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Nestedness of small mammal assemblages and role of indicator species in isolated marshland habitats

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Horváth, Gy., Herczeg, R., Tamási, K. & Sali, N.: N*estedness of small mammal assemblages and role of indicator species in isolated marshland habitats.*

Abstract: The concept of nestedness has important role in community ecology of fragmented habitats that measures the order in presence-absence matrices of species in different communities, and the vulnerability of species to habitat change can be quantified. We have been examining the composition of small mammal assemblages of Kis-Balaton Landscape Protection Area since 1999 within the framework of Hungarian Biodiversity Monitoring System Programme. Our basic question was how much the species turnover processes and the water-level increase following bountiful precipitation as a natural disturbance predominate in directing the composition of small mammal assemblages and in the nestedness pattern in human disturbed habitat patches. Our investigation was based on nestedness analysis and the IndVal method. The results of nestedness analysis showed that the small mammal assemblages of the isolated Kis-Balaton marshland habitat patches are ordered contrary to the random pattern and showed nested pattern. The endangered habitat-specialist root vole appeared as an asymmetrical indicator species regarding its optimal habitat patch, and we evaluated it as an idiosyncratic species in the nestedness analysis. These results proved admittedly that the root vole – as a habitat specialist species – is very sensitive to habitat fragmentation and human disturbance, so the pattern of its presence influences considerably the nestedness of small mammal assemblages of the examined marshlands.

Keywords: small mammals, presence-absence, nestedness, indicator value, marshland, disturbance

Introduction

One of the most important objects and aims of community ecology is to describe and evaluate the community patterns (Gee & Giller 1987, Southwood 1996, Weiher & Keddy 1999) and formulate testable null-hypotheses for these examinations (Diamond & Giplin 1982, Gotelli & Graves 1996, Gotelli 2000, Moore & Swihart 2007). Null models are pattern-generating methods that intentionally exclude a mechanism of interest to determine whether a specific pattern can be produced randomly (Gotelli 2000; Gotelli & Graves 1996, Ulrich & Gotelli 2007a, b). Leibold (2002) listed six hypothetical patterns of species' distribution among sites: nested subsets (1), checkerboards (2), Clementsian gradients (3), Gleasonian gradients (4), evenly spaced gradients (5) and random pattern (6). Patterns represent idealized characteristics hypothesized to result from at least one (and generally more than one) potentially important ecological or biogeographical process (Leibold 2002). We can find a detailed overview about the sto-

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chastic – i.e. random – or other differring patterns describing studies in the review of BÁLDI (2003) which discusses the nestedness of communities.

This study (BÁLDI 2003) has a great importance in the comparing surveys of island communities in the description of metapopulation- and community patterns, therefore the nestedness was interpret firsly by the analysis of species compositon. Nestedness is a pattern where the species composition of one island can be found in the species composition of an other, larger island at the same time, and futhermore it contains the species composition of differring smaller islands too (PATTERSON & ATMAR 1986, CUTLER 1994). Nestedness is among the most frequently cited patterns (WRIGHT et al. 1998, BLOCH et al. 2007, ULRICH et al. 2009). Nestedness pattern most often is used to explore the structure of communities, such as islands within an archipelago (PATTERSON & ATMAR 1986, KRIŠTUFEK & KLETEČKI 2007), habitat fragments within a landscape (ATMAR & PATTERSON 1993, PATTERSON & ATMAR 2000, GANZHORN & EISENBEISS 2001), isolated peaks along a mountain range (PATTERSON 1990, MCDONALD & BROWN 1992, COOK 1995), temporal changes on disturbed (BLOCH et al. 2007) and coevolutionary relationships in non-isolated areas. The nestedness also is useful to describe spatial distribution of species in less discrete habitats (PATTERSON & BROWN 1991, BAKER & PATTERSON 2011).

Significant nestedness was extensively manifested in case of different taxons and ecosystems. However, the most important questions by the examination of nestedness patterns are that (1) which species and in what kind of measure are responsible for the unexpected incidences and (2) which islands, isolated fragments or habitat patches are those where we are able to detect more or less presences than the expected (SIMBERLOFF & MARTIN 1991, BÁLDI 2003). We can show these unexpected occurrences with the study of nestedness and these objects will be called idiosyncratic species or areas (ATMAR & PATTERSON 1993). Thus the important aim of nestedness analysis was always identifying such 'deviating' species and to infer the causes of idiosyncracy. With the knowledge of these we can value which species have an indication characteristic, which cause-effect factors are indicated by these species and which species are responsible for the pushing away of ordered nestedness pattens. The identification of idiosyncratic sites are practical applications in conservation ecology, wich have been discussed with regard to the single-large-or-several-small (S.l.o.s.s) debate (ULRICH et al. 2009). This has a great importance in the planning of environmental management of endangered species in fragmented habitats.

The fragmentation of habitats by human land use and disturbences is one of the most important impact modifying the composition of natural species assemblages (e.g. WILCOX & MURPHY 1985, GAINES et al. 1992, NOSS & CSUTI 1997, BROKAW 1998; LOMOLINO & PERAULT 2000). The effects of these activities accompany the substitution and local extinction of some species, which is the one of the key problems of nature conservation (BÁLDI 2003). The analysis of nestedness patterns of assemblages can be a useful method for nature conservation management (PATTERSON 1987), because nestedness subsets can also be generated through extinction (PATTERSON & ATMAR 1986, GANZHORN & EISENBEISS 2001).

The negative effects of natural and human disturbances are even more obvious in the marshlands. Wetlands and marshlands all around the world have been lost in the past century and the remaining marshlands have been degraded to different degrees because of the adverse influences of human activities (EPPINK et al. 2004, FRASER & KEDDy 2005, ZHIJUN et al. 2010, TOUSIGNANT et al. 2010). Kis-Balaton is worth considering as one of these endangered areas of Hungary, being the biggest near-natural wetland habitat in our country (14745 ha). The marshland area was drained in the l920s and the Kis-Balaton as a Landscape Protection Area has been legally protected since 1976. The Kis-Balaton Landscape Protection Area today is a flood prevention system consisting of two main parts. Kis-Balaton Water Protection System stage 1 (KBWPS-I) (1985) is characterized by open water surfaces with relatively narrow reedbedts along the dikes, while KBWPS-II (1992) contains vast reedbeds and sedgy marshes, and less open water. The building of infrastructure necessary for the filtering system accompanying the increased water level after the 1992 reconstruction has fragmented considerably the original marshland area and isolated the refuge habitats.

