

Quantitative classification of macrohabitats for small mammals' habitat segregation surveys in a forest reserve

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GÁBOR, A., HORVÁTH, GY., ORTMANN-NÉ AJKAI, A., & CSICSEK, G.: *Quantitative classification of macrohabitats for small mammals' habitat segregation surveys in a forest reserve.*

Abstract: To investigation of coexistent small mammals' macro-habitat association first we discriminated three habitat groups of the 13 small mammal monitoring quadrats which were placed in Kőszegi-forrás Forest Reserve based on their age and structure using biotic variables. Than we used number of captures to show how dominant small mammal species differed between groups.

Keywords: habitat, old-growth forests, PCA, cluster analysis

Introduction

Old-growth forests of the different climatic zones include a remarkable variety of habitats for plants, animals, fungi and micro-organisms, representing a diversity hotspot. Diverse macro- and micro-habitats harbours many communities, not only representing higher taxonomic diversity due to their complex food web system, but also have greater functional or ecological diversity. However, this biodiversity is threatened by natural and human disturbance such as direct and indirect human activities, including deforestation, fragmentation and the degradation of forest habitats which may lead to species replacement, for example increasing the distribution of non-native species (KLENNER et al. 2009). Thus it is important to investigate how habitat diversity affects ecosystem functions such as productivity and ecosystem stability via taxonomic diversity (ANGELSTAM et al. 1997, BENGTSSON et al. 2000).

Small mammals, due to their high reproduction rate, rapid demographic changes, and short turnover are often used as a sensitive indicator species group to demonstrate and evaluate these negative effects in different managed and unmanaged forest habitats (e.g. CAREY & JOHNSON 1995, PEARCE & VENIER 2005, CONVERSE et al. 2006). They are important elements of food webs; among other they are dispersers of seeds and micor-rhizae and also important seed predators and seed dispersers (VANDER WALL et al. 2001, FRANK et al. 2009). Small mammal communities are good indicators of habitat quality

changes due to different forest management activities, e.g. selection felling or clear-cutting.

The classical and current studies of resource partitioning (e.g. BROWN & LIEBERMAN 1973, SCHOENER 1974, ROSENZWEIG et al. 1979, MESERVE 1981) and competitive coexistence (e.g. PIANKA 1976, ROSENZWEIG 1979, ABRAMSKY et al. 1979, KOTLER & BROWN 1988, KELT et al. 1994, MARSH & HARRIS 2000) have shown that the habitat selection and the resource or habitat partition play important role in the avoidance of competition or reduction of competitive situation which allows the stable coexistence of species in space and time.

Most of the classical habitat selection studies were performed in deserts or semi-deserts (e.g. AMBRAMSKY et al. 1979). Segregation studies between coexistent small mammals in well-structured forests (e.g. CARREY & HARRINGTON 2001, BELLOWS et al. 2001) had been made possible at the end of 1970's, based on the seminal methodological papers of DUESER & SHUGART (1978; 1979).

As the abundance of small mammals is affected by both macro-and micro-habitat structure, the scale of habitat selection is an important issue in more studies (e.g. MORRIS 1987, JORGENSEN 2004). Habitat-scale studies provide direct information on the resource utilization of each species, so they are appropriate for community structure analysis (POINDEXTER et al. 2012). Therefore, the above studies have shown that small mammals are an appropriate indicator group to investigate and understand the mechanisms of habitat selection and segregation in different forest types (structure, age, management).

In this study segregation of habitat types and habitat segregation of the three most common small mammal species of Kőszegi-forrás Forest Reserve in 2013 – *Apodemus flavicollis*, *Apodemus sylvaticus* and *Myodes glareolus* - was tested, based on environmental variables selected from literature, and using method new in Hungary, although proven to be appropriate in more countries.

Material and methods

Study area and forest characteristics

Our study was executed in the core area and buffer zone of the Kőszegi-forrás Forest Reserve. It is situated in southern Hungary, in Mecsek Middle Mountains (46°09'28.88" N, 18°17'09.90" E), in Danube-Drava National Park, managed by Mecsek Forestry Ltd. Core area of the forest reserve is 33.0 ha, buffer zone is 116.2 ha (BARTHA & ESZTÓ 2002). It is among the best-studied hungarian forest reserves (HORVÁTH et al. 2012). Mean annual temperature is 9°C, annual precipitation is 750-800 mm (AMBRÓZY & KOZMA 1990). The bedrock is Miocene conglomerate covered by fluvisols. Since the majority of the core area lies on a north-facing slope, the most typical plant community here is the beech forest *Helleboro odori-Fagetum*, despite the low altitude. The canopy consists of *Fagus sylvatica*, although *Carpinus betulus* and *Quercus cerris* individuals are also present. The shrub layer is lacking or sparse. The cover of the herb layer varies considerably, and it has a lot of geophytes (e.g. *Allium ursinum*, *Galanthus nivalis*, *Isopyrum thalictroides*) and several plants with a sub-Mediterranean character (e.g. *Calamintha sylvatica*, *Lathyrus venetus*, *Ruscus hypoglossum*). The stand within the forest reserve is ca. 170 years old, and no forestry activities have been carried out since 1973. On the more xeric sites of the forest reserve, the turkey oak-sessile oak forest *Potentillo micranthae-Quercetum dalechampii* can be found. The canopy is formed by *Quercus petraea* agg. and *Qu. cerris*, but other species such as *Acer campestre* and

