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QUANTITATIVE BIOGEOGRAPHIC CHARACTERIZATION OF HUNGARY BASED ON THE DISTRIBUTION DATA OF LAND SNAILS (MOLLUSCA,GASTROPODA): A CASE OF NESTEDNESS OF SPECIES RANGES WITH EXTENSIVE OVERLAP OF BIOTIC ELEMENTS

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Biogeographic classifications of Hungary in past decades were based on qualitative data, and since than, data have increased significantly and more efficient methods become available. I used UTM based distribution data of 121 land snail species to quantitatively assess biogeographic patterns in Hungary. Hierarchical cluster analysis identified two main clusters of areas: highlands and lowlands. This dichotomy can be attributed to mainly climatic and altitudinal differences. One fourth of the species were present in the whole country (general species), one fourth was characteristic to highlands, and half of the species (including all the endemics) were localized in smaller regions. The distribution of localized species revealed historical effects in regional faunas: Carpathian influences in the Northern Mountains, Alpine influences in the Western Marginal Area, and southern-Illyric influences in Southern Transdanubia. Biotic element analysis revealed that clustering of species ranges did not differed significantly from the null model, but species' areas were significantly more nested that under the null model. Based on the high degree of nedtedness in species' areas and the composition of various biogeographical influences, representativeness can be achieved with relative efficiency in Hungary.

Key words: biodiversity, biotic elements, endemic species, nestedness, species groups

INTRODUCTION

Biogeography aims to describe and interpret the patterns of biodiversity from a historical point of view and on a large spatial scale (Whittaker *et al.* 2005). Developing regional classifications of landmasses on Earth's surface was a traditional activity of early biogeographers since the time of Wallace (1876), and it has also remained a fundamental step in modern biogeographic analyses (Cox 2001). Originally its emphasis was on continental level that shifted to smaller, i.e. regional, spatial level by time (Hengeveld 1999, Heikinheimo *et al.* 2007).

Soós (1934, 1943) was among the firsts to characterise the fauna of the Carpathian Basin (and Hungary as part of it) and his work became a milestone in Hungarian biogeographic literature. He based his qualitative and descriptive assessment on the distribution of molluscs. In the next decades, distribution data of molluscs have increased, but unfortunately the Mollusc Collection of the Hungarian Natural History Museum was almost completely destroyed in the fights of 1956. After these, data collection has restarted and resulted in the works of PINTÉR *et al.* (1979) and PINTÉR and SZIGETHY (1979, 1980). These publications listed detailed distribution data of the species in 10 × 10 km UTM grid system. Based on these data, BÁBA (1981, 1982) has analysed the similarity of regional faunas within Hungary and tried to explain the results within an area-analytical framework (DE LATTIN 1967, VARGA 1977). He defined these regions a priori based on the results of plant geography, thus his work was semi-quantitative, because he did not use mollusc distribution data directly to delineate and classify regions, but adopted other botanical and zoological works in this field (for references see BÁBA 1981, 1982).

Since that time, more sophisticated methods have become available and the use of personal computers has been a standard tool in scientific analysis. Besides these, data have increased considerably (FEHÉR & GUBÁNYI 2001, PINTÉR & SUARA 2004). Based on the data, conservation priorities have been set up for species (FEHÉR *et al.* 2006, SÓLYMOS 2004, 2007) and areas (SÓLYMOS & FEHÉR 2005) as well. Biogeographic studies may help in the long term conservation of the mechanisms and processes that maintain diversity (WHITTAKER *et al.* 2005).

Here I use quantitative (UTM based) distribution data of Hungarian land snails to hierarchically classify spatial units and identify spatially coherent regions. Further, I identify species groups (indirectly by species that are characteristic to these hierarchical units and directly by biotic elements) and I assess range size relations of these species. I also discuss these results in a general biogeographic context and outline conservation implications.

MATERIALS AND METHODS

I used the distribution data of land snails based on PINTÉR *et al.* (1979), PINTÉR and SZIGETHY (1979, 1980) and FEHÉR and GUBÁNYI (2001). Invasive and introduced species were excluded because their conservation implication is doubtful (PATTEN & ERICKSON 2001). Slugs were also excluded due to collecting and identification problems (WIKTOR & SZIGETHY 1983, CAMERON & POKRYSZKO 2005). In total, 121 species were involved in the analysis, for nomenclature I followed PINTÉR (1984).

Out of the 1052 10 km × 10 km UTM cells covering Hungary, 704 (66.9%) contained distribution data. For analysis, I merged these 10 × 10 km grid cells into 50 × 50 km to account for uneven sampling coverage and intensity (SÓLYMOS 2005). In some cases, it was necessary to unite more 50 × 50 km cells, too, because of the shape of the country border and the arrangement of empty cells. A main criterion in merging was, that the resulting units should contain at least five 10 × 10 km UTM cells containing distribution data. As a result, I used pooled data of 49 approximately 50 × 50 km grid cells (Fig. 1). Mean area of the explored area in the analytical units (excluding empty cells) was 1415.4 ± 581.1 SD km^2.

Species were grouped according to range size, based on the range size scores listed by SÓLYMOS (2004). The geographic range size scores were as follows: 1, beyond Europe (e.g., Eurosiberian, western Palearctic, Palearctic, Holarctic species). 2, large within Europe (in more biogeographic regions, e.g., central European, boreo-montane, Alpine-Carpathian species). 3, restricted to one well-defined biogeographic region (e.g., Carpathian endemic species). 4, narrow within one biogeographic region (e.g., endemic to northern Carpathians) (Appendix). These scores has direct biogeographic interpretation, although they do not represent faunal types or biogeographic elements (HAUSDORF 2002). HAUSDORF and HENNIG (2004) grouped the northwest European land snails into eight groups based on recent distribution (after filtering noise elements): 1, widespread species (Holarctic, Palaearctic, European), 2, western Alpine (polycentric) species, 3, Alpine-Carpathian, 4, Pyrenean, 5, western European, 6, south Alpine, 7, east Alpine, and 8, Carpathian species. The first faunal group corresponds to range size score 1, faunal groups 1–2 correspond to range size score 2, faunal groups 4–8 correspond to range size score 3–4. Although the classification of HAUSDORF and HENNIG (2004) apparently excludes south European (Balcanic) and Pontic species, that also occur in Hungary.

I did not use faunal types in this study, because faunal type categorization of Hungarian land snails worked out by BÁBA (1982) is not fully accepted in Hungary and can be criticized on several grounds: the research is not reproducable because it lacks a full reference list, it is statistically questionable in some points, and applies centers of endemism based on other taxa, i.e. Lepidoptera and higher plants, instead of investigating directly the available mollusc distribution data. The first step in this area analytical method was also the identification of areas of extensive overlap of narrow range species (BÁBA 1981, 1982, HAUSDORF 2002, VARGA 1971), because these species can be associated with certain centers of endemism. My aim was not to provide a revision of faunal type categorization of the species, but to categorize areas based on faunal similarities, and to explore zoogeographical patterns.

I used the Sørensen index of similarity and Ward-Orlóci fusion method in hierarchical cluster analysis to study the relationship among the 49 spatial units. For clustering I used the SYNTAX software (PODANI 1993).

