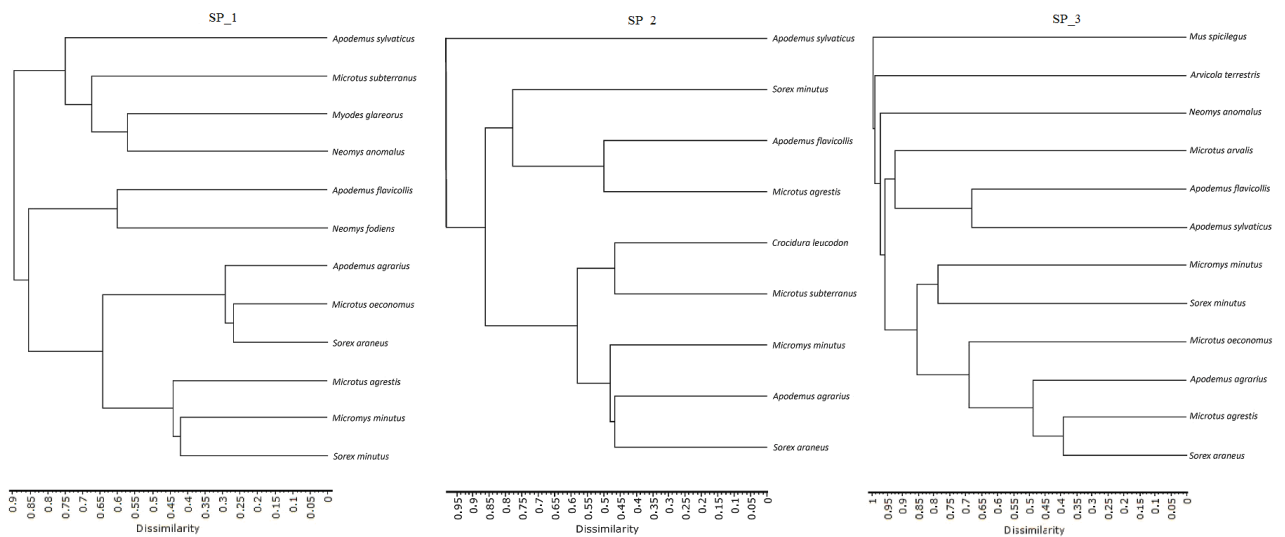


Fig. 4. Bray-Curtis classification of small mammal species recorded in the two marshland habitats during three sampling periods.

undisturbed (SP_S1) and the third period (SP_S3), characterizing a regenerated habitat (Table 4). The two relict vole species showed contrary trends: while root vole was the dominant species in the first period and field vole was less frequent, we observed the opposite trend in the third period (Table 4).

The distribution of captures, relative abundance of species and parameters of community ecology indicate the species turnover process between the communities of disturbed and undisturbed periods. We

used the Sørensen index for quantitative evaluation (Table 5). The first sampling period represented the intact, disturbance-free habitat quality and a small mammal community characterized by the dominant presence of the typical, habitat-specialist root vole in both the northern and southern habitat patches (SP_N1, SP_S1). We received the greatest homogeneity value (0.857) for these two habitats in the first period of monitoring. Comparing the communities of the first and second periods, we obtained higher similarity values again in the northern site (SP_N3). Despite

of the termination of human disturbances and the improvement of habitat quality, we observed a considerable turnover in the third period compared to the communities of both the first and second period, as indicated by the lowest, equal values (0.533) of the Sørensen similarity index. It is important to highlight that regarding the similarity values, the greatest value occurred between communities of the two degraded habitat patches due to anthropogenic disturbances (0.889), which confirms that disturbance, through the alteration of habitat quality, caused the same changes in both sampled sites (Table 5).