Fraxinus ornus are also typical in the lower canopy (<http://www.erdorezervatum.hu/node/154>). Both the shrub (e.g. *Cornus mas*, *Crataegus monogyna*, young individuals of *Fraxinus ornus* and *Acer campestre*) and the herb layers (e.g. *Helleborus odoratus*, *Melica uniflora*) are well developed. A detailed survey of the canopy, shrub and herb layers of the whole core area had been executed between 2011-2013., according to the Forest Reserve Research Protocol (HORVÁTH et al. 2012).

Five sampling sites in the core area are situated in a stand above 130 years, belonging to the most valuable old-growth stands of Mecsek Mountains. Abandoned since the 1970's, natural forest dynamic processes take place here (gap building, accumulation of a considerable amount of deadwood of various ages and sizes, spontaneous regeneration).

Eight sampling sites are placed in the buffer zone, which is characterized by horn-beam-oak (*Asperulo taurinae-Carpinetum*) and turkey oak-sessile oak forests (*Potentillo micranthae-Quercetum dalechampii*); and secondary stands consisting of turkey and sessile oak, with a smaller amount of non-native species (e.g. *Pinus sylvestris*, *Robinia pseudacacia*). Stands in the buffer zone are of different ages (1-80 years) and of complex structure. According to the prescriptions of the Forest Act of 2009, continuous cover management (group felling) is realized in the buffer zone, complemented by planting of small oak sapling in the open parts. These management results in a mosaic of different stands, partly with dense shrub layer and with old tree groups, providing a rich habitat complex for small mammals.

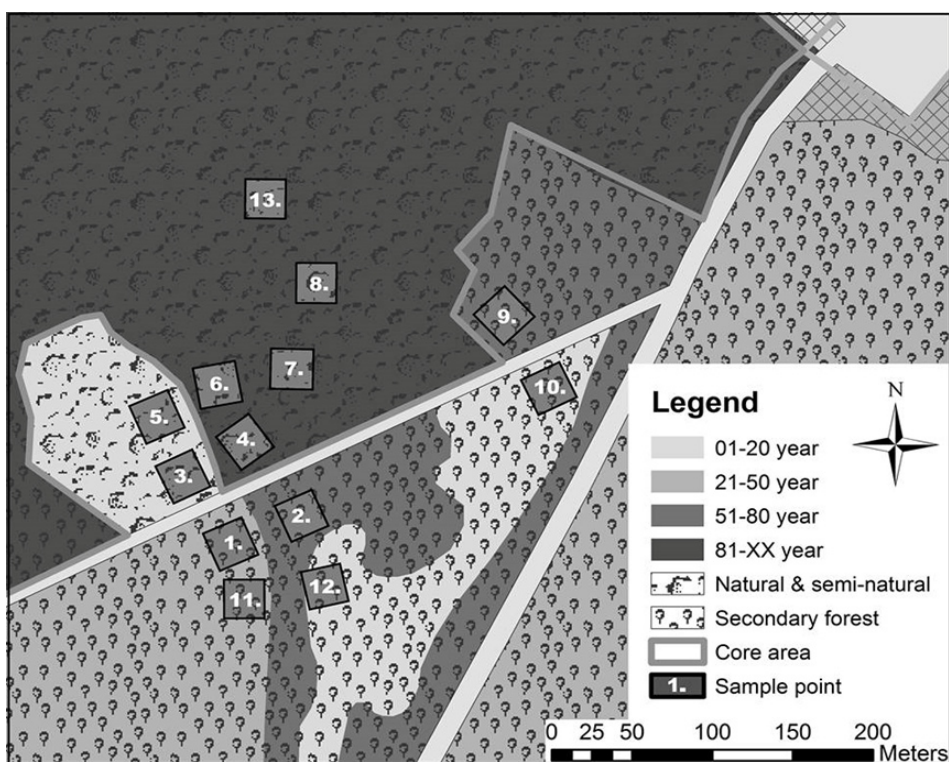


Fig. 1. Naturalness and age-group map of the Kőszegi-forrás Forest Reserve in the neighborhood of the sampling sites

Grid-based microhabitat mapping and environmental variables

Grid-based microhabitat mapping was executed by a purposefully developed unique method, published first in this paper. 13 small mammal sampling sites, 36 traps in each, were permanently marked in the forest reserve, and divided into 36 individual micro-quadrats of 5×5 m positioned with the traps in their centre. Environmental variables were estimated in a total of 468 micro-quadrats were mapped.