I identified characteristic species of the resulting cluster hierarchy indirectly by the IndVal method (DUFRÉNE & LEGENDRE 1997). I used relative frequency of occurrence of each species in the 49 spatial units. The IndVal method considers both the specificity and fidelity of the species, and the IndVal index is maximal, when a given species occurs in only a certain group of the classification hierarchy, and it occurs in all sites within that cluster group. These species are called symmetrical character species (IndVal < 55%) because their occurrence is specific and can be well predicted. A species is called asymmetrical character species when it is specific to certain partition of the classification but it occurs infrequently and thus can not be well predicted in that partition. IndVal index of a species is independent that of other species' values. Significance values were calculated based on 1000 random permutations by the software IndVal2. This program can handle only 25 partitions thus I used the lowest 25 internal nodes closest to terminal nodes of the classification tree instead of original terminal nodes.

I checked the data set for general trends in species clustering by using the distance ratio test based on the Kulczynski distances and 1000 simulated data sets (HAUSDORF & HENNIG 2004). The test statistic is the ratio between the 25% smallest and the 25% largest Kulczynski distances between the ranges of the examined taxa is used. The null model simulates the case in which all inhomogeneities (clustering) of the data can be attributed to the range size distribution, to varying numbers of taxa per geographic unit and to the spatial autocorrelation of the occurrences of a taxon

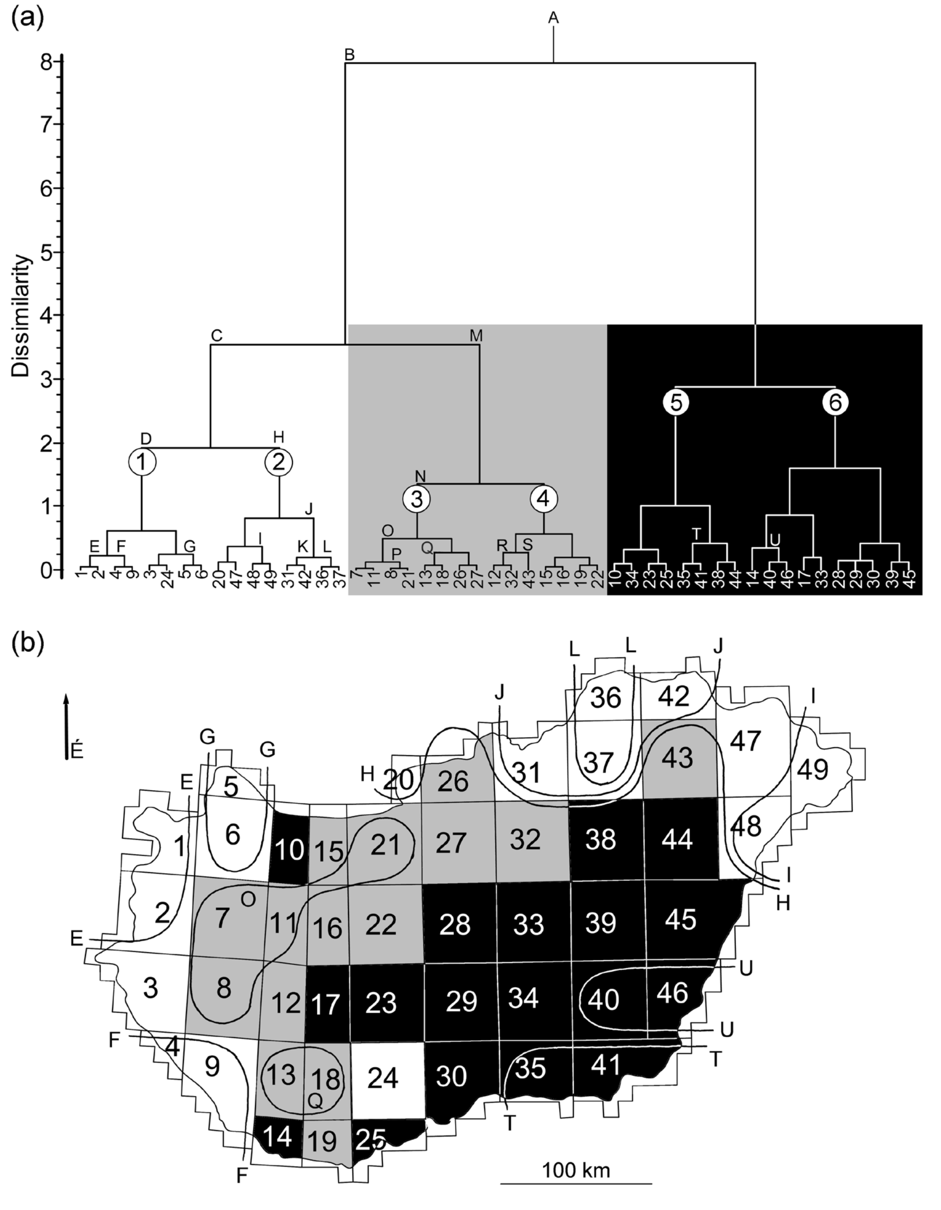

Fig. 1. Biogeographic classification of Hungary based on distribution data of land snails according to the (a) hierarchical clustering of the (b) spatial units (ca. 50 km × 50 km). For clustering, the Sørensen–index and Ward–Orlóci fusion method was used. Shades of grey indicate main partitions of the cluster hierarchy, circled numbers 1–6 indicate lower level partitions mentioned in the text, numbers 1–49 identify spatial units (a) in the cluster foot and (b) in the map. Capital letters correspond to IndVal species groups listed in the text and in Appendix, lines associated to letters refer to spatially coherent clusters with character species (a) encircled also in the map (b).

(HAUSDORF & HENNIG 2003*a*, 2003*b*). I also tested the nestedness of species ranges on this null modell. The test statistics was the number of strict inclusions (supersets) in the species-by-species nestedness matrix based on the regions-by-species matrix (HAUSDORF & HENNIG 2003*a*).

For the Hungarian range data I obtained the disjunction probability for original data was 0.0485. This low value of indicates that the occurrences of the examined land snail species are highly clumped. This underlines the necessity to consider spatial autocorrelation in the null model. For this test I used the PRABCLUS package (HENNIG 2006).

I identified biotic elements based on model based Gaussian clustering applied on the outcome of a metrical multidimensional scaling by using the package MCLUST (FRALEY & RAFTERY 2007). This method provides decisions about the number of meaningful clusters and the number of points, which cannot be assigned adequately to any cluster. Initial estimation of noise was done by the package NNCLEAN (BYERS & RAFTERY 1998). All mentioned packages are add-ons for the statistical software R (R Development Core Team 2007).

I grouped species according to the IndVal categorization. Species were cross tabulated according to IndVal species groups and range size groups and biotic elements. The associations between the three cross-tabulations were evaluated by the Chi-squared test (simulated p values with with 10000 replicates).