Marshlands are important habitats for small mammals (MARTIN et al. 1991, KRITŠOFĬK 2001, BIAS & MORRISON 2006, SCOTT et al. 2008, MICHELAT & GIRAUDOUX 2006) and thus small mammals are typical objects of biodiversity monitoring of the relict Kis-Balaton marshlands. Small mammals are often used as an indicator species group (CAREY & JHONSON 1995, PEARCE & VENIER 2005); they have an important role in ecosystem and foodwebs, because they are primary consumers (HAYWARD & PHILLIPSON 1979, HUNTLY 1991), they are also prey for many carnivore mammals and birds of prey (KORPIMÄKI & KREBS 1996, KLEMOLA et al. 2003, TOME 2003). Small mammals respond rapidly to disturbance and other anthropogenic effects (FOX 1996, BUTET et al. 2006, PANZACCHI et al. 2010). Changes in the structure of their communities indicate the possible degradation of their environment (habitat degradation, fragmentation, antropogenic distrubance etc.). Because of the relict characteristic of these marshlands, the water-reserve system maintaining human interventions affect appreciably the biodiversity, thus the hypothesis-testing control of these effects are highlighted projects in the Hungarian Biodiversity Monitoring System (HBMS). In the view-point of composition of the small mammal communities existing in the refuge marshland habitats of Kis-Balaton there is a habitat specialist character species which has great importance and appears on the Habitat Directive list; this species is the root vole, *Microtus oeconomus* (Pallas 1776), whose conservation and maintenance is one of the greatest problems of local environment protection. With special regard to the isolated occurrence of this species in the Kis-Balaton region there were several projects applied for examining the composition of small mammal assemblages of the area. These researches have examined whether (1) human interventions and disturbances related with the marshlands have measurable effect on the diversity and temporal composition of small mammal assemblages (LELKES & HORVÁTH 2000, HORVÁTH 2001, 2004) and if (2) they fulfilled the examination of small mammal assemblages of different-sized and isolated islands (FARKAS et al. 1998, FARKAS & CZABÁN 2007).

We have been examining the composition of small mammal fauna of Kis-Balaton Landscape Protected Area since 1999 within the framework of HBMS program where our main aim is the spatial-and temporal monitoring of subpopulation patterns of the relict root vole. In the sampling approach of the 11-year long period we have applied two successive strategies. When we could catch root vole individuals in habitat patches which are adequate for the species, we applied population-level monitoring that concentrates on smaller areas. However, when the state of the habitat had deteriorated and the number of the individuals of the given species had decreased dramatically or the species disappeared from the area because of human interventions or weather conditions, we switched from population-level monitoring to faunistical monitoring approach that needs greater trapping expenditure and associates with more habitats.

In the present study we have evaluated the presence-absence data derived from a 3-year long period of the faunistical mapping of several micro-habitats after the local extinction of the endangered root vole. Based on the nestedness analysis and the counted character- or indicator values derived from the hierarchical classification of habitat patches (*i*), we examined the composition and structure of small mammal assemblages living in differently isolated patches, (*ii*) we described those habitat patches and animals which showed unexpected presence values, (*iii*) we evaluated how similar results are produced by the methods of nestedness and IndVal concerning the indicator characteristics of the species, and how could these results be used for qualitatively typifying the marshland habitat patches.

Material and methods

Study areas

During the period between 2001-2004 within the small mammal monitoring programme having been performed in the Kis-Balaton area for 11 years, the root vole largely disappeared from the HBMS study locations, due to unfavourable weather conditions and associated anthropogeneic effects, and trapping efforts yielded lesser results for other small mammal species as well. With the aim of surveying new habitats suitable for the ecological requirements of the root vole, and to search for new populations of this strictly protected species, sampling was performed with increased trapping investment in the successive 3 years (2005-2007). Thus, new habitats were designated compared with former population-level monitoring, and trapping frequency was increased too.

In the present study our data collected between 2005-2007 in isolated macrohabitats of the Kis-Balaton area are analysed (Fig. 1.)

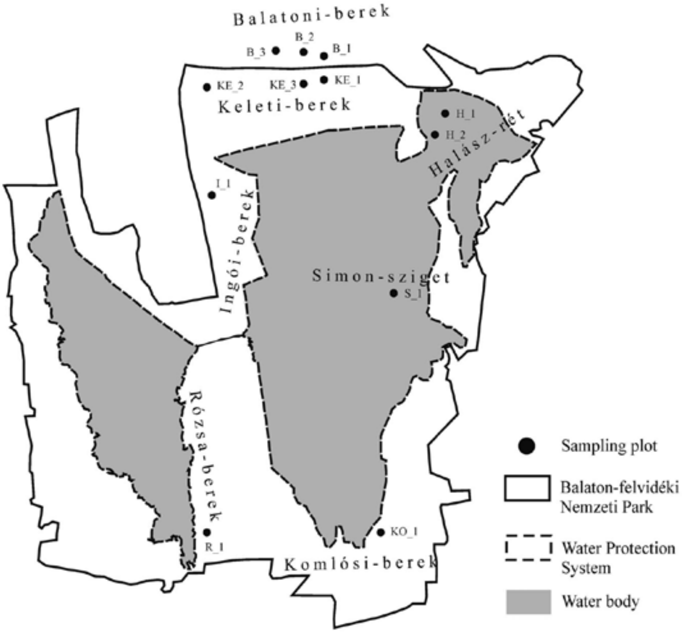


Fig. 1: Distribution of the investigated seven macrohabitats and different sampling plots in the Kis-Balaton Protected Area

Table 1: GPS coordinates of sampling plots and parameters of trapping effort

Macrohabitat	Sampling plot	GPS coordinate		2005			2006			2007		
		N	E	*TN*	*S*	*C*	*TN*	*S*	*C*	*TN*	*S*	*C*
Balatoni-berek	B_1	46°42'50"	17°11'20"	418	4	46	165	3	17	-	-	-
	B_2	46°42'29"	17°11'03"	-	-	-	-	-	-	2057	8	129
	B_5	46°42'29"	17°10'54"	-	-	-	-	-	-	847	5	45
Keleti-berek	KE_1	46°42'43"	17°11'20"	3872	8	244	605	3	10	-	-	-
	KE_2	46°42'03"	17°10'52"	3025	11	149	2079	11	432	1331	8	214
	KE_3	46°42'25"	17°11'09"	-	-	-	-	-	-	2541	9	246
Halász-rét	H_1	46°42'04"	17°15'15"	1474	10	121	3707	10	206	1537	7	50
	H_2	46°42'00"	17°14'51"	-	-	-	120	5	21	-	-	-
Simon-sziget	S_1	46°38'20"	17°13'14"	-	-	-	22	2	17	-	-	-
Komlósi-berek	KO_1	46°34'59"	17°13'19"	484	3	45	-	-	-	-	-	-
Ingói-berek	I_1	46°40'52"	17°11'22"	2047	9	96	-	-	-	-	-	-
Rózsa-berek	R_1	46°35'08"	17°10'25"	688	5	58	-	-	-	-	-	-

TN: trap night, *S*: number of species, *C*: capture number of specimens

Altogether seven macrohabitats (groves) were studied during the three years which were different in their number of sampling plots and trapping intensity. For each sampling habitat patch we indicated GPS coordinates, the number of trap nights representing trapping effort, the indicated level of species richness (S), and the numbers of small mammal captures (Table 1.).

Balatoni-berek

The Balatoni-berek is a boggy area stretching between Sármellék and Keszthely, reaching the canal "Északi-keresztcsatorna", an "*ex lege*" protected nature conservation area before 2001 but not part of the Balaton Uplands National Park. A large stretch of the Balatoni-berek in the south, neighbouring the national park was privatized in 2002, meaning that the monitored area in the analysed study years was managed by a private owner. This macrohabitat rose due to the filling up of a former freshwater marshland. These heterogeneous macrohabitats consist of some different degraded sedgy habitat patches, where the high density of *Calamagrostis epigeios* indicates the negative effects of eutrophication (accumulation of nutrients). The altitudes are increasing uniformly from the reedy part towards the road, which clearly shows the gradual thinning and shrinkage of the common reed's stocks (*Phragmites australis*). In the period before privatization, it was this boggy area among the sampled macrohabitats that represented habitat patches with the most suitable conditions for the root vole, with undisturbed, homogeneous sedge vegetation and water cover. The very dry period in the Balatoni-berek in 2001, and successive human impact i.e. regular hay cutting in 2002-2003 altered the physiognomic structure and vegetation composition of the homogeneous sedgy habitat. The higher amounts of precipitation in 2004 replenished the water supplies of the bog area, preventing the owner from utilising the land, including grass cutting. As a result, vegetation in the area could gradually regenerate itself, allowing us to lay out sampling spots in three regenerated habitat patches in 2005-2007 (B_1, B_2, B_3).