5 m		5 m					
5 m	1.	2.	3.	4.	5.	6.	
	11	21	31	41	51	61	
	7.	8.	9.	10.	11.	12.	
	12	22	32	42	52	62	
	13.	14.	15.	16.	17.	18.	
	13	23	33	43	53	63	
5 m	19.	20.	21.	22.	23.	24.	
	14	24	34	44	54	64	
	25.	26.	27.	28.	29.	30.	
	15	25	35	45	55	65	
	31.	32.	33.	34.	35.	36.	
	16	26	36	46	56	66	

Fig. 2. Location of botanical quadrats around of each small mammal trapping point

Environmental variables, relevant for small mammals and describing habitat complexity were selected, based on literature. Many studies show that height and cover of vegetation layers, especially of herb layer, even its species composition, are relevant for small mammals (e.g., SUCHOMEL et al. 2009, ROSSELL & ROSSELL 1999, HEROLDVÁ et al. 2008). The abundance and thickness of the dead wood is a key feature of natural state in the forest reserves (DUDLEY et al. 2006) which is important role for small mammals as hiding places and food resource (STEVENS 1997). Many of case studies investigated the relation between abundance and thickness of dead wood, cut logs, presence of wood-piles and spatial distribution and microhabitat use of appear small mammals species (e.g. CHAMBERS 2002, MIKLÓS & ZIAK 2002, LIN & SHIRAISHI 1992).

Survey of environmental variables

13 sites of small mammal trapping quadrats (900 m² each), situated in different forest types, were mapped in the Kőszegi-forrás Forest Reserve (Fig. 1.). Environmental variables were documented in a grid covering each of the quadrats in summer 2013.

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Table 1. Description of environmental variables

Variables	Code	Description	Units/Categories
<i>Canopy layer and tree stand structure</i>			
Cover of canopy layer	CanC	Cover of trees above 500 cm	%
Number of trees	TreeN		numbers
Diameter in 130 cm height (DH) for each tree in 4 categories	TreeD130		Categories: D1 >40 cm D2 20-40 cm D3 10-20 cm D4 <10 cm
Average diameter of trees	AvD	Calculated as a mean of TreeN and TreeD130	cm
<i>Shrub layer</i>			
Cover of shrub layer	SC	Cover of shrubs between 50-500 cm	%
Average height of shrub layer	AvHS	Calculated as a height and cover of dominant (cover is above 5 %) shrub species	cm
<i>Herb layer</i>			
Cover of herb layer	HC	Cover of herbs, and also woody plants < 50 cm	%
Average height of herb layer	AvHH	Calculated as a height and cover of dominant (cover is above 5 %) herb species	cm
<i>Soil surface cover</i>			
Cover of litter	Lit		%
Cover of rocks	Rock		%
Cover of nude soil	Soil		%
<i>Deadwood</i>			
Cover of lying deadwood (LDW)	CLDW		%
Length of LDW		Length of LDW in three diameter categories:	m for each categories
	LDWD1	D1: 5-10 cm	
	LDWD2	D2: 10-40 cm	
	LDWD3	D3: >40 cm	
Number of branch heaps	BH	Shelter for small mammals	number
Number of cut trunks	CT	Indicator of forestry management	number

in the forest reserves (DUDLEY et al. 2006) which is important role for small mammals as hiding places and food resource (STEVENS 1997). Many of case studies investigated the relation between abundance and thickness of dead wood, cut logs, presence of wood-piles and spatial distribution and microhabitat use of appear small mammals species (e.g. CHAMBERS 2002, MIKLÓS & ZIAK 2002, LIN & SHIRAIISHI 1992). The measured abiotic and biotic variables are summarized in Table 1.

Trapping method

13 sites of small mammal trapping quadrats (900 m² each), situated in different forest types were used. The trapping method applied in each of the plots was capture-mark-recapture (CMR), with 6×6 live-trapping plastic box traps (75×95×180 mm), placed in 5 m distance from each other. Small mammal monitoring was done eight trapping periods in 2013: from March to October. In every month, a standard five-night capture occasions was carried out. Just like the traps themselves, the trapping technique was also alike in all cases: bacon and cereals mixed with aniseed extract and vegetable oil were used as bait. The traps were checked one times a day in the morning. Captured animals were marked individually and we also recorded the sex (by females: gravidity or lactation too), age and body mass.