RESULTS

Hierarchical clustering revealed the separation of lowland and highland areas based on faunal similarity among the 49 spatial units (Fig. 1). Highlands further separated into mountain areas (Western Marginal Area forming cluster 1 in Fig. 1, and the Northern Mountains forming cluster 2 in Fig. 1) that are peripheral parts of high mountain systems (i.e. the Alps and the Carpathians respectively), and mountains and hills of Transdanubia that are relatively independent from high mountain systems (the Transdanubian Mountanis, the Mecsek Mountain and the Gödöllő Hills forming cluster 3 in Fig. 1, and other hills forming cluster 4 in Fig. 1). Separation within the lowland cluster did not revealed spatially coherent units at lower hierarchical levels.

Based on the IndVal analysis, 33 species were generally characteristic to the whole country (general species, labelled with A in Fig. 1 and the Appendix), 26 species were characteristic to highland areas (highland species, labelled with B in Fig. 1 and the Appendix). The remaining 62 species were localized character species in smaller geographical areas (localized species, labelled from C to U in Fig. 1 and the Appendix).

The Western Marginal Area and the Northern Mountains (clusters 1 and 2 in Fig. 1) had two joint species: *Perforatella bidentata* and *Ena montana* (labelled with C in Fig 1 and Appendix). *Semilimax semilimax*, *Perforatella umbrosa*, *Aegopis verticillus* and *Aegopinella ressmanni* were characteristic to the Western Marginal Area (labelled with D in Fig 1 and Appendix). *Pagodulina pagodula*, *Coch-*

lodina fimbriata, *Pseudofusulus varians* and *Macrogastra densestriata* were characteristic to the Soproni and Kőszegi Mountains (labelled with E in Fig 1 and Appendix). *Helicigona planospira* and *Pomatias elegans* were characteristic to the south-western Transdanubia (labelled with F in Fig 1 and Appendix). *Aegopinella nitens*, *Trichia striolata* and *Cochlicopa nitens* were characteristic to the Szigetköz (labelled with G in Fig 1 and Appendix).

Joint character species of the Northern Mountains and the Szatmár-Bereg Plain (which is part of the Great Plain in the upper Tisza region) were *Perforatella vicina*, *Ruthenica filograna*, *Bulgarica cana*, *Helix lutescens* and *Vertigo substriata* (although the latter species does not occur in the lowlands) (labelled with H in Fig 1 and Appendix). *Perforatella dibo*thrion and *Pomatias rivulare* were characteristic to the Szatmár-Bereg Plain and the Nyírség region (labelled with I in Fig 1 and Appendix). The Mátra, Bükk, Aggteleki and Zempléni Mountains had several joint character species: *Cochlodina orth*ostoma, *Oxychilus orientalis*, *Helicigona faustina*, *Hygromia transsylvanica*, *Cochlodina cerata*, *Isognomostoma isognomostoma*, *Oxychilus depressus*, *Trichia unidentata* and *Macrogastra latestriata* (labelled with J in Fig 1 and Appendix).

Trichia lubomirskii, *Balea stabilis* and *Discus ruderatus* were characteristic to the Mátra and the Zempléni Mountains (labelled with K in Fig 1 and Appendix). The species *Vestia gulo* occurred in the Zempléni Mountains, however, it was characteristic to the cluster S because border of neighbouring cells divided the Zempléni Mountains into two parts in clusters K and S. The species *Clausilia cruciata*, *Vestia turgida*, *Spelaeodiscus* triarius, *Phenacolimax annularis* and *Chondrina clienta* were characteristic to the Bükk Mountain and the Aggteleki Karst area (labelled with L in Fig 1 and Appendix).

Joint character species of the Transdanubian Mountains, the Mecsek and the Cserhát Mountains, and Gödöllői Hills were *Pupilla triplicata*, *Truncatellina claustralis*, *T. callicratis*, *Zebrina detrita*, *Orcula doliolum*, *Discus rotundatus* and *Orcula dolium* (labelled with M and N in Fig 1 and Appendix). *Acicula polita*, *Macrogastra plicatula*, *Pyramidula rupestris*, *Vertigo alpestris*, *Bulgarica vetusta*, *Cepaea nemoralis*, *Clausilia parvula*, and *Balea perversa* were characteristic to the Transdanubian Mountains (labelled with O and P in Fig 1 and Appendix). *Trichia filicina*, *Acicula banatica* and *Trichia erjaveci* were characteristic to the Mecsek Mountains (labelled with Q in Fig 1 and Appendix).

Lowland areas lacked any higher level joint character species (except for the general species of the country). Localizes character species in the lowlands (*Helicigona banatica*, *Hygromia kovacsi*, *Cecilioides petitiana* and *Oxychilus hydatinus*) were associated to smaller areas (labelled with R, T and U in Fig 1 and Appendix).

Table 1. Cross-tabulation of the species groups according to the IndVal and biotic element analysis, and their geographic range size distribution.*

Biotic elements	Range size	IndVal species groups			Total
		A	B	C-U	
1	1	3	7	–	10
	2	3	13	4	20
	3–4	–	–	–	–
	Total	6	20	4	30
2	1	16	1	–	17
	2	7	–	–	7
	3–4	–	–	–	–
	Total	23	1	–	24
3	1	–	–	–	–
	2	–	1	15	16
	3–4	–	–	8	8
	Total	–	1	23	24
4	1	–	1	–	1
	2	3	–	12	15
	3–4	–	–	4	4
	Total	3	1	16	20
Noise	1	–	1	1	2
	2	1	2	10	13
	3–4	–	–	8	8
	Total	1	3	19	23
Total		33	26	62	121

*Biotic elements are indicated in Appendix and in Figs. 2–3; range size scores follow SÓLYMOS (2004), 1: widespread beyond Europe, 2: widespread within Europe, 3–4: endemic; IndVal groups are labelled in Appendix and in Fig. 1.

The cross tabulation of species according to main IndVal groups and range size scores revealed significant association between the two grouping factors ($Chi^2 = 50.8$, $p < 0.001$). The majority of the general species were widespread in the Palaearctic, majority of the highland species had European distribution. Localized species were Palaearctic in only one case (*Discus ruderatus*), the majority was European, and all the endemic and narrow endemic species (20 species) belonged to this group (Table 1).

The test statistic of the distance ratio test for the Hungarian land snail species data set was 0.232. The statistic varied between 0.14 and 0.348 for 1000 artificial data sets generated under the null model (mean 0.258). Thus the observed value fell within the 95% percentile range of the values generated under the null model ($p = 0.183$).

There are 3119 cases in which a range of a Hungarian land snail species is a subset of the range of another species. Such a high number of supersets has not been observed in any of 1000 data sets obtained by Monte Carlo simulations (1421–2947 supersets were observed, mean 2021.66). Thus, the test indicates that the ranges of the Hungarian land snail species are significantly nested ($p < 0.001$).

The association between biotic elements and range size scores revealed was significant ($Chi^2 = 58.05$, $p < 0.001$). Species in elements 1 and 2 tended to be widely distributed in Europe and beyond, species in elements 3 and 4 were European or endemic with all endemic species in these elements and the noise category (Table 1).