Keleti-berek

Keleti-berek is located south of Road 76, being part of the Balaton Uplands National Park, and as such, of the Natura 2000 habitat network. The macrohabitat is 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*). Further down the area is characterized by higher water availability.

Between 2001 and 2003 habitat qualities in this area, too, were greatly determined by the drier weather period together with negative human impacts (burning, grass cutting). Due to rainier weather in 2004, vegetation in the area could regenerate. The quality improvement of habitats was partly due to negotiations with national park staff regarding locations of habitat management activities, i.e. only vegetation patches dominated by the invasive *Solidago gigantea* were cut down in the following years. In the monitoring period between 2005-2007 in the Keleti-berek, sampling spots were designated in three habitat patches (KE_1, KE_2, KE_3).

Halász-rét

Halász-rét is a microhabitat patch in the northeastern part of the Kis-Balaton Landscape Protected Area, towards the village Balatonszentgyörgy. Sampling locations (H_1, H_2) were laid out about 100 m west of the river Zala. The mosaic-like mixture of patches including homogeneous sedge, deeper areas with reed and elevated, drier areas dominated by *Solidago* contributed to an increased macrohabitat heterogeneity. Water cover in the Halász-rét area is to a great degree determined, besides precipitation, by water management in Stage 2 of the Kis-Balaton Water Protection System. From the point of view of small mammals, i.e. in the spring-autumn period, the most important abiotic constraint factor was changes in water level, as evoked by the combined effect of water management and weather.

Simon-island

Simon-island is one of the largest islands, with the most variable vegetation cover, located in the eastern part of Stage 2 of the Kis-Balaton Water Protection System. Its northern part is covered by forests (locust maple, oak), whereas in its southern parts there is an abandoned pasture with scattered hawthorn bushes, used currently as a hayfield. In its higher elevations along these areas there are edge zones with *Solidago* cover. The perimeter of the island is lined by a zone of tall tussock sedge, with as high as 50-100 cm water cover under rainy weather conditions. The sampling location was designated in the homogeneous tussock sedge area east of the forest-covered part of the island (S_1).

Komlósi-berek

Komlósi-berek is located in the southernmost part of Stage 2 of the Kis-Balaton Water Protection System, between the water buffalo reserve of Kápolnapuszta and the village of Sávoly, where the sampling plot (KO_1) was laid out in a large expanse of homogeneous tall-sedge vegetation. This area extends towards the north to the village Főnyed, with the physiognomic structure of its vegetation potentially suitable for supporting subpopulations and populations of the strictly protected root vole. However, our experience showed that one of the most important ecological constraint factors influencing small mammals and their dispersion was the rapidly changing levels of water cover.

Rózsa-berek

Rózsa-berek is a mosaic-pattern boggy area stretching between Balatonmagyaród and the areas of Stage 1 of the Kis-Balaton Water Protection System, i.e. the expanse between the village and the Hídvégi lake. The low-lying macrohabitat east of the village is typically heterogeneous in its vegetation, due to the presence of sedgy areas and patches of wooded areas, shrubs and forest pathes in a mosaic pattern. The sampling plot is a mosaic area but is dominated by sedgy areas (R_1). This habitat patch is more elevated than the lakeside area of the Hídvégi lake, thus the drastic increase in water levels was not characteristic.

Ingói-berek

Ingói-berek is a large, homogeneous sedgy area located west of Fenéki-lake. Water levels in Ingói-berek are greatly influenced by water amounts passing in Ingói canal between the sedgy area and the dyke of Fenéki-lake. The sampling area (I_1) was laid out near the automatic pumping station of Ingó, in a tussock sedge area under permanent water cover, to the east along the western dyke.

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). From the number of traps in each of sampling plots and the number of sampling nights in the three monitoring years (2005-2007) we can count the summarized amount of trap occasions, which was as many as 12008 trapping nights for the present study. Captured animals were marked individually and we also recorded the sex (by females: gravidity or lactation too), age and body mass. Ages were determined based on body mass and overall appearance.

Statistical methods

The nestedness analysis of small mammal assemblages in sampling locations (habitat patches) of various macrohabitats in the Kis-Balaton area was based on presence-absence data of recorded species. The presence-absence matrix is the fundamental unit of analysis in community ecology and biogeography (MCCOY & HECK 1987). In such a matrix, rows are species, columns are sites or samples, and entries are the presence (1) or absence (0) of a species in a site. Few issues in community ecology have been more contentious than the statistical analysis of these data matrices (GOTELLI 2000).

Based on presence-absence matrices ATMAR & PATTERSON (1993, 1995) introduced a concept that considers also the placement of a cell in a give matrix. The software published by these authors is the most popular approach for estimating nestedness; based on temperature of the matrix, *T*, was the Nestedness Temperature Calculator, (NTC) (ATMAR & PATTERSON 1993). *T* measures the degree of order in "packed" distribution matrices and takes values from 0 (perfect nestedness) to 100 (maximum disorder). This simple thermodynamic term, *T*, describes a continuum between the extremes of perfect nestedness (maximally "cold", 0) and hyper-dispersed, checkerboard arrangement (maximally "hot", 100), where matrices that contain both a degree of nested order and randomness will exhibit an intermediate "temperature" (ATMAR & PATTERSON 1993). Nevertheless, several other new softwares have since been released for the analysis of the nestedness of communities (ULRICH et al. 2009). WINE (Weighted-Interaction Nestedness Estimator) is a new nestedness estimator that takes into account the weight or intensity of each interaction (e.g., in a plant-pollinator network, the number of registered visits of a particular interaction). Thus, instead of using presence-absence matrices, this esimator calculates nestedness from quantitative data matrices that include the number of events of each interaction (GALEANO et al. 2009). We used the “bipartite” package of R (DORMANN et al. 2008) to calculate the weighted-interaction nestedness estimator (WINE), where d_{max} is the distance of the completely packed matrix. The WIN of the data matrix can then be normalized by comparing it to the average WIN of equivalent random matrices and to the WIN of the maximal nestedness matrix (WRIGHT & REEVES 1992) to obtain the weighted-interaction nestedness estimator (GALEANO et al. 2009):

$$\eta_w = \frac{d^w - d_{rnd}}{d_{\max} - d_{rnd}}$$

where the d_w is the mean weighted distance of all its non-zero elements, d_{rnd} is the average value of 1000 replication random matrix. The value of this estimator approaches (η_w) 0 when the WIN of the original data matrix is close to the average WIN of the equivalent random matrices. It approaches 1 as it gets closer to the nestedness of the maximal nestedness matrix. The estimator evaluates the relative position of the data matrix between the corresponding random matrices and the maximal nestedness matrix. Negatives values for this estimator can be found in some synthetic matrices that have been described as “anti-nestedness” matrices (ALMEIDA-NETO et al. 2007). Negative values indicate that the synthetic matrices are less nested than the corresponding random matrices (GALEANO et al. 2009). The program WINE calculates the standardized static variable z-score to assess the significance of WIN. This score assesses how different WIN d_w is from average random WIN d_{rnd}. It is important to mention that the original data is just one combination of all possible permutations of registered events. z values below -1.65 or above 1.65 indicate approximate statistical significance at the 5% error level (one-tailed test). WINE calculates a weighted-interaction distance (d_{ij}^{w}), which estimates nestedness taking into account the number of events in the links, whose values are expressed in a colour scale of the weighted distance matrix. The colour plot is relevant in depicting the relative importance of each interaction, for instance, in the identification of idiosyncratic species or in the evaluation of extinction sequences in species distribution in fragmented habitats (GALEANO et al. 2009).