Statistical methods

Sites were grouped by cluster analysis (Ward's method) using normalized values of the 16 environmental variables. Segregating variables were identified by principal component analysis (PCA). Statistics were calculated using the PAST free software (HAMMER et al. 2001). Differences between the abundances of dominant small mammal species (*Apodemus flavicollis* (Afl), *Apodemus sylvaticus* (Asy) and *Myodes glareolus* (Mgl) in the whole study area and in the different site groups determined by the cluster analysis were analysed by Pearson's χ^2 test.

In case of each investigated rodent species the distribution of the yearly number of captures was tested with nonparametric Kruskal-Wallis median test among the different forest types. When significant differences were detected in the Kruskal-Wallis test, we employed the Mann-Whitney U tests with the Bonferroni correction for post hoc multiple comparisons (ZAR 2010).

Results

According to the cluster analysis based on the 16 environmental variables, the 13 sites were segregated into three groups: young stands (1) (sites 1, 11); disturbed stands (2) (sites 2, 3, 5, 10, 12); old stands (3) (sites 4, 6, 7, 8, 9, 13) in the core area and in its close neighborhood. The oldest beech stands were segregated inside this group (Fig. 3). Disturbed stands had been affected either by clear-cutting 15 years ago, or by artificial gap regeneration complemented by planting seedlings (Fig. 3.). Regarding relevant variables, differentiating between groups, young stands (Group 1: sites 1 and 11) were associated positively to variables characteristic for young managed stands (age: 20-50 years) after a recent thinning: lots of cut stumps and thin deadwood (D<10 cm) and relatively low canopy cover, and negatively to high canopy cover and quantity of medi-

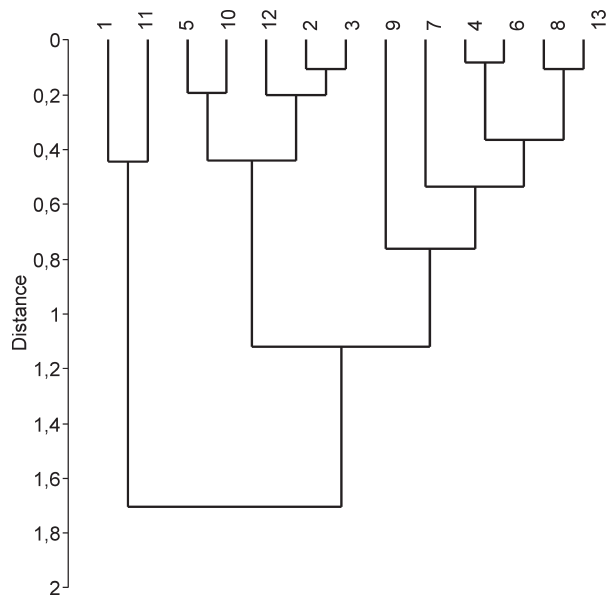


Fig. 3. Separation of the three habitat groups according to the results of cluster analysis

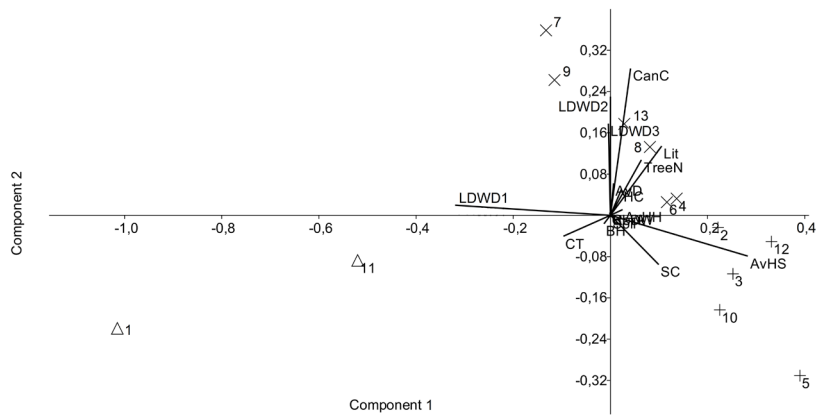


Fig. 4. Segregation of the three group were supported also by PCA (Fig. 3), where 77,3% of total variance was explained by the first two axes (61,8% and 15,5% accordingly)

um and thick deadwood (D 10-40 cm, D>40cm). Disturbed sites (Group 2: sites 2, 3, 5, 10, 12) were associated positively to cover and height of shrub layer; negatively to canopy cover and quantity of all types of deadwood. They display the characteristic physiognomy of stands managed with gaps: well-developed shrubs in the gaps and deadwood removal (Fig. 4.).

Old stands (Group 3: sites 4, 6, 7, 8, 9, 13) associated positively to canopy cover, to the quantity of medium and thick deadwood and to litter cover; negatively to cover and height of shrub layer, thin deadwood ($D < 10$ cm) and number of cut stumps. According to these results, old abandoned stands are characterized by a canopy above 80% cover (not old enough yet for gap opening), large deadwood and thick litter layer due to profuse foliage production; lack of management is indicated by the lack of cut stumps; they may be regarded as most natural stands (Fig. 4.).