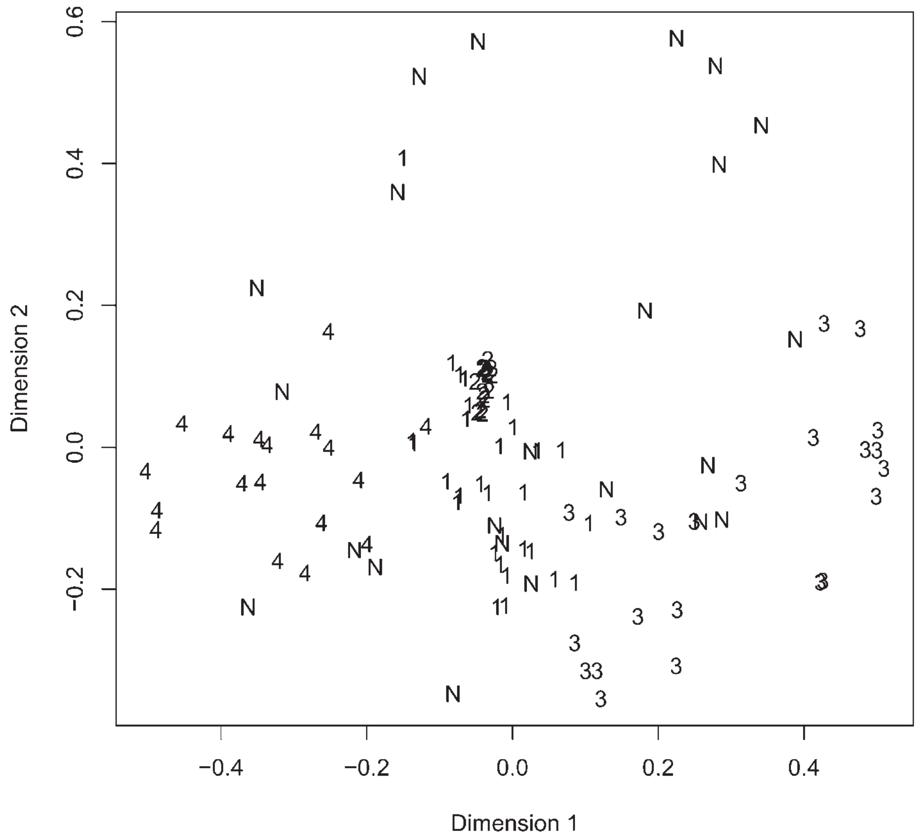

Fig. 2. First two dimensions of the metric multidimensional scaling of the range data of the Hungarian land snail species. 1–4: biotic elements found by PRABCLUS; N: noise component.

The agreement between the indirect (IndVal based) and direct (PRABCLUS based) grouping of the species was high (83.7% excluding the noise component) and significantly associated ($Chi^2 = 130.19$, $p < 0.001$) (Table 1). In congruences were found in 16 cases (18%) (Appendix).

DISCUSSION

The first biogeographic synthesis of the mollusc fauna in the Carpathian Basin was made by SOÓS (1926, 1928, 1934, 1943). He put great emphasis on endemics and stressed the importance of historical factors operating on evolutionary time scale. According to his qualitative analysis, "the mollusc fauna in the Carpathian Basin is allochtonous with widespread and central European species, and influenced by southern, Alpine and Dinaric species" (SOÓS 1943). Similar conclusions were made earlier by MÉHELY (1918) on merely qualitative and intu-

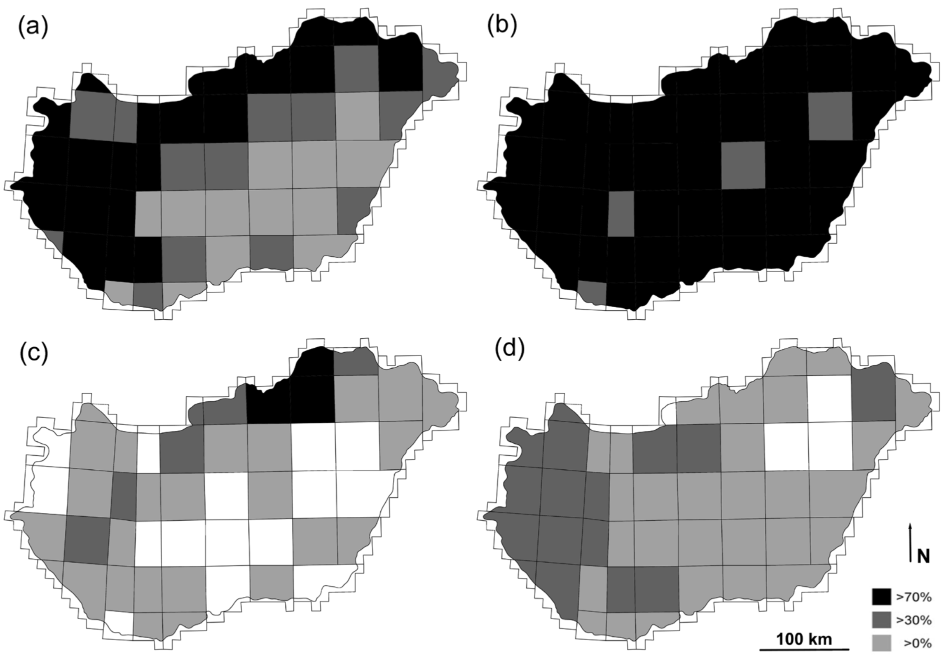

Fig. 3. Distribution maps of four biotic elements found by PRABCLUS: (a) highland species, (b) general species, (c) localizes species distributed in the northern and (d) south–eastern parts of Hungary. The different shadings indicate the areas where >70%, >30%, and >0% of the species of an element was present.

itive basis. He also noted, that central European species send to occur in the mountains. These conclusions were reconfirmed by the present quantitative analysis. "Widespread" (range size score = 1) and "central European" (range size score = 2) species comprise 81.5% of the studies species (101 out of 121 species), comprising the "general" and "highland" species groups based on both the IndVal and PRABCLUS classification.

SOÓS (1943) pointed out that "the fauna formed and changed mainly in situ, and is a resultant of changing environment and the interaction between organisms reacting to environmental change", and "outline of the mollusc fauna was formed before the glacial, and the glacial has made only minor changes through the extinction of few species" (SOÓS 1943). These correspond to latest quarter-malacological evidence (KROLOPP 1995, KROLOPP 2003), namely that during and after the Pleistocene only 14 testaceous snail species have gone extinct, 16 have became locally extinct (their ranges shifted to north and east or west). Besides of these, 29 species have colonised Hungary in post Pleistocene times, out of which 13 have been introduced in the past decades. Total number of species has remained almost the same for long time, and third of the fauna turned over. Two third of the fauna has continuous or temporarily discontinuous presence in Hungarian Quaternary deposits (FŰKÖH *et al.* 1995, KROLOPP 2003) with some species dating back to the Tertiary (SOÓS 1926). These species are termed as "members of the ancient tribe" (not in a taxonomical sense) and "central European" by SOÓS (1934, 1943).