Similarity of the species composition was ca1culated by the Bray-Curtis quantitative index, and similarity structure was analysed by hierarchical cluster analysis applying the UPGMA fusion method. The SYN-TAX package (PODANI 1993) was used for these computations. To find character species of the cluster hierarchy the IndVal method (DUFRÊNE & LEGENDRE 1997) was used:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

$$A_{ij} = N_{(individuals)ij} / N_{(individuals)i}$$

$$B_{ij} = N_{(traps)ij} / N_{(sites)i}$$

In the equation A_{ij} a stands for specificity where N_{ij} is the mean number of individuals of the i^{th} species in the j^{th} habitat (habitat type), and N_j is the totalised mean number of individuals of the i^{th} species in all of the habitats (or habitat groups). B_{ij} is the degree of fidelity where $N_{(traps)ij}$ stands for the number of traps in the j^{th} group in which the i^{th} species was captured. $N_{(sites)i}$ is the total number of traps in the j^{th} habitat group. This method combines the mean number of species individuals with its relative frequency of occurrence in the various groups of sites in the cluster hierarchy. The index has a maximum when all individuals of a species are found in a single group of sites, and when the species occurs in all sites of that group, it is a symmetrical indicator (its presence contributes to the habitat specificity and its presence can be predicted in all sites of the group, IndVal >55 %). Other species must be considered as accidental ones, these are asymmetrical indicators (their presence cannot be predicted in all samples of one habitat, but contributes to the habitat specificity, IndVal <55 %). The statistical significance of the species indicator values is evaluated using a randomisation procedure by 1000 random permutations. The IndVal2 package (DUFRÊNE & LEGENDRE 1997) was used for these computations.

Results

Pattern of nestedness

The number of small mammal species differed through the three examined years as well as the number of sampling patches within the macro-habitats. This determined the size of given matrices that we used by the exploration of nestedness patterns in the analysis.

The program estimated higher weighted-interaction nestedness (WIN) values for every year than we got from the randomisation process (d_{rnd}). Therefore, all of the nestedness patterns of small mammal assemblages of the three years indicated that the counted nestedness values can not be random, but they differed significantly from it. This assumption was proved by the significance of z scores. The statistical results of compared nestedness values of random and original data matrix showed that the small mammal assemblages of the isolated Kis-Balaton marshland habitat patches are ordered contrary to the random pattern, and showed structured pattern (Table 2).

The value of the weighted-interaction nestedness estimator was positive in all three years, which expressed the relative position between the maximum nestedness and the random pattern. The highest value of this estimator was calculated for the year of 2006 which therefore showed the greatest nestedness, however the relative value of this arose

Table 2: Summarised statistic of nestedness analysis based on Weighted-Interaction Nestedness Estimator (WINE)

Nestedness / years	2005	2006	2007
WIN	0.334	0.432	0.325
d_{max}	0.400	0.472	0.401
d_{rnd}	0.266	0.350	0.268
z-score	4.503	5.407	2.778
P - value	3.34E-06	3.19E-08	0.002
η (WINE)	0.505	0.672	0.428

WIN: weighted-interaction nestedness

η (WINE): weighted-intercation nestedness estimator

d_{max}: weighted-interaction nestedness of the maximal nestedness matrix.

d_{rnd}: average weighted-interaction nestedness of random replicates

z-score: z score of the weighted-interaction nestedness

P - value: probability of the matrix having WIN value, less than expected by chance y 0.5 in 2007, which reflects that the level of nestedness of assemblages recorded for this year was lower and the pattern was less ordered. It is important to highlight in the results of year 2007 that the smallest difference can be seen between the weighted-interaction nestedness (WIN) value and the mean value of randomisation process (d_{rnd}), so the level of significance of z score was the lowest by this analysis. The summarized statistical values of nestedness analysis – based especially on the species composition of 2005 and 2006 – confirmed the nestedness of small mammal assemblages of examined habitat patches (Table 2). Beside the evaluation of the nestedness patterns of data matrices of the three years characterized by different trapping expenditure we were curious what kind of nestedness patterns can be seen by the small mammal assemblages of the 7 variously isolated groves (macro-habitats) on the basis of the summarized data of the three years. The latter three years were characterized by habitat regeneration following the bountiful rainwater and the ceasure of human disturbances.

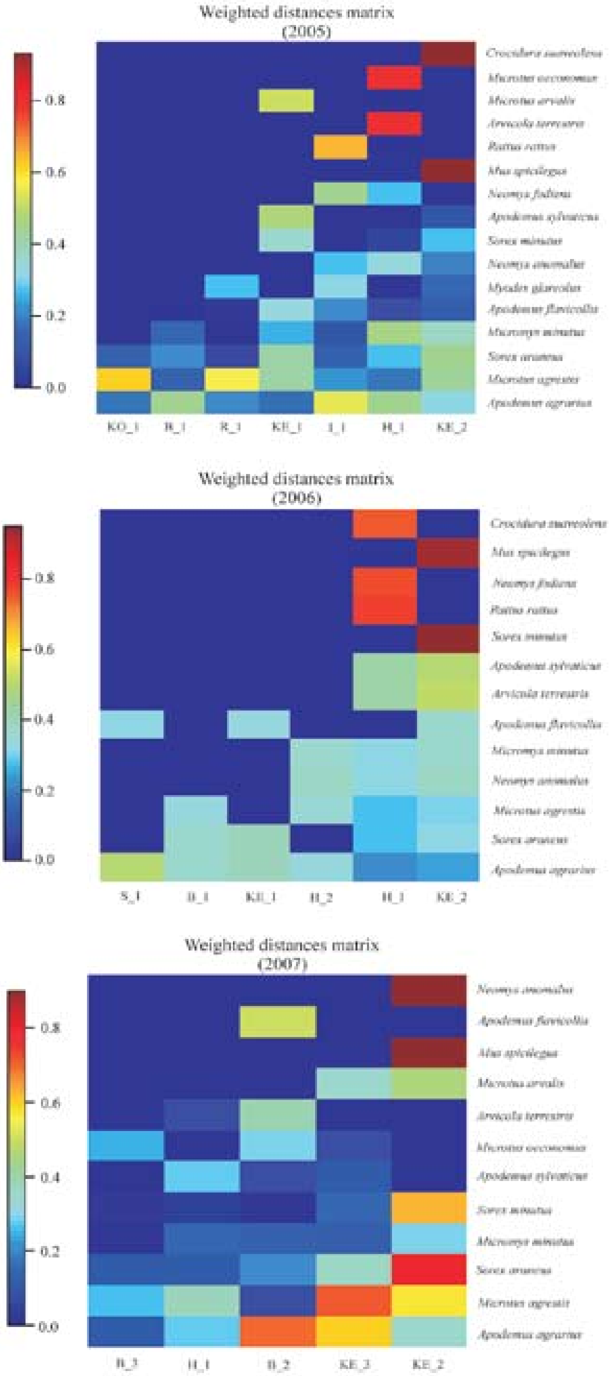
WINE calculates a weighted-interaction distance (d_{ij}^{w}), which estimates nestedness taking into account the number of events in the links (Fig. 2). Based on the pattern of colour plots we are able to explain the peak values of idiosyncratic species and isolated habitats. In 2005 six idiosyncratic species contributed to the disorder (*C. suaveolens, M. oeconomus, M. arvalis, A. terrestris, R. rattus, M. spicilegus*). Common vole (*M. arvalis*) did not increas the disorder with its high value, but with its presence. From the perspective of investigated areas the idiosyncratic habitats were KE_1 and H_1. In the Keleti-berek habitat (KE_1) we found that the habitat altering effects of previous disturbances were the main community organiser external constraint factor, while in case of the Halász-rét (H_1) it was the effect of bountiful rainwater and the water regulations in the neighbourhood of River Zala.