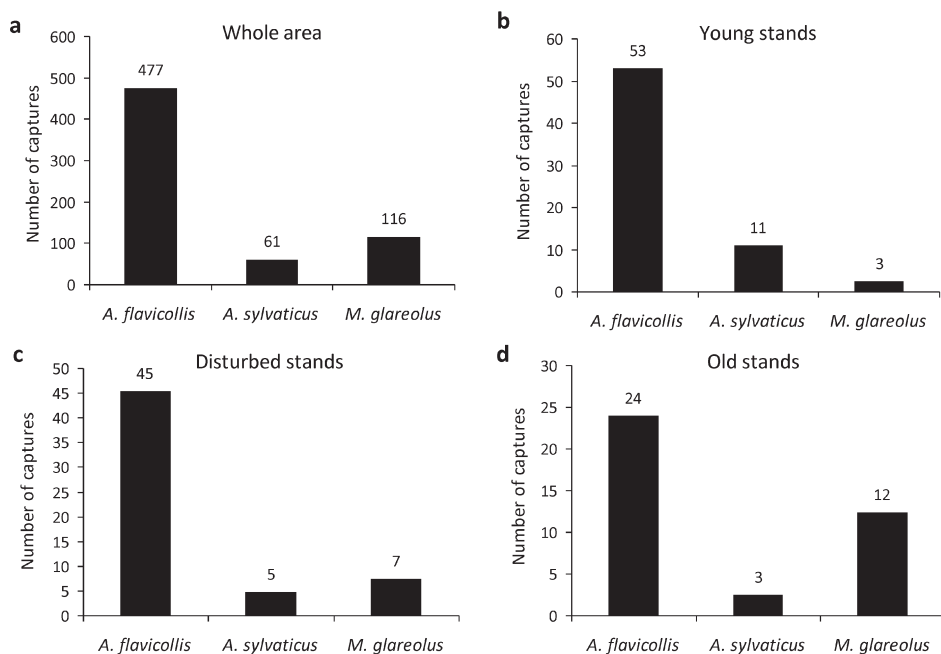


Fig. 5. Capture number of dominant species within the whole area (a) and the habitat groups (b, c, d)

Abundance values of the three dominant small mammal species were compared between these three groups. *Apodemus flavicollis* was highly dominant on the whole area and in each of the types too. Other two species occurred in smaller numbers. *Myodes glareolus* dominated over *Apodemus sylvaticus* in old and disturbed stands, but their relation was the opposite in young stands (Fig. 5.). Differences in abundances of species were significant in the whole area and also in each of the types, compared to the theoretical even distribution (whole area: $\chi^2 = 468.5$, $P < 0.001$, young stands: $\chi^2 = 131.9$, $P < 0.001$; disturbed stands: $\chi^2 = 269.02$, $P < 0.001$; old stands: $\chi^2 = 107.4$, $P < 0.001$) (Fig. 5.).

Differences were found also regarding habitat use of the species. *Apodemus flavicollis*, occurring in large numbers in each of the three types, displayed significant differences between the types ($H = 18.31$, $P < 0.001$). Young and disturbed stands were preferred, as shown by significant differences of capture numbers (post hoc tests $P < 0.001$ for young and old, and disturbed and old stands).

Abundance distribution of *Apodemus sylvaticus* was similar to that of *Apodemus flavicollis*. It was captured in largest numbers in the young stands, in smallest number in

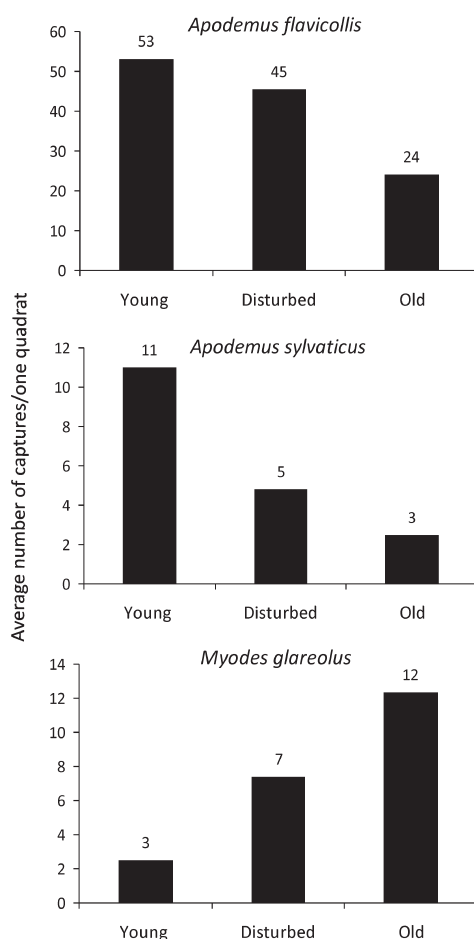


Fig. 6. Average number of captures for one quadrat of species in different macrohabitats (Y: Young stands, D: Disturbed stands, O: Old stands)

the old ones (post hoc test: $P < 0.001$); significant difference was found between disturbed and young stands also (post hoc test: $P < 0.05$).