Directions of historical influences can be identified based on the distribution of endemic species (range size score ≥3). Alpine influence is most expressed in the Soproni and Kőszegi Mountains with occurrences of the species *Pagodulina pagodula*, *Cochlodina fimbriata*, *Pseudofusulus varians*, *Macrogastra densest*riata. These areas can be defined as "Praenoricum" following the terminology of VARGA (1964). East Alpine and Dinaric influences are diffuse throughout the Transdanubian area with the species *Aegopis verticillus*, *Aegopinella ressmanni*, *Truncatellina claustralis*, *T. callicratis*, *Bulgarica vetusta*. Dinaric influences are sharply present along the River Dráva (with occurrences of *Helicigona planospira*) and in the Mecsek Mountains (with species *Trichia filicina*, *Acicula banatica*, *Trichia erjaveci*), and these areas can be defined as "Praeillyricum" following the terminology of VARGA (1964).

Based on the occurrences of many Carpathian species (*Perforatella vicina*, *Oxychilus orientalis*, *Helicigona faustina*, *Hygromia transsylvanica*, *Cochlodina cerata*, *Macrogastra latestriata*, *Trichia lubomirskii*, *Balea stabilis*, *Vestia gulo*, *V. turgida*, *Spelaeodiscus triarius*) in the Northern mountains it can be defined as part of the Carpathicum region accepting the classification of Soós (1943). The number of endemic species was highest here that indicates the profound significance of historical effects in this region. KASZAB (1961) noted that the Northern Carpathians are the most species poor region among the Carpathian chains, thus the fauna of the Northern Mountains with its high endemicity must be treated as a part of this relatively species poor Carpathian region.

The results presented here results support the hypothesis of DELI and SÜMEGI (1999) which states that the Bereg-Szatmár plain, the Nyírség region (both in North-East Hungary) and the plain along the Körös Rivers are fluctuation zones of Carpathian species (e.g. *Perforatella vicina*, *Perforatella dibothrion*, *Helicigona banatica*). DELI and SÜMEGI (1999) identified these parts of the Great Plain as "Praecarpathicum", where number of species belonging to the same faunal group decreases gradually (VARGA 1971, 2002) due to differential dispersal from centers of endemism (HAUSDORF & HENNIG 2003*a*). For ground beetles, KÖDÖBÖCZ and MAGURA (1999) also identified the hills in the Bereg area as part of the "Praecarpathicum". These alluvial plains along the rivers originating from high-diversity areas function as "green corridors" and promote the transfer of different faunal elements (DELI *et al.* 1995, OBRDLÍK *et al.* 1995).

Regional classification based on land snail distribution data corresponds reasonably well with geographical classification (e.g. MAROSI & SOMOGYI 1990). Although minor deviations were also identified. The north-eastern part of the Great Plain (Nyírség, Szatmár-Bereg Plain) was more similar to the Northern Mountains (with joint occurrences of the species *Perforatella dibothrion*, *Perforatella vicina*, *Balea stabilis*; cf. SOÓS 1928) than to other parts of the Great Plain. The fauna of the Cserhát Mountains and the Gödöllő Hills resembled at a higher degree to Transdanubian areas than to the other parts of the Northern Mountains. This disagreement between biogeographic and pure geographical classification was also identified by (VARGA 1964) for Macrolepidoptera. On the contrary, BÁBA (1981) found the Gödöllői Hills more similar to the Great Plain.

BÁBA (1981, 1982, 1986) used the area analytical method developed for Macrolepidoptera (DE LATTIN 1967, VARGA 1977) on land snail distribution data. BÁBA (1981, 1982) used data of 17 well studied regions based on the data of PINTÉR *et al.* (1979). He grouped the species according to faunal types, than he studied the correlation between frequency of faunal types in regions and climatic variables. He found that the fauna of the regions were differentiated, and the pattern corresponded to results of plant geographical classification. He failed to identify clear relationship between regions because of inadequate data and methods.

The main dichotomy of highlands and lowlands found here can be attributed to mainly climatic and altitudinal differences. The semiarid continental climate in the Great Plain precludes the occurrence of many species (AGÓCSY 1965). The general forest-steppe vegetation of the plains enables the occurrence only of widespread and xerotolerant species (general species group). Those rare species that occur in the plains are associated with wetlands (e.g. *Vertigo moulinsiana*, *Vallonia enniensis*) and riparian forests (e.g. *Helicigona banatica*). Forests in the highlands serve adequate habitats for species of the highland species group. The fauna shows nested pattern along climatic and altitudinal gradient with many widespread general and highland species, and than localized and endemic species in the Northern Mountains and Western Marginal Area. This corresponds to the general pattern found in North-Western Europe of HAUSDORF and HENNIG (2003*a*), which analysis involved the area of Hungary, too.

The agreement between the indirect (IndVal based) and direct (PRABCLUS based) representation of the species groups was high. Although indirect methodology lacks the power of testing the deviation from a null modell. By using direct biotic element analysis, the spatially autocorrelated nature of species richness and species' occurrences can be modelled. Species' ranges were significantly more nested than in the null modell, but clustering of species' ranges did not differed from the null modell. This indicates that differential dispersal of the species is an important process in shaping regional land snail faunas (HAUSDORF & HENNIG 2003*a*). Species clusters were obscured by this dispersal process, which underlines the "biogeographic crossroad" (SPECTOR 2002) effect (multiple mass effect, SHMIDA & WILSON 1985) in the Carpathian Basin.

The pattern of land snail distribution is driven by both contemporary environmental and historical effects. General highland-lowland pattern of species composition is influenced primarily by climate and elevation. The historical effects result in the faunal dissimilarities between highland regions through the occurrence of endemic species. These are of two main sources, Alpine-Carpathian and southern-Illyric influences. The land snail fauna of the Northern and Transdanubian Mountains are distinct, the border between them is termed as "middle Danube floristic (biotic) barrier" (ZÓLYOMI 1942). Transdanubian areas are influenced primarily by species with southern distribution, while Northern Mountains are influenced primarily by Carpathian species. This separation can be attributed to the fact, that the Northern Mountains are direct continuation of the Northern Carpathians, and as such, is part of a high mountain system. Contrary to this, mountains in Transdanubia are independent of such high mountains.

Here, I used UTM based distribution data of 121 land snail species and quantitative methods to assess the biogeographic classification of Hungary. The results reconfirmed, that regions in Hungary possess different environmental histories from the Pleistocene up to the present (FŰKÖH *et al.* 1995, KROLOPP & SÜMEGI 1995, RUDNER & SÜMEGI 2001) and different biogeographic influences make up a fauna with unique composition (VARGA 1995, VARGA 2002) and relatively high species richness compared to European standards as a result of mass effect (SHMIDA & WILSON 1985). In such areas, representativeness can be achieved with relative efficiency in such areas. Saving the biota requires greater efforts to preserve not only the pattern of biodiversity but also the processes and mechanisms that generate and maintain it.

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REFERENCES

AGÓCSY, P. (1965) Hazai csigafajaink elterjedését megszabó klímatényezők vizsgálata. *Állattani Közlemények* **52**: 21–27. [In Hungarian]

BÁBA, K. (1981) Magyarország szárazföldi csigáira vonatkozó új állatföldrajzi felosztás tanulságai. *Soosiana* **9**: 13–22. [In Hungarian]

BÁBA, K. (1982) Eine neue zoogeographische Gruppierung der ungarischen Landmollusken und die wertung des Faunenbildes. *Malacologia* **22**: 441–454.