Although, in the next year (2006) the nestedness pattern resembled to the maximum nestedness matrix based on the higher value of WINE that is demonstrated by the graphic illustration of the results. We could also identify several idiosyncratic species – *S. araneus, M. agrestis* and *A. flavicollis* – in this year based on the unexpected appearance and absence (Fig. 2.). Five species (*C. suaveolens, M. spicilegus, Neomys fodiens, R. rattus, S. minutus*) had higher weighted distance values, which decreased the orderedness of the system. By analysing the habitats we found that three of them (KE_1, KE_2 and H_1) were idiosyncratic. Regarding the identification of the idiosyncratic habitats we can conclude the same like for the previus year.

We received the lowest level of nestedness for 2007 based on the original data matrix, and WINE placed the position of the pattern between the random pattern and maximum nestedness. This year is the most unorganised among the three examined years, which is caused by the following species: *N. anomalus, M. spicilegus, S. araneus, M. agrestis, A. agrarius*. The presence or absence of several species was unexpected (*A. flavicollis, A. terrestris, M. oeconomus, A. sylvaticus*). Considering the habitats it can be laid down that KE_2, KE_3 and B_2 habitats were responsible for the disorder (Fig. 2.).

Determining the indicator values (IndVal) of species

The greater trapping effort that was applied in 2005 aiming at the rediscovery of root vole (*M. oeocnomus*) resulted data from 6 macro-habitats and 7 habitat patches, from which data we could perform the IndVal analyses. In this year 11 species received the significant indicator or character value from the 16 small mammals (Table 3). The most important result of the 2005 sampling period is that we could catch several individuals of the critically endangered root vole in the Halász-rét (H_1) area among the sampled habitats. In 8 of the 11 species characterized by maximum indicator value the IndVal values were lower than 55% (Table 3). Through the classification performed on the basis


Weighted distances matrix (2005)

Weighted distances matrix (2006)

Weighted distances matrix (2007)

Fig. 2: Weighted distances matrices of small mammals assemblages in the three investigated years (2005-2007)

Table 3: Table of the indicator values of the species, based on the hierarchy level of the habitat patches in 2005, where the first value is the number of caught individuals by single habitat patch and the second value is the number of those trap points where the species occurred in the given patch

Macrohabitat / Sampling plot	IndVal (%)	Keleti-berek		Halász-rét	Ingói-berek	Komlósi-berek	Balatoni-berek	Rózsa-berek
Species		KE_1	KE_2	H_1	I_1	KO_1	B_3	R_1
S. araneus	77.59	66/10	38/11	22/9	11/4	7/5	11/4	4/2
S. minutus	50.91**	10/7	4/4	1/1	0/0	0/0	0/0	0/0
C. suaveolens	27.27*	0/0	3/3	0/0	0/0	0/0	0/0	0/0
N. anomalus	11.89	0/0	1/1	2/2	2/1	0/0	0/0	0/0
N. fodiens	32.59*	0/0	0/0	1/1	2/2	0/0	0/0	0/0
M. glareolus	51.31**	0/0	3/2	0/0	8/2	0/0	0/0	9/5
M. agrestis	82.76	68/11	41/10	16/6	18/4	30/8	7/4	33/5
M. oeconomus	18.18 *	0/0	0/0	3/2	0/0	0/0	0/0	0/0
M. arvalis	63.64**	18/7	0/0	0/0	0/0	0/0	0/0	0/0
A. terrestris	45.45**	0/0	0/0	6/5	0/0	0/0	0/0	0/0
R. rattus	20*	0/0	0/0	0/0	1/1	0/0	0/0	0/0
A. agrarius	82.76	23/11	26/10	34/9	39/4	8/5	20/5	11/4
A. flavicollis	43.14**	19/8	4/4	3/3	8/1	0/0	0/0	1/1
A. sylvaticus	69.26**	10/8	1/1	0/0	0/0	0/0	0/0	0/0
M. spicilegus	9.09	0/0	1/1	0/0	0/0	0/0	0/0	0/0
M. minutus	69.82**	32/11	27/7	33/10	7/2	0/0	8/4	0/0
Total		243/73	149/54	121/48	96/21	45/18	46/17	58/17

**: $P < 0.01$; *: $P < 0.05$

of quantitative values we separated three smaller clusters (one incorporated 3 habitats, two of them contained 2) in the 2005 analysis. In the first cluster the habitat patches of Keleti-berek (KE_1, KE_2) and the Halász-rét (H_1) were joined on the basis of their similarities. In the second cluster the Ingói-berek (I_1) and the Balatoni-berek (B_1) were joined at the same dissimilarity value range like the previous ones. This fact is caused by the high frequency of striped field mouse (*A. agrarius*) in case of the latter two habitats (Table 3). In the south-western part of KBWPS-II the examined sedgy habitat patches of the Komlósi-berek (KO_1) and Rózsa-berek (R_1) were joint with the lowest distance value, which showed the highest similarity of the small mammal assemblages of these two habitats (Fig. 3).

Every species that was characterized with lower IndVal values than 55 % were typical only in the given habitat patch, where they can be considered as asymmetrical indicator species. In the sampling plot of Halász-rét (H_1) laying by River Zala the root vole showed up with low IndVal values as an asymmetrical indicator species. The european water vole (*A. terrestris*) appeared in the same patch as a significant species, however its character values were higher than those of the root vole and thus we can state that both of these vole species appear as indicators of the reedy-sedgy habitat patches characterized by higher water level close to River Zala. Regarding the two vole species the significant character value – typified locally for every habitat patch – indicates such optimal habitat quality that provides suitable environmental conditions for root vole settling (colonisation). In case of the Keleti-berek (K_2) the lesser white-toothed shrew (*C. suaveolens*) was an asymmetrical indicator species characterized by significant IndVal values revealing one habitat type, while in the area of Ingó-berek (I_1) water shrew (*N.*