Myodes glareolus also has shown significantly different abundance values between habitat types ($H = 5.59$, $P < 0.01$), but this species displayed a distribution pattern just opposite to *Apodemus* species. It was extremely abundant in the old stands and occurred in very low numbers in the young stands (post hoc test: $P < 0.001$). Capture numbers differed significantly also between other habitat combinations.

These results show that different species segregate by habitat types. Both *Apodemus* species prefer young and disturbed stands, till *Myodes glareolus* displayed opposite distribution, avoiding former ones (Fig. 6.).

Discussion

Habitat segregation of three dominant small mammal species in forest stands differing by age and structure were analyzed using faunistic and environmental data of 13 small mammal trapping quadrats in the Kőszegi-forrás Forest Reserve. Based on 16 environmental variables three markedly different stand types were identified, as young (sites 1, 11), disturbed (sites 2, 3, 5, 10, 12) and old stands (4, 6, 7, 8, 9, 13), representing also different levels of naturalness due to different forestry management (thinning, gap management, abandonment).

Our results supported that proper identifying of site types is of key importance in studies on macrohabitat association of small mammals. Although visual habitat grouping is appropriate in case of habitats of apparently different structure or in topographically far from each other, as e.g. in the habitat differentiation study of JÜCH (2000) on four structurally different habitats (forest, shrubland, burned shrubland and grassland); more other studies also demonstrate the usefulness of this type of grouping (e.g. STEVENS et al. 2009, PREVEDELLO et al. 2010). However, in case of habitats of complex structure, neighboring or spatially close to each other, as it was in our case, checking the visual differentiation by statistical methods, using field-based data may be advisable. Differentiation of habitats in forests of complex structure may be tested by different statistical methods (e.g. ORROCK & PAGELS 2003, MORRIS 1984); however, ordination also was used by HARRINGTON (2006) and MANSON et al. (1999) like our study.

Our results suggested that small mammal species occur in different numbers in the types identified by multivariate methods, according to their macrohabitat preferences. Younger, more fragmented, managed stands were preferred by *Apodemus flavicollis*. Similar results are reported e.g. by SUCHOMEL et al. (2009) and TATTERSALL et al. (2001). According to our data, *Apodemus sylvaticus* also preferred stands of younger ages. Literature data demonstrated that this species is less selective, using a wider spectra available habitats (GURNELL 1985, MARSH & HARRIS 2000, SUCHOMEL et al 2012). Contrasting to the two *Apodemus* species, *Myodes glareolus* occurs in the old-growth stands of the core area in the highest numbers, so it may regarded as an indicator of high naturalness. Studying the coexistence of *Apodemus flavicollis* and *Myodes glareolus* MIKLOS & ZIAK (2002) found that *Apodemus flavicollis* occupies microhabitats of younger age with more dense undergrowth, shrubs and deadwood, when occurring together with *Myodes glareolus*.

Our results proved that small mammal species segregate according to macrohabitat types. One more question is, whether refining the spatial scale of the study provides more comprehensive data on association of certain small mammal species to certain environmental variables; and whether micro-scale variables may yield a more appropriate grouping of the study sites. In the future, the analysis of environmental data on the „trap scale” (5×5m) is planned. Studying the microhabitat association of small mammal species in these same fixed quadrats, the comparison of habitat association both on micro- and macro-scale will also be possible.

The naturalness of forest management technologies influences the creation and subsistence of macro- and microhabitats in forests in a large extent (ORROCK et al. 2000). Retaining deadwood or shrubs may increase naturalness, till clear-cutting of large areas or the removal of dried-out trees causes degradation. Accurate revealing of habitat association of small mammals on micro and macro scale may greatly support the long-term conservation of protected and/or endangered small mammal populations (e.g. *Sorex araneus*, *Microtus agrestis*), and the development of proper near-natural forest management methods.