BÁBA, K. (1986) Magyarország szárazföldi csigáinak besorolásához felhasznált fajarea térképek és értelmezésük II. *Folia Historico-naturalia Musei Matraensis* **11**: 49–69. [In Hungarian]

BYERS, S. & RAFTERY, A. E. (1998) Nearest neighbor clutter removal for estimating features in spatial point processes. *Journal of the American Statistical Association* **95**: 781–794.

CAMERON, R. A. D. & POKRYSZKO, B. M. (2005) Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology* **38**: 529–547.

COX, C. B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography* **28**: 511–523.

DE LATTIN, G. (1967) *Grundriss der Zoogeographie*. Gustav Fischer, Stuttgart, 602 pp.

DELI, T. & SÜMEGI, P. (1999) Biogeographic characterisation of Szatmár-Bereg plain based on the mollusc fauna. Pp. 471–477. *In:* HAMAR, J & SÁRKÁNY-KISS, A (eds): *The Upper Tisa Valley. Preparatory proposal for Ramsar site designation and an ecological background*. Hungarian, Romanian, Slovakian and Ukrainian co-operation, Szeged.

DELI, T., DOBÓ, T., KISS, J. & SÜMEGI, P. (1995) Hinweise über dei Funktion eines "grünen Korridors" Entlang der Tisza (Theiß) auf Grund der Molluskenfauna. *Malacological Newsletter* **14**: 29–32.

DUFRÉNE, M. & LEGENDRE, P. (1997) Species assemblages and indicator species: the need for a flexibile asymmetrical approach. *Ecological Monographs* **67**: 345–366.

FEHÉR, Z. & GUBÁNYI, A. (2001) *The distribution of Hungarian Molluscs. The catalogue of the Mollusca Collection of the Hungarian Natural History Museum.* Hungarian Natural History Museum, Budapest, 466 pp.

FEHÉR, Z., MAJOROS, G. & VARGA, A. (2006) A scoring method for the assessment of rarity and conservation value of the aquatic molluscs in Hungary. *Heldia* **6**: 101–114.

FRALEY, C. & RAFTERY, A. (2007) mclust: Model-Based Clustering / Normal Mixture Modeling. R package version 3.1–1. URL: http://www.stat.washington.edu/mclust

FŰKÖH, L., KROLOPP, E. & SÜMEGI, P. (eds) (1995) *Quaternary Malacostratigraphy in Hungary*. Malakológiai Tájékoztató **Suppl.** 1, 219 pp.

HAUSDORF, B. (2002) Units in biogeography. *Systematic Biology* **51**: 648–652.

HAUSDORF, B. & HENNIG, C. (2003*a*) Nestedness of north-west european land snail ranges as a consequence of differential immigration from pleistocene glacial refuges. *Oecologia* **135**: 102–109.

HAUSDORF, B. & HENNIG, C. (2003*b*) Biotic element analysis in biogeography. *Systematic Biology* **52**: 717–723.

HAUSDORF, B. & HENNIG, C. (2004) Does vicariance shape biotas? Biogeographic tests of the vicariance model in the north-west european land snail fauna. *Journal of Biogeography* **31**: 1751–1757.

HENNIG, C. (2006) prabclus: Test for clustering of presence-absence data. R package version 2.0–2. URL: http://www.homepages.ucl.ac.uk/~ucakche

HEIKINHEIMO, H., FORTELIUS, M., ERONEN, J. & MANNILA, H. (2007) Biogeography of European land mammals shows environmentally distinct and spatially coherent clusters. *Journal of Biogeography* **34**: 1–12.

HENGEVELD, R. (1999) *Dynamic biogeography*. Cambridge University Press, 249 pp.

KASZAB, Z. (1961) A Kárpátok és medencéinek állatföldrajzi kapcsolatairól. *Folia Entomologica Hungarica* **14**: 261–269. [In Hungarian]

KÖDÖBÖCZ, V. & MAGURA, T. (1999) Biogeographic connections of the carabid fauna (Coleoptera: Carabidae) of the Beregi-síkság to the Carpathians. *Folia Entomologica Hungarica* **60**: 195–203.

KROLOPP, E. (1995) Biostratigraphic division of Pleistocene formations in Hungary according to their Mollusc fauna. Pp. 17–78. *In:* FŰKÖH, L,, KROLOPP, E. & SÜMEGI, P. (eds.): *Quaternary Malacostratigraphy in Hungary*. Malakológiai Tájékoztató, Suppl. 1, Gyöngyös.

KROLOPP, E. (2003) Mollusc species of the Hungarian Pleistocene formations (as of Dec 31 of year 2002). *Malakológiai Tájékoztató* **21**: 13–18.

KROLOPP, E. & SÜMEGI, P. (1995) Palaeoecological reconstruction of the Late Pleistocene, based on loess malacofauna in Hungary. *GeoJournal* **36**: 213–222.

MAROSI, S. & SOMOGYI, S. (1990) *Magyarország kistájainak katasztere, I–II.* MTA Földrajztudományi Kutatóintézet, Budapest. [In Hungarian]

MÉHELY, L. (1918) A magyarországi fauna földrajzi vázlata. *In:* LÓCZY, L. (ed.): *A Magyar Szentkorona Országainak földrajzi, társadalomtudományi, közművelődési és közgazdasági leírása*. Magyar Földrajzi Társaság, Budapest, pp. 94–96. [In Hungarian]

OBRDLÍK, P., FALKNER, G. & CASTELLA, E. (1995) Biodiversity of Gastropoda in European floodplains. *Archiv für Hydrobiologie*, *Suppl.* **101**: 339–356.

PATTEN, M. A. & ERICKSON, R. A. (2001) Conservation value and rankings of exotic species. *Conservation Biology* **15**: 817–818.

PINTÉR, L. (1984) A revised catalogue of the recent molluscs of Hungary. *Folia Historico-naturalia Musei Matraensis* **9**: 79–90.

PINTÉR, L. & SUARA, R. (2004) *A magyarországi puhatestűek elterjedése II.* Magyar Természettudományi Múzeum, Budapest, 547 pp. [In Hungarian]

PINTÉR, L. & SZIGETHY, A. S. (1979) Die Verbreitung der rezenten Mollusken Ungarns: Neunachweise und Berichtigungen, I. *Soosiana* **7**: 97–108.

PINTÉR, L. & SZIGETHY, A. S. (1980) Die Verbreitung der rezenten Mollusken Ungarns: Neunachweise und Berichtigungen, II. *Soosiana* **8**: 65–80.

PINTÉR, L., RICHNOVSZKY, A. & SZIGETHY, A. (1979) *Distribution of the recent Mollusca of Hungary*. Budapest, 351 pp.

PODANI, J. (1993) Syn-tax 5.0: computer programs for multivariate data analysis in ecology and systematics. *Abstracta Botanica* **17**: 289–302.

R Development Core Team (2007). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, URL http://www.R-project.org

RUDNER, Z. E. & SÜMEGI, P. (2001) Recurring taiga forest-steppe habitats in the Carpathian Basin in the Upper Weichselian. *Quaternary International* **76–77**: 177–189.