For further community ecological analyses, we performed the hierarchic classification of small mammal communities in the two marshland habitats, recorded in the 3+3 periods separated on the basis of their disturbances. Cluster analysis was run using binary Sørensen and quantitative Bray-Curtis indices. The dendrograms obtained using the two different methods were not identical. Classification based on the binary Sørensen index ordered the communities of the northern and southern habitat patches in the expected way. Greater similarity was found between small mammal communities of the undisturbed and the regenerated periods. The dendrogram obtained using quantitative data (Bray-Curtis index) showed that the community in the regenerated northern area (SP_N3) was more similar to the communities recorded in the northern and southern habitat patches in the undisturbed period (SP_N1, SP_S1) than the community that established itself after disturbance had ceased in the southern habitat (SP_S3). Accordingly, the disturbing effect of human disturbance, through the dissimilarity of small mammal communities in degraded habitat patches, was supported also by the dendrogram drawn up based on the Bray-Curtis index (Fig. 3).

Changes in the structure of the small mammal community are clearly revealed by the dendrograms charted from the cluster analysis of each sampling period. In the first, undisturbed period when the two studied habitat patches were covered by marshland vegetation, two clusters showed up in separation according to the small mammal species recorded in

them. Within the cluster including several species, the typical marshland species were organized in two smaller groups. Among these, the first group contained the common species such as root vole that had been dominant in the two habitat patches of the first period, common shrew and striped field mouse, the latter showing an expansive radiation also in the marshland area. The other group included species that are typical for the Kis-Balaton marshland but with lower dominance rate (*M. agrestis*, *M. minutus*, *S. minutus*). Connected with a greater distance value to the cluster made up by these two groups, the water shrew *Neomys fodiens* (Pennant, 1771) indicated the improving water supply in the area, whereas the yellow-necked wood mouse, *Apodemus flavicollis* (Melchior, 1834) appeared from greater distances, traveling along linear habitats (e.g. railway embankments, ditches, canals). The second distinct group had 4 infrequent species that appeared only occasionally during the studies. Among these, the appearance of particular species in the two habitats primarily indicated the effects of patch dynamical changes induced by water-level changes (Fig. 4).

In the third period with increased disturbance, the community structure transformed. The striped field mouse became the most frequent species, in separation together with the common shrew and harvest mouse, *Micromys minutus* (Pallas, 1771) within the larger cluster of five common species. Within the same cluster, a separate group was represented by bicolored white-toothed shrew and common pine vole, indicating drying processes in the marshland habitat and physiognomic changes in the vegetation. At the same time, the habitat-specialist root vole that had been a dominant species in the former period disappeared from the community. In greater separation from these species in the second period, we recorded species with lower dominance, among which the typical marshland species such as the field vole and pygmy shrew, *Sorex minutus* (Linnaeus, 1766) declined strongly in the two studied patches due to habitat disturbance (Fig. 4).

In the third period, because of habitat regeneration, the root vole reappeared and became a char-

acteristic species of the community. This species formed a single cluster together with other dominant species such as the striped field mouse, field vole and common shrew. Although these typical marshland species became part of the same cluster, their hierarchy showed a different pattern from that of the first, undisturbed period. Recolonization by marshland character species, especially the habitat-specialist root vole, again played a determining role in forming the structure of the small mammal community in the studied marshland area. Community response by small mammals indicated changes in habitat quality.

DISCUSSION

The community-level response of small mammals in a marshland area of Kis-Balaton Landscape Protection Area, western Hungary, was investigated. The area that was once continuous but was later cut in two by a major road is under state nature conservation. Two habitat patches under different landscape use and management were investigated using data from live trapping. Because small mammals play a fundamental role in food webs in wetland and marshland ecosystems (Abernethy et al., 1985, Bowland and Perrin, 1993, Krištofik, 2001, Gubányi et al., 2002, Scott et al., 2008), they are distinguished subjects in the nature conservation monitoring of the refugial marshlands of Kis-Balaton Landscape Protection Area. One of the main objectives of small mammal monitoring is to map the remaining sub-populations of the endangered root vole and provide data for nature conservation management. A local subspecies of the Hungarian root vole, *Microtus oeconomus mehelyi* is the rarest vole species in Hungary according to the Hungarian Red Data Book. Another objective has been to follow changes in the structure and composition of small mammal communities in refugial marshland areas, as induced by changes in habitat quality (disturbance, human activity, water management).