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References

- AMBRÓZY P. & KOZMA F. 1990: A Közép-Tisza-vidék éghajlata. - In: MAROSI S. és SOMOGYI S. (szerk.): Magyarország kistájainak katasztere I. MTA FKI, Budapest, pp. 175-192.
- ANGELSTAM P., ANUFRIEV V., BALCIAUSKAS L., BLAGOVIDOV A., BORGEÅRD S.-O., HODGE S., MAJEWSKI P., PONOMARENKO S., SHVARTS E., TISHKOV A., TOMIALOJC L. & WESOŁOWSKI, T. 1997: Biodiversity and sustainable forestry in European forests how west and east can learn from each other. - *Wildlife Society Bulletin* 25: 38-48.
- ABRAMSKY Z., DYER M. I. & HARRISON P. D. 1979: Competition among small mammals in experimentally perturbed areas of the short grass prairie. - *Ecology* 60: 530-536.
- BARTHA D. & ESZTÓ P. 2002: Az erdőrezervátumok bemutatása az Országos Erdőállomány-Adattár alapján. - In: HORVÁTH F. & BORHIDI A. (szerk.): A hazai erdőrezervátum-kutatás célja, stratégiája és módszerei, TermészetBÚVÁR Alapítvány Kiadó, Budapest, pp. 60-82.
- BELLOWS A. S., PAGELS J. F. & MITCHELL J. C. 2001: Macrohabitat and microhabitat affinities of small mammal in fragmented landscape on the upper coastal plain of Virginia. - *American Midland Naturalist* 146: 345-360.
- BENGTSOON J., NILSSON S. G., FRANC A. & MENOZZI, P. 2000: Biodiversity, disturbances, ecosystem function and management of European forests. - *Forest Ecology and Management* 132: 39-50.
- BROWN J. H. & LIEBERMAN G. A. 1973: Resource utilization and coexistence of seed eating desert rodents in sand dune habitats. - *Ecology* 54: 788-797.
- CAREY A. B. & HARRINGTON C. A. 2001: Small mammals in young forests: implications for management for sustainability. - *Forest Ecology and Management* 153: 147-160.
- CAREY A. B. & JOHNSON M. L. 1995: Small mammals in managed, naturally young, and old-growth forests. - *Ecological Applications* 5: 336-352.
- CHAMBERS C. L. 2002: Forest Management and the Dead Wood Resource in Ponderosa Pine Forests: Effects on Small Mammals. - USDA Forest Service General Technical Report PSW-GTR-181.
- CONVERSE S., WHITE G., FARRIS K. & ZACK S. 2006: Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. - *Ecological Applications* 16: 1717-1729.
- DUDLEY N., VALLAURI E. & VALLAURI D. 2006: Holtfa - az élő erdőkért. Az öreg fák és a holtfa természetvédelmi és erdészeti szerepe. (Deadwood-Living forests. WWF International, Gland). - WWF Magyarország, Budapest, 19 pp.
- DUESER R. D. & SHUGART H. H. 1978: Microhabitats in a forest-floor small mammal fauna. - *Ecology* 59(1): 89-98.
- DUESER R. D. & SHUGART H. H. 1979: Niche pattern in a forest-floor small-mammal fauna. - *Ecology* 60: 108-118.
- FRANK J. L., ANGLIN S., CARRINGTON E. M., TAYLOR D. S., VIRATOS B. & SOUTHWORTH D. 2009: Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. - *Botany* 87: 821-829.
- GURNELL J. 1985: Woodland rodent communities. - *Symposia of the Zoological Society of London* 55: 377-411.
- HAMMER Ø., HARPER D. A. T. & RYAN P. D. 2001: PAST: Paleontological Statistics Software Package for Education and Data Analysis. - *Palaeontologia Electronica* 4(1): p. 9.
- HARRINGTON E. 2006: Small Mammals, Habitat, and Forest Restoration at Seney National Wildlife Refuge. - Thesis book, University of Michigan. 29 pp.
- HEROLDOVÁ M., SUCHOMEL J., PURCHART L. & HOMOLKA M. 2008: Impact intensity of rodents on the forest regeneration in artificial plantations in the Smrk – Kněhyně area. - *Beskydy* 1(1): 33-36.
- HORVÁTH F., BIDLÓ A., HEIL B., KIRÁLY G., KOVÁCS G., MÁNYOKI G., MÁZSA K., TANÁCS E., VÉPERDI G., & BÓLÓNI J. 2012: Abandonment status and long-term monitoring of strict forest reserves in the Pannonian Biogeographical Region. - *Plant Biosystems* 146(1):189-200.
- JORGENSEN E. E. 2004: Small mammal use of microhabitat reviewed. - *Journal of Mammalogy* 85: 531-539.