SHMIDA, A. & WILSON, M. V. (1985) Biological determinants of species diversity. *Journal of Biogeography* **12**: 1–20.

SÓLYMOS, P. (2004) Magyarország szárazföldi mollusca-faunájának ritkaságon alapuló értékelése és alkalmazási lehetőségei. *Természetvédelmi Közlemények* **11**: 511–520. [In Hungarian]

SÓLYMOS, P. (2005) *Természetvédelmi prioritások meghatározása magyarország szárazföldi puhatestűinek elterjedési adatai alapján (Mollusca, Gastropoda).* PhD Thesis, University of Debrecen (manuscript). [In Hungarian]

SÓLYMOS, P. (2007) Are current protections of land snails in Hungary relevant to conservation? *Biodiversity and Conservation* **16**: 347–356.

SÓLYMOS, P. & FEHÉR, Z. (2005) Conservation prioritization using land snail distribution data in Hungary. *Conservation Biology* **19**: 1084–1094.

SOÓS, L. (1926) A magyar mollusca-fauna multja. *Annales Musei Nationales Hungarici* **24**: 392–421. [In Hungarian]

SOÓS, L. (1928) A bátorligeti ősláp mollusca-faunája és az Alföld multjának kérdése. *Állattani Közlemények* **25**: 103–113. [In Hungarian]

SOÓS, L. (1934) Magyarország állatföldrajzi felosztása. *Állattani Közlemények* **31**: 1–25. [In Hungarian]

SOÓS, L. (1943) *A Kárpát-medence Mollusca-faunája*. Akadémiai Kiadó, Budapest, 478 pp. [In Hungarian]

SPECTOR, S. (2002) Biogeographic crossroads as priority areas for biodiversity conservation. *Conservation Biology* **16**: 1480–1487.

VARGA, Z. (1964) Magyarország állatföldrajzi beosztása a nagylepkefauna komponensei alapján. *Folia Entomologica Hungarica* **17**: 119–167. [In Hungarian]

VARGA, Z. (1971) A szétterjedési centrumok és a szétterjedési folyamat jelentősége a földrajzi izoláció kialakulása és a mikroevolúció szempontjából. *Állattani Közlemények* **58**: 142–149. [In Hungarian]

VARGA, Z. (1977) Das Prinzip der areal-analytischen Methode in der Zoogeographie und die Faunenelemente-Einteilung der europäischer Tagschmetterlinge (Lep.: Diurna). *Acta Biologica Debrecina* **14**: 223–285.

VARGA, Z. (1995) Geographical patterns of biological diversity in the Palaearctic Region and the Carpathian Basin. *Acta Zoologica Academiae Scientiarum Hungaricae* **41**: 71–92.

VARGA, Z. (2002) Biodiversity and phylogeography – general and regional aspects. *Acta Biologica Debrecina* **24**: 5–38.

WALLACE, A. R. (1876) *The geographical distribution of animals*. Harper, New York,

WHITTAKER, R. J., ARAÚJO, M. B., JEPSON, P., LADLE, R. J., WATSON, J. E. M. & WILLIS, K. J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions* **11**: 3–23.

WIKTOR, A. & SZIGETHY, A. S. (1983) The distribution of slugs in Hungary (Gastropoda: Pulmonata). *Soosiana* **10–11**: 87–111.

ZÓLYOMI, B. (1942) A középdunai flóraválasztó és a dolomitjelenség. *Botanikai Közlemények* **39**: 209–231. [In Hungarian]

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APPENDIX
Characteristics of species used in this study

Abbreviations used: Cluster = Occurrences are given according to clusters with circled numbers 1–6 in Fig. 1. IndVal = IndVal species groups refer to clusters in Fig. 1 with capital letters. E = Biotic elements are indicated in Appendix and in Figs 2–3. R = Range size scores follow SÓLYMOS (2004). 1: beyond Europe, 2: large within Europe, 3: restricted to one well-defined biogeographic region, 4: narrow within one biogeographic region. P = p group.

Species names follow (PINTÉR 1984)	Cluster	IndVal	E	R	%	P
Succinella oblonga DRAPARNAUD, 1801	1, 2, 3, 4, 5, 6	100	ns	A	2	1
Pupilla muscorum (LINNÉ, 1758)	1, 2, 3, 4, 5, 6	100	ns	A	2	1
Zonitoides nitidus (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	100	ns	A	2	1
Cepaea vindobonensis (FÉRUSSAC, 1821)	1, 2, 3, 4, 5, 6	100	ns	A	2	2
Cochlicopa lubrica (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	98	ns	A	2	1
Vallonia pulchella (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	98	ns	A	2	1
Monacha cartusiana (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	98	ns	A	1	2
Perforatella rubiginosa (A. SCHMIDT, 1853)	1, 2, 3, 4, 5, 6	98	ns	A	2	1
Vallonia costata (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	95.9	ns	A	2	1
Chondrula tridens (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	95.9	ns	A	2	2
Helix pomatia LINNÉ, 1758	1, 2, 3, 4, 5, 6	95.9	ns	A	2	2
Oxyloma elegans (RISSO, 1826)	1, 2, 3, 4, 5, 6	93.9	ns	A	2	1
Truncatellina cylindrica (FÉRUSSAC, 1807)	1, 2, 3, 4, 5, 6	93.9	ns	A	2	2
Cochlicopa lubricella (PORRO, 1837)	1, 2, 3, 4, 5, 6	91.8	ns	A	2	1
Punctum pygmaeum (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	91.8	ns	A	2	1
Vitrina pellucida (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	91.8	ns	A	2	1
Helicella obvia (MENKE, 1828)	1, 2, 3, 4, 5, 6	91.8	ns	A	2	2
Carychium minimum O. F. MÜLLER, 1774	1, 2, 3, 4, 5, 6	87.8	ns	A	2	1
Bradybaena fruticum (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	87.8	ns	A	1	1
Succinea putris (LINNÉ, 1758)	1, 2, 3, 4, 5, 6	85.7	ns	A	2	1
Vertigo pygmaea (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	85.7	ns	A	2	1
Granaria frumentum (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	83.7	ns	A	4	2
Euomphalia strigella (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	83.7	ns	A	2	2
Vertigo antivertigo (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	81.6	ns	A	1	1
Vitrea crystallina (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	81.6	ns	A	2	1
Euconulus fulvus (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	81.6	ns	A	2	1
Aegopinella minor (STABILE, 1864)	1, 2, 3, 4, 5, 6	81.6	ns	A	2	2