Today, wetland ecosystems in various biomes are made up of a complex of fragmented habitats where the remaining, often refugial habitats exist in discrete patches within the landscape matrix. As a result, the

local population of wetland species are isolated and endangered (Gibbs, 2000). This is particularly true for the Kis-Balaton marshlands where fragmentation caused by human landscape use and water management poses a serious threat to the survival of a number of species, and in particular to the glacial relict root vole. The isolated populations of the root vole subspecies surviving here had key importance in the community level evaluation of monitoring data. As a habitat-specialist species, it appeared as a characteristic and dominant species component of the small mammal community of natural, disturbance-free sedgy habitat patches. The 10-year monitoring period was separated into three periods in both marshland areas on the basis of the onset of disturbance and the termination of these detrimental anthropogenic effects. In the two areas together, the 10-year trapping yielded altogether 16 small mammal species, but the composition of the small mammal communities and the relative abundance of their species were considerably different in the two areas in relation to disturbance effects and management activities affecting the two habitats. In the first, the disturbance-free period with homogeneous sedge beds and natural environment, as well as Period 3 when the vegetation was regenerated and habitat quality improved after the effects of disturbance, altogether 5 typical marshland species were identified (*S. araneus*, *M. agrestis*, *M. oeconomus*, *A. agrarius*, *M. minutus*) in both areas. Small mammal studies in Slovakia in reed stands of similar wetland environment resulted in 16 species, with the community dominated by *S. araneus*, *M. glareolus*, and *A. sylvaticus* (Krištofik, 2001). Scott et al. (2008) studied the influence of habitat and landscape heterogeneity of wetlands on small mammals in western Estonia, where 7 species were recorded and the reed-bed sites were dominated by *A. agrarius* followed by *M. agrestis* and then *S. araneus*. Despite the difference in geographic location, the small mammal community data obtained for the Kis-Balaton marshland were similar in species composition and relative abundance values. Dominant species that were indicated in the Estonian study site proved to be frequent character species in the refugial Hungarian wetland as well, and it is important to note for this comparison that the habitat gener-

alist striped field mouse was a determining element of the small mammal community in both northern and central European wetland habitats. Its successful expansion that is seen also in wetland areas is assisted, in addition to its wide tolerance in habitat use, by its ability to move large distances beyond its home ranges, a well-investigated feature in heterogeneous habitats (Liro and Szacki, 1987; Szacki and Liro, 1991). The synchrony between small mammal population dynamics was investigated in marshes and adjacent grassland habitat in France, with 9 species being monitored. Based on capture data in the marshy area, this study showed the dominance of *M. agrestis* and *S. araneus* as well, although *A. terrestris* is typical mostly in the grassland areas (Michelat and Giraudoux, 2006). In a study of the small mammal communities of lake coastal zones in Poland seven small mammals were revealed, with removal analyses also done in some experimental plots, focusing on the importance of the spatial distribution of species and their interspecific interactions (Kozakiewicz, 1987). In lake coastal areas, bank vole was found to be the dominant species and striped field mouse the second most frequent one. Bank vole, recorded with the highest number of captures, occupied the drier areas, whereas the striped field mouse was present in patches near the side of the lake. However, when bank voles were removed from the dry areas, striped field mice rapidly colonized them. The study pointed out that habitat selection by species is determined, besides habitat quality, by interspecific interactions. Both root vole and field vole were present in the investigated community of the coastal lake habitat. Between these two sympatric species, root vole was the more frequent: its individuals were captured in both the experimental and the control plots, whereas field voles were detected in the experimental area. The Polish capture data also referred to the results of earlier studies investigating the coexistence of these two species in Finnish Lapland habitats, suggesting that root vole is the stronger competitor in the interaction of the two species. In this region, the ecological niches of the two species largely overlap, leading to competition between them (Tast, 1968, Henttonen et al., 1977). The coexistence of root voles and field voles in both of the studied marshland