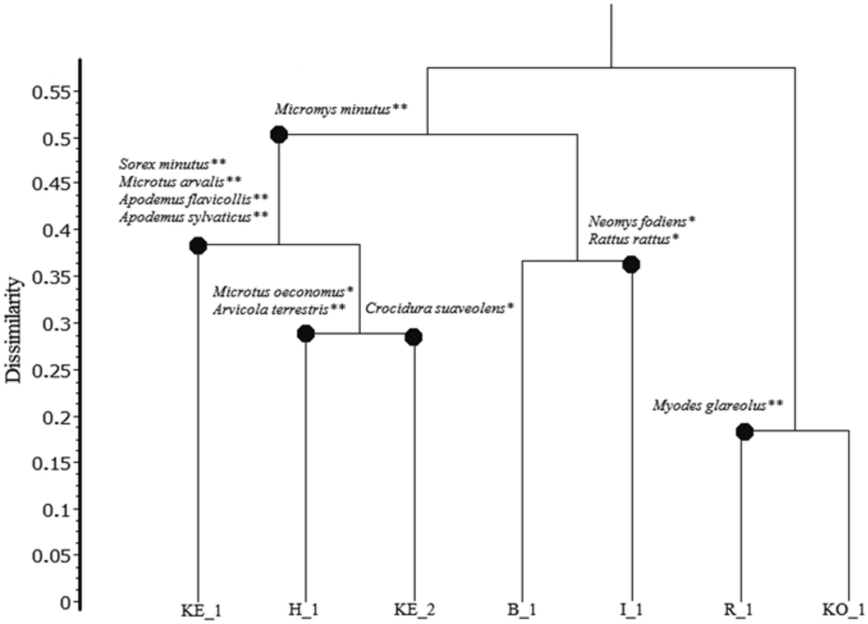


Fig. 3: Dendrogram of the habitats in 2005 (Bray-Curtis-index, UPGMA). Species possessing significant maximum indicator values are marked (*: P < 0.05, **: P < 0.01)

fodiens) and black rat (*R. rattus*) seemed to be indicator species. While the lesser white-toothed shrew indicated habitat alteration occurring because of human disturbances (regular mowing) in the area of Keleti-berek between 2001-2004, the two other species indicated the higher water level of the canal-flanked Ingói-berek (Fig. 3).

Receiving significant indicator value in case of the bank vole (*M. glareolus*) appeared as an unexpected result through the analysis, because this species can not be considered as a character species regarding marshland habitats. The IndVal values of the bank vole were not expoundable for a group of habitats based on the quantitative data, but for a single habitat – Rózsa-berek (R_1) – where it appeared as a rare species of the small mammal community (Fig. 3). The recorded presence of bank vole in the small mammal assemblage of the examined mosaic-like sedgy habitats was due to the isolated willow groups. Contrary to species characterized by lower character values there were three species that received higher IndVal values than 55 % (*M. minutus, M. arvalis, A. sylvaticus*), however only the highest value for the harvest mouse (*M. minutus*) (68.82 %) can be considered as a symmetrical indicator species among them. Since the harvest mouse was present in the habitat patches of Keleti-berek and the Halász-rét, therefore it appeared as a character species of one habitat group of the Kis-Balaton marshland area. On the fourth level of the habitat hierarchy the two *Apodemus* species (*A. flavicollis, A. sylvaticus*) showed up in the disturbed habitats of Keleti-berek, and the bank vole indicated altered habitat quality due to the disturbances (Fig. 3).

On the basis of the 2006 trapping data some species occurred in smaller proportion in more habitats. Among others we received smaller abundance values for the water shrews (*N. fodiens, N. anomalus*) and the lesser white-toothed shrew (*C. suaveolens*), however in terms of faunistical and nestedness analyses these are valuable information. In this year we performed the IndVal analysis on the basis of data derived from 6 habitat patches of 4 macro-habitats. We recorded 13 small mammal species with the trapping of 6 habitat patches and 6 of them received significant value (Table 4). The yellow-necked mouse (*A. flavicollis*) got the highest IndVal value, however, despite of this fact its significant indicator value was expoundable only for that patch of Keleti-berek (KE_1), where human activities altered considerably the structure of vegetation in the previous years (Fig. 4). Furthermore, we received maximum indicator values for two other species (*A. agrarius, M. minutus*), but it was only the harvest mouse whose IndVal value was significant, which can be jointly construed for two habitat patches (H_1, KE_2) on the second level of hierarchy. Therefore, the harvest mouse was a component of small mammal assemblages of several habitat patches as an asymmertic indicator species. Miller's water shrew (*N. anomalus*) showed up as an asymmetric character species of one habitat patch (H_2) with significant maximum value, which indicated the higher level of water on this sedgy-reedy transient habitat mosaic (Fig 4). The european water vole (*A. terrestris*) with its 60% IndVal value can be considered as a symmetrical indicator species (> 55% IndVal) (Table 4). Its significant maximum character value characterized the second habitat patch of Keleti-berek (KE_2) on the fifth level of the hierarchy, where the water level of the homogeneous sedgy area was higher in springtime (Fig. 4). Trapping throughout the year 2006 cannot prove the permanent presence of root vole subpopulation in the Halász-rét or rather its colonisation in the area of Keleti-berek. In this year the other endangered vole species, the field vole (*M. agrestis*) – that characterises the Kis-Balaton marshy relict area – appeared in the second habitat patch of Keleti-berek (KE_2). There had been no human disturbance through the preceding few years, so the field vole got significant maximum IndVal value for the typical homogeneous sedgy habitat (Fig. 4).

Table 4: Table of the indicator values of the species based on the hierarchy level of the habitat patches in 2006, where the first value is the number of caught individuals by single habitat patch and the second value is the number of those trap points where the species has occurred in the given patch.

Macrohabitat / Sampling plot	IndVal (%)	Keleti-berek		Halász-rét		Balatoni-berek	Simon-sziget
Species		KE_1	KE_2	H_1	H_2	B_3	S_1
S. araneus	50.77	6/5	41/13	18/13	0/0	4/2	0/0
S. minutus	11.76	0/0	2/2	0/0	0/0	0/0	0/0
C. suaveolens	7.41	0/0	0/0	2/2	0/0	0/0	0/0
N. anomalus	37.37**	0/0	18/9	5/4	2/2	0/0	0/0
N. foediens	7.41	0/0	0/0	2/2	0/0	0/0	0/0
M. agrestis	35.41**	0/0	12/10	11/7	0/0	1/1	0/0
A. terrestris	58.56*	0/0	60/11	10/4	0/0	0/0	0/0
R. rattus	7.41	0/0	0/0	3/2	0/0	0/0	0/0
A. agrarius	70.77*	3/3	262/16	89/21	2/1	14/3	14/2
A. flavicollis	84.87*	1/1	3/3	0/0	0/0	0/0	3/2
A. sylvaticus	9.09	0/0	2/2	2/2	0/0	0/0	0/0
M. spicilegus	29.41**	0/0	5/5	0/0	0/0	0/0	0/0
M. minutus	74.55*	0/0	46/16	85/21	8/3	0/0	0/0
Total		10/9	451/87	227/78	12/6	19/6	17/4