- JÜCH P. 2000: Habitat Preferences of small Mammals on Mount Elgon, Uganda. - *Bulletin de la Société des Naturalistes Luxembourgeois* 100: 83-96.
- KELT D. A., MESERVE P. & LANG B. K. 1994: Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. - *Journal of Mammalogy* 75: 890-904.
- KLENNER W., ARSENAULT A., BROCKERHOFF E. G. & VYSE A. 2009: Biodiversity in forest ecosystems and landscapes: A conference to discuss future directions in biodiversity management for sustainable forestry. - *Forest Ecology and Management* 8S: S1-S4.
- KOTLER B. P. & BROWN J. S. 1988: Environmental heterogeneity and the coexistence of desert rodents. - *Annual Review of Ecology, Evolution, and Systematics* 19: 281-307.
- LIN L.-K. & SHIRAISHI S. 1992: Home range and microhabitat utilization in the formosan wood mouse, *Apodemus semotus*. - *Journal of the Faculty of Agriculture Kyushu University* 37(1): 13-27.
- MANSON R. H., OSTFELD R. S. & CANHAM C. D. 1999: Responses of a small mammal community to heterogeneity along forest-old-field edges. - *Landscape Ecology* 14: 355-367.
- MARSH A. & HARRIS S. 2000: Living with yellow-necked mice. - *British Wildlife* 11: 168-174.
- MESERVE P. L. 1981: Thropic relationship among small mammals in Chilean semiarid thorn shrub community. - *Journal of Mammalogy* 62: 304-314.
- MIKLÓS P. & ZIAK D. 2002: Microhabitat selection by three small mammal species in oak-elm forest. - *Folia Zoologica* 51(4): 275-288.
- MORRIS D. W. 1984: Patterns and scale of habitat use in two temperate-zone, small mammal faunas. - *Canadian Journal of Zoology* 62: 1540-1547.
- MORRIS D. W. 1987: Ecological scale and habitat use. - *Ecology* 68: 362-369.
- ORROCK J. L., PAGELS J. F., MCSHEA W. J., & HARPER E. K. 2000: Predicting presence and abundance of a small mammal species: the effect of scale and resolution. - *Ecological Applications* 10(5): 1356-1366.
- ORROCK J. L. & PAGELS J. F. 2003: Tree communities, microhabitat characteristics, and small mammals associated with the endangered rock vole, *Microtus chrotorrhinus*, in Virginia. - *Southeastern Naturalist* 2: 547-558.
- PEARCE J. L., VENIER L. A., ECCLES G., PEDLAR J. H. & MCKENNEY D. W. 2005: Habitat Islands, Forest Edge and Spring-active Invertebrate Assemblages. - *Biodiversity and Conservation* 14: 2949-2969.
- PIANKA E. R. 1976: Competition and niche theory. In: May, R. M. (eds) *Theoretical Ecology*. Blackwell Scientific publications, Oxford, pp. 114-141.
- POINDEXTER C. J., SCHNELL G. D., SANCHEZ-HERNANDEZ C., ROMERO-ALMARAZ M. L., KENNEDY M. L., BEST T. L., WOOTEN M. C. & OWEN R. D. 2012: Variation in habitat use of coexisting rodent species in a tropical dry deciduous forest. - *Mammalian Biology* 77: 249-257.
- PREVEDELLO J. A., RODRIGUES R. G., & MONTEIRO-FILHO E. L. A. 2010: Habitat selection by two species of small mammals in the Atlantic Forest, Brazil: Comparing results from live trapping and spool-and-line tracking. - *Mammalian Biology* 75: 106-114.
- ROSSELL C. R. JR., & ROSSELL I. M. 1999: Microhabitat selection by small mammals in a southern Appalachian fen in the USA. - *Wetlands Ecology and Management* 7: 219-224.
- ROSENZWEIG M. L. 1979: Optimal habitat selection in two-species competitive systems. - *Fortschritte der Zoologie* 25: 283-93.
- SCHOENER T. W. 1974: Resource partitioning in ecological communities. - *Science* 185: 27-39.
- STEVENS R. D., & TELLO J. S. 2009: Micro- and macrohabitat associations in Mojave desert rodent communities. - *Journal of Mammalogy* 90(2): 388-403.
- STEVENS V. 1997: The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. - Research Branch, British Columbia Ministry of Forests, Victoria, B.C. Work. Pap. 30/1997
- SUCHOMEL J., KROJEROVÁ-PROKEŠOVÁ J., HEROLDOVÁ M., PURCHART L., BARANČEKOVÁ M. & HOMOLKA M. 2009: Habitat preferences of small terrestrial mammals in the mountain forest clearings. - *Beskydy* 2(2): 195-200.
- SUCHOMEL J., PURCHART L., CEPELKA L. 2012: Structure and diversity of small-mammal communities of lowland forests in the rural central European landscape. - *European Journal of Forest Research* 131: 1933-1941.
- TATTERSALL F. H., MACDONALD D. W., HART B. J., MANLEY W. J. & FEBER, R. E. 2001: Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. - *Journal of Zoology* 255: 487-494.
- VANDER DER WALL S. B., THAYER T. C., HODGE J. S., BECK M. J. & ROTH J. K. 2001: Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). - *Western North American Naturalist* 61: 109-113.
- ZAR J.H. 2010: *Biostatistical Analysis*. 5th Edition. - Pearson Prentice-Hall, Upper Saddle River, NJ. 944 pp.

internet:

Kőszegi-forrási Erdőrezervátum alapadatai: <http://www.erdorezervatum.hu/node/154>, viewed: 25.03.2015.