habitat patches of Kis-Balaton was recorded in the disturbance-free periods. During these periods field vole had lower frequency in the small mammal community, thus, with its sub-dominant presence in relation to the root vole, our results suggest the relevance of the stronger competitor status of the root vole. Species belonging to the genus *Microtus*, especially populations of the habitat-specialist root vole, have been used in a number of studies as an experimental model system (EMS) to investigate the effect of both fragmentation (Andreassen et al., 1998; Bjørnstad et al., 1998) and habitat destruction (Johannesen and Ims, 1996, Andreassen and Ims, 1998, Johannesen et al., 2003) on space use and demographic parameters. These studies have yielded results that can be utilized in the conservation management of endangered populations surviving in refugial habitats, and have pointed out that the population-level responses to habitat fragmentation and destruction are very complex, depending on spatial scale, species-specific characteristics (e.g. home-range size, natal dispersal) and social organization (Johannesen et al., 2003). During our studies, habitat destruction was caused by human interventions (burning and mowing), and the population-level response of both of the mentioned *Microtus* species was indicated. According to our findings, it was clearly the root vole whose loss was brought about by the disturbance-laden periods in both habitat patches. Both *Microtus* species and especially the root vole that is a species with narrow ecological valence with regard to changes of habitat quality, dominated the area in both homogeneous sedgy habitat patches before the onset of disturbance. They played an important role at the community level response of small mammals to disturbance, and in the transformation of species composition and community structure.

We first described the community-level changes in small mammal populations through differences in species richness. Regarding the two investigated marshland areas that differed in their disturbance and land use, it was the southern sampling plot inside the National Park that had a community with greater difference in species richness values. Nine species were detected in both the first and the third

periods, whereas the number of species decreased to five in the second period, a consequence of burning, consecutive mowing and drier weather, together representing cumulative disturbance effects. Several studies have dealt with the importance of vegetation cover from the aspect of small mammals (e.g. Beck and Vogl, 1972, Cook, 1959, Getz, 1961, Peles and Barrett, 1996, Schmidt and Olsen, 2003, Schmidt et al., 2005). Habitat destruction (whether because of burning, grass cutting, overgrazing or drying due to loss of water supply) has an effect on animal assemblages including small mammal communities through decreased vegetation coverage and density, thinning of greenery. Over the course of monitoring activities in the Kis-Balaton marshland areas, we proved the presence of the combined effect of these disturbance factors. In the southern habitat patch, human disturbance included burning and grass cutting activities, so that the loss of species and the changes in species composition and relative abundance were more dramatic than in the northern area. Small mammals are specifically vulnerable to habitat perturbation, with increased predation risk (Eccard et al., 2000; Tabeni and Ojeda, 2003, Tattersall et al., 2001). Scott et al. (2008) reported similar results in the case of a small mammal community of a wetland habitat, concluding that small mammal relative abundance, diversity and richness were positively correlated with tall grass habitat and negatively correlated with short grass, bare ground and lower shore herbaceous vegetation. The change in the diversity of small mammals was higher in the southern sampling plot where burning appeared as a human perturbation. In the third period of our investigations, the comparison of areas differing in land use and protection status showed that diversity became leveled again as a result of habitat regeneration after the discontinuation of disturbance, suggesting that community level responses to habitat regeneration were similar regarding small mammal diversities. Calculations of similarity indices measuring species substitution also suggested that changes in community structure because of habitat improvement lead to a community composition similar to the initial, perturbation-free period of the monitoring.

Our monitoring experience so far has proved that populations of typical habitat-specialist species of marshland areas (e.g. root vole) are very sensitive to the negative effects of environmental and human disturbances. If there are no appropriate ecological corridor retreat areas, these populations become completely isolated, their size falling between the minimum viable limits, so that local extinction may follow in patches and habitat fragments. Changes in land use and management and various types of associated anthropogenic disturbances, can affect the species frequency relations of small mammal communities even in the case of a single effect. The outcome of these effects and natural stochastic events is that species that stabilize the original community vanish and are substituted by other species. Thereby these events modify the species composition and structure of small mammal communities.

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