**: $P < 0.01$; *: $P < 0.05$

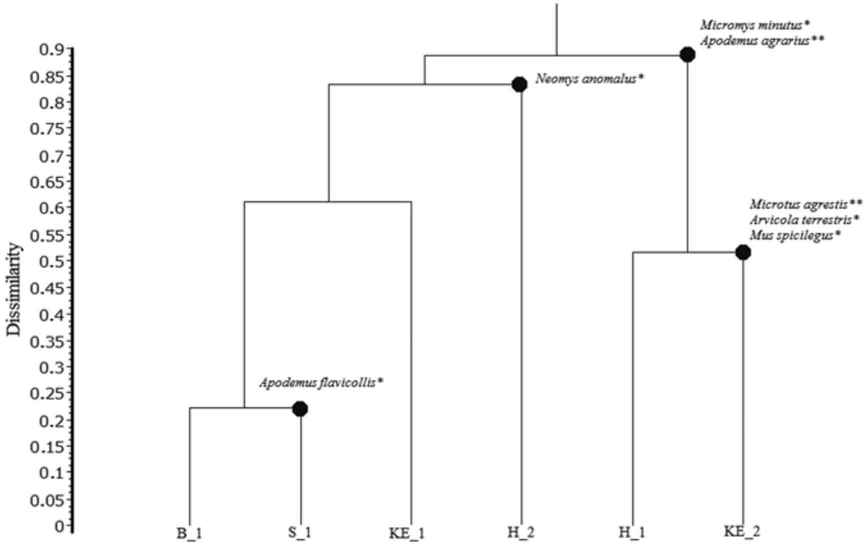


Fig. 4: Dendrogram of the habitats in 2006 (Bray-Curtis-index, UPGMA). Species possessing significant maximum indicator values are marked (*: $P < 0.05$, **: $P < 0.01$)

The mound-building mouse (*M. spicilegus*) appeared in the same habitat patch of the Keleti-berek (KE_2) as a colouring element of the small mammal assemblage in 2006, and its maximum indicator value can be considered to be significant based on the statistical calculations of IndVal program (Fig. 4). This result can be regarded as an opposite result in relation to the character values of field vole and european water vole. The appearance of mound-building mouse was due to the environmental background variables of autumn 2006 and the presence of plough-lands beside the sampled patch. This allowed this mouse species which uses mostly agricultural areas to ensconce more often to the sedgy marshes from the fields. Mound-building mouse was typical for one habitat patch from the 6 sampled areas, therefore its significant indicator value was caused by its rareness and we could characterise it as an absolute asymmetrical indicator species.

On the basis of 2007 trapping we computed the input matrices of IndVal analysis based on trapping data of 3 macro-habitats and 5 habitat patches. We recorded 12 small mammal species and 6 of them received significant maximum indicator value. It was a very important result of this year that we indicated the recolonised individuals of root vole in many habitat patches of Keleti-berek. Through the analysis we received greater than 80 % indicator values for the common shrew (*S. araneus*) and the striped field mouse (*A. agrarius*), therefore these two species can be considered as symmetrical indicator species of more habitat patches. We received lower than 55 % values for every other species and those which were characterized by significant maximum Indval values appeared as asymmetrical character species of certain habitat patches (Table 5).

Based on the quantitative data the root vole appeared in this study with significant maximum indicator value in the regenerated sedgy area of Balatoni-berek following the mowings. Then the rediscovered root vole was a typical indicator species in the Balatoni-berek in an enclosed, treatment-free, regenerated sedgy habitat which is beyond the pale of the national park. The same habitat patch and the regenerated habitat quality were characterized by the appearance of european water vole individuals as well (Fig. 5).

Table 5: Table of the indicator values of the species based on the hierarchy level of the habitat patches in 2007, where the first value is the number of caught individuals by single habitat patch and the second value is the number of those trap points where the species has occurred in the given patch

Macrohabitat / Sampling plot	IndVal (%)	Balatoni-berek		Keleti-berek		Halász-rét
Species		B_1	B_2	KE_2	KE_3	H_1
S. araneus	81.61**	6/5	22/9	88/11	48/10	6/6
S. minutus	33.77**	0/0	0/0	10/5	3/3	1/1
N. anomalus	18.18*	0/0	0/0	2/2	0/0	0/0
M. agrestis	80.00	13/7	9/7	69/11	105/11	20/8
M. oeconomus	44.57**	20/9	19/8	0/0	4/4	0/0
M. arvalis	9.09	0/0	0/0	1/1	1/1	0/0
A. terrestris	23.38*	0/0	3/3	0/0	0/0	1/1
A. agrarius	85.01**	5/4	71/11	39/10	82/11	13/4
A. sylvaticus	27.97*	0/0	1/1	0/0	1/1	5/4
A. flavicollis	9.09	0/0	1/1	0/0	0/0	0/0
M. spicilegus	9.09	0/0	0/0	1/1	0/0	0/0
M. minutus	16.36	0/0	3/2	4/3	2/2	4/2
Total		129/42	44/25	17/4	245/43	59/26

***: $P < 0.01$; *: $P < 0.05$*

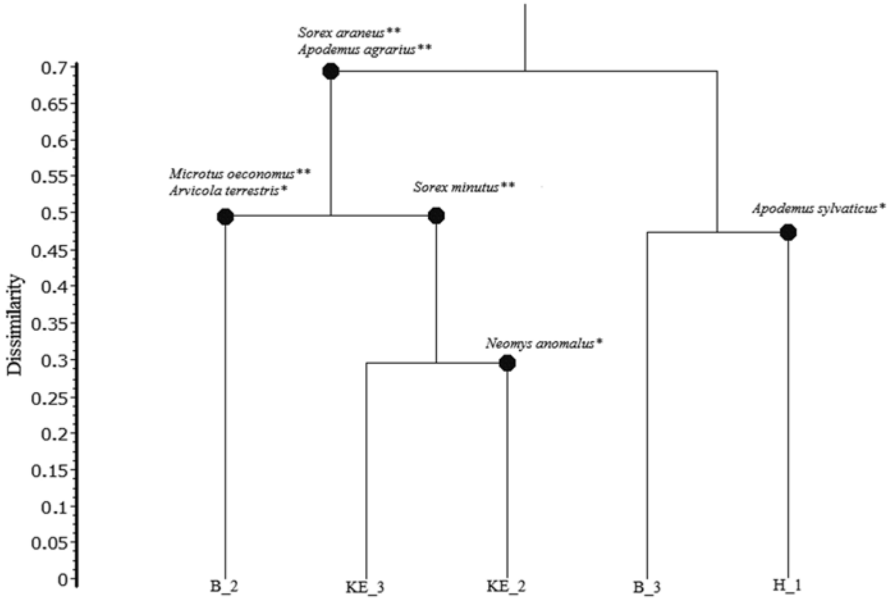


Fig. 5: Dendrogram of the habitats in 2007 (Bray-Curtis-index, UPGMA), Species possessing significant maximum indicator values are marked (*: $P < 0.05$, **: $P < 0.01$)

The IndVal analysis of 2007 suggested that whenever the root vole appears in a given macrohabitat, it can be characterized as a significant character species in the comparing studies of community ecology. Its typical indicator feature appears even if its individuals cannot be detected in a high proportion – this could be seen by the appearance of the species in the Halász-rét in 2005 as a good example. The eurasian pygmy shrew (*S. minutus*) – a typical species of marshy-moorish habitats – was a significant character species of two macrohabitat patches on the third level of the habitat hierarchy. The significant maximum character value of the wood mouse (*A. sylvaticus*) was typical in the Halász-rét in this quantitative data based analysis (Fig. 5).

Discussion

Nestedness pattern is most often used to explore the structure of communities (ATMAR & PATTERSON 1993, PATTERSON & ATMAR 2000, GANZHORN & EISENBEISS 2001), which has a great importance by the protection of meta-communities, where species loss decrease immediately the predictability of species composition (PATTERSON 1987, CUTLER 1991, BÁLDI 2003b). By analyzing mammal communities there were several case studies which described the nestedness, for instance islands within an archipelago (KRIŠTUFEK & KLETEČKI 2007), isolated peaks along a mountain range (MCDONALD & BROWN 1992, HADLEY & MAURER 2001), habitat fragments within a landscape (PATTERSON & ATMAR 2000) and by the approach describing spatial distribution of species and interspecific interactions (BAKER & PATTERSON 2011). These studies have a great importance regarding both biogeographical, community ecological and environmental protection view points, and some of the previous works (e.g.: MCDONALD & BROWN 1992) draw the attention to the problems of using nestedness approach (BÁLDI 2003a).

Nestedness pattern can originate from many different factors such as extinction, colonization, disturbance, spatial distribution of habitats and hierarchical niche associations (PATTERSON & ATMAR 2000, BÁLDI 2003a). These processes have big significance related with the fragmented refuge relict wetlands, primarily by those habitat patches which are isolated on different levels and can be typified by different land-use intensity and the negative effects of considerable human disturbances prevail – these are important questions concerning several animal assemblages of the Kis-Balaton Landscape Protection Area in terms of environment protection and management activities.

Because of the relict characteristic of Kis-Balaton marshlands the water-reserve system maintaining human interventions affect appreciably the biodiversity, thus the hypothesis-testing control of these effects are highlighted projects in the Hungarian Biodiversity Monitoring System (HBMS). Small mammal species abundances or community compositions – as disturbance indicators – have potential to be important tools for land- and conservation management to evaluate effects of disturbance (LEIS et al. 2008), therefore small mammals are important objects by the conservational monitoring of Kis-Balaton marshland area. In case there are relict, habitat specialist species in a fragmented, refuge community, then the latter effects can cause local extinctions, species turnovers and they may induce the alteration of the community structure.

One goal of nestedness analysis has always been to identify such ‘deviating’ species and to infer the causes of idiosyncrasy (ULRICH et al. 2009). ATMAR & PATTERSON (1993) explained the existence of idiosyncratic species by post-isolation immigration, geographic barriers and competitive exclusion. Because the base of the nestedness analysis made by ATMAR & PATTERSON (1993) is extinction, therefore we can draw important inferences about the extinction sequence by the nestedness community patterns (BÁLDI et al. 2003a, b; GALEANO et al. 2009). In terms of the mammals of Kis-Balaton marshlands one of the main tasks of the project is connected with the critically endangered root vole, which proved to be the most vulnerable species in the analysis of small mammal responses to disturbing effects. Therefore, in the case of the macro-habitats of Kis-Balaton the most important question in the conservation management of root vole is how large habitat fragments does the species occurs in?

The main aim of the 11-year long small mammal monitoring programme applied in the wetlands of Kis-Balaton area was the population-level examination of the root vole. However, the joint effects of human disturbance, interventions (burning, mowing, enclosure) and the dry weather altered the habitat structure, because of which the structure of small mammal assemblages has changed significantly. After the dry period the extensive sampling of the sedge-dominated macro-habitats provided the ecological evaluation of the typical small mammal assemblages based on the nestedness pattern and definition of indicator and character species. For the evaluation of nestedness we used a recently developed program, the wieghted-interaction nestedness (WINE), which contains many innovations: it is independent from matrix size and fill, in addition to taking into account the relative position of the links in the matrix, it accounts for the number of events of links (GALEANO et al. 2009).

Our basic question was how much the species turnover processes and the water-level increase following bountiful precipitation as a natural disturbance predominate in directing the composition of small mammal assemblages and in the nestedness pattern in human disturbed habitat patches. The results of the WINE randomization statistic showed that the small mammal assemblages of Kis-Balaton marshland habitat patches show, instead of a random pattern, an ordered one. The value of the weighted-interaction nestedness estimator was positive all in the three years, which expressed the relative position between the maximum nestedness pattern and the random state. The summarised statistical results of the nestedness analysis showed – especially in 2005 and 2006 – that the small mammal assemblages of the isolated Kis-Balaton marshland habitat patches are nested without doubt.

Comparing the results of the nestedness and the IndVal analysis we can highlight 5 species as idiosyncratic species based on the 2005 data matrix. These species determined the nestedness patterns and they got significant maximum indicator values for a given habitat patch. We suggest that the root vole (*M. oeconomus*), as a habitat specialist species has a great importance because it indicates on the one hand its own optimal environment, on the other hand its local extinction influenced considerably the nestedness patterns because it is one of the most vulnerable species of the community. However, the lesser white-toothed shrew (*C. suaveolens*) appeared as an asymmetrical indicator species in that habitat patch, where human interventions and disturbances changed the structure of tha habitat. This unexpected presence was confirmed by the high weighted-interaction distance received through the nestedness analysis and thus it appeared as a idiosyncratic species. The rare occurrence in 2005 of some species that are not typical in original homogeneous sedgy habitats showed that despite of the bountiful precipitation following the dry season the previously disturbed habitat patch of Keleti-berek (KE_1) can not recover properly through one year compared to the undisturbed state.

Synthesizing the results of the two community typifying approaches in 2006 we could highlight only three species that received significant indicator value in the IndVal analysis as an idiosyncratic species. The yellow-necked mouse (*A. flavicollis*) as a symmetrical-, while the mound-building mouse (*M. spicilegus*) as an asymmetrical indicator have decreased the nestedness with their unexpected presence regarding the sampled marshlands. Although the field vole (*M. agrestis*) indicated the regeneration of the given habitat, yet – because of its absence in some patches – it is a idiosyncratic species in the nestedness analysis. This result showed that this species is a good indicator of regenerating sedgy habitat patches, but it has not even appeared generally in every marshland where the difference of environmental factors and the fragmentation of macro-habitats play an important role.

We received other results by analyzing which species are responsible for the nestedness pattern and how high indicator values do they have in the habitat structure according the 2007 data. The assemblage structure seemed to be the less nested and altogether we could highlight 8 small mammal species as idiosyncratic ones. We received maximum indicator values at 5 occasions from the 8, the striped filed mouse (*A. agrarius*) and the common shrew (*S. araneus*) were symmetrical indicators, although they had the least importance in the variance of the theoretical maximum nestedness pattern.

Miller's water shrew (*N. anomalus*) as an asymmetrical indicator appeared in a given habitat patch of Keleti-berek, therefore both of its significant value and idiosyncratic nature was caused by its unexpected presence. Finally, we emphasize the values of root vole, because we could record its recolonized groups in the habitat patches of Balatoni-berek, where it indicated the regenerated, undisturbed environment. The root vole as a habitat specialist indicator has appeared in the nestedness analysis as an idiosyncratic species. These results proved admittedly that the root vole – as a habitat specialist species – is very sensitive to the habitat fragmentation and the human disturbances, so the pattern of its presence influences considerably the nestedness of small mammal assemblages of the examined marshlands.

The nestedness analysis and calculation of indicator values of the species provide useful information for the environment protection about the organisation of small mammal assemblages in an altering environment, about the habitat use and colonization abilities of generalist and specialist species and the species turnover processes, especially about the presence-absence relations changing within the small mammal assemblages through human disturbances and water states. Based on the two parallel community ecological analyses we are able to draw inferences about the relation between small mammals and their occupied habitat patches within isolated refuge macrohabitats, about the relation between habitat quality and the habitat selection of small mammals. These results provide more useful information for nature protection than we can receive with the diversity analysis of those small mammal assemblages which are characterized by low species richness.

In the near future it is very important to evaluate long-term monitoring data in terms of exploring the nestedness patterns, where the changes in the structure of assemblages could be examined not only spatially but temporally as well (BÁLDI 2003a, BLOCH et al. 2007), focusing on recolonisation and species turnover processes.

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