Species names follow (PINTÉR 1984)	Cluster	IndVal	E	R	%	P
Cecilioides acicula (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	77.6	ns	A	1	2
Nesovitrea hammonis (STRÖM, 1765)	1, 2, 3, 4, 5, 6	77.6	ns	A	1	1
Oxychilus draparnaudi (BECK, 1837)	1, 2, 3, 4, 5, 6	75.5	ns	A	1	2
Helicopsis striata (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	67.4	ns	A	4	2
Cepaea hortensis (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	49	ns	A	4	2
Helicigona arbustorum (LINNÉ, 1758)	1, 2, 3, 4, 5, 6	46.9	ns	A	N	2
Acanthinula aculeata (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	85.6	*	B	1	1
Perforatella incarnata (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	83	*	B	1	2
Carychium tridentatum (RISSO, 1826)	1, 2, 3, 4, 6	82.9	*	B	1	1
Vitrea contracta (WESTERLUND, 1871)	1, 2, 3, 4, 6	81.8	*	B	1	1
Trichia hispida (LINNÉ, 1758)	1, 2, 3, 4, 5, 6	81.7	*	B	1	1
Cochlodina laminata (MONTAGU, 1803)	1, 2, 3, 4, 5, 6	81.5	*	B	2	1
Balea biplicata (MONTAGU, 1803)	1, 2, 3, 4, 5, 6	81	*	B	1	2
Vallonia enniensis (GREDLER, 1856)	1, 2, 3, 4, 5, 6	79.3	*	B	1	2
Laciniaria plicata (DRAPARNAUD, 1801)	1, 2, 3, 4, 5	75.7	*	B	1	2
Vertigo angustior JEFFREYS, 1830	1, 2, 3, 4, 5, 6	75.3	*	B	1	1
Discus perspectivus (MEGERLE VON MÜHLFELD, 1816)	1, 2, 3, 4	74.2	*	B	1	2
Oxychilus glaber (ROSSMÄSSLER, 1838)	1, 2, 3, 4	74.2	*	B	N	2
Daudebardia rufa (DRAPARNAUD, 1805)	1, 2, 3, 4, 6	74.1	*	B	1	2
Clausilia pumila C. PFEIFFER, 1828	1, 2, 3, 4, 5	72.5	*	B	1	2
Macrogastra ventricosa (DRAPARNAUD, 1801)	1, 2, 3, 4, 5, 6	69	*	B	1	2
Clausilia dubia DRAPARNAUD, 1805	1, 2, 3, 4, 5	69	*	B	1	2
Oxychilus inopinatus (ULIČNY, 1887)	1, 2, 3, 4, 5, 6	68.8	*	B	1	2
Aegopinella pura (ALDER, 1830)	1, 2, 3, 4, 5, 6	66.7	*	B	1	2
Columella edentula (DRAPARNAUD, 1805)	1, 2, 3, 4, 6	61.4	*	B	1	1
Vertigo pusilla O. F. MÜLLER, 1774	1, 2, 3, 4	61.3	*	B	1	1
Ena obscura (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	60.9	*	B	N	1
Daudebardia brevipes (DRAPARNAUD, 1805)	1, 2, 3, 4, 6	56.6	*	B	1	2
Vitrea diaphana (STUDER, 1820)	2, 3, 4, 6	51.9	*	B	3	2
Helicodonta obvoluta (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5	50.2	*	B	1	2
Vitrea subrimata (REINHARDT, 1871)	1, 2, 3, 4	48.4	*	B	N	2
Vertigo moulinsiana (DUPUY, 1849)	1, 2, 3, 4, 5, 6	47.5	*	B	4	1
Perforatella bidentata (GMELIN, 1788)	1, 2, 3, 4, 5, 6	43.1	*	C	N	2
Ena montana (DRAPARNAUD, 1801)	1, 2, 3, 5	30.7	*	C	N	2
Semilimax semilimax (FÉRUSSAC, 1802)	1, 2, 3	61.8	*	D	4	2
Perforatella umbrosa (C. PFEIFFER, 1828)	1, 3, 4, 5, 6	57.4	*	D	4	2
Aegopis verticillus (LAMARCK, 1822)	1, 3	55.7	*	D	4	2
Aegopinella ressmanni (WESTERLUND, 1883)	1, 3, 4, 6	52.1	*	D	4	3
Pagodulina pagodula (DES MOULINS, 1830)	1	50	ns	E	4	2
Cochlodina fimbriata (ROSSMÄSSLER, 1835)	1	50	ns	E	4	3
Pseudofusulus varians (C. PFEIFFER, 1828)	1	50	ns	E	4	2
Macrogastra densestriata (ROSSMÄSSLER, 1836)	1	50	ns	E	4	3
Helicigona planospira (LAMARCK, 1828)	1	100	*	F	N	3

Species names follow (PINTÉR 1984)	Cluster	IndVal	E	R	%	P
Pomatias elegans (O. F. MÜLLER, 1774)	1, 3, 4	28.6	ns	F	4	2
Aegopinella nitens (MICHAUD, 1831)	1, 3	83.3	ns	G	4	2
Trichia striolata (C. PFEIFFER, 1828)	1, 2, 3, 5	63.6	ns	G	4	2
Cochlicopa nitens (GALLENSTEIN, 1848)	1, 2, 3, 4	58.8	ns	G	4	2
Perforatella vicina (ROSSMÄSSLER, 1842)	2	100	*	H	3	3
Ruthenica filograna (ROSSMÄSSLER, 1836)	2, 3	82.9	*	H	3	2
Bulgarica cana (HELD, 1836)	2, 3	49.6	*	H	3	2
Helix lutescens ROSSMÄSSLER, 1837	2, 4, 5, 6	47.7	*	H	N	3
Vertigo substriata (JEFFREYS, 1833)	2	37.5	*	H	3	2
Perforatella dibothrion (M. KIMAKOWICZ, 1884)	2	50	ns	I	N	3
Pomatias rivulare (EICHWALD, 1829)	1, 2	44.4	ns	I	1	2
Cochlodina orthostoma (MENKE, 1830)	2	100	*	J	3	2
Oxychilus orientalis (CLESSIN, 1887)	2	100	*	J	3	4
Isognomostoma isognomostomos (SCHRÖTER, 1784)	1, 2	93.2	*	J	N	2
Helicigona faustina (ROSSMÄSSLER, 1835)	2, 4	93.1	*	J	3	3
Macrogastra latestriata (A. SCHMIDT, 1857)	2	80.7	*	J	3	3
Hygromia transsylvanica (WESTERLUND, 1876)	2, 4	67.9	*	J	3	3
Cochlodina cerata (ROSSMÄSSLER, 1836)	2, 3	66.7	*	J	3	3
Oxychilus depressus (STERKI, 1880)	2, 3	52.9	*	J	3	2
Trichia unidentata (DRAPARNAUD, 1805)	1, 2, 3, 5	43	*	J	3	2
Trichia lubomirskii (SLÓSARSKI, 1881)	2	100	*	K	N	4
Balea stabilis (L. PFEIFFER, 1847)	2	33.3	ns	K	N	3
Discus ruderatus (FÉRUSSAC, 1821)	2	30.8	ns	K	N	1
Clausilia cruciata (STUDER, 1820)	1, 2	92.3	*	L	N	2
Vestia turgida (ROSSMÄSSLER, 1836)	2	61.5	*	L	3	3
Spelaeodiscus triarius (ROSSMÄSSLER, 1839)	2	50	ns	L	3	3
Phenacolimax annularis (STUDER, 1820)	2	50	ns	L	3	2
Chondrina clienta (WESTERLUND, 1883)	2, 3, 4	41.9	*	L	3	2
Pupilla triplicata (STUDER, 1820)	1, 2, 3, 4, 5	70	*	M	1	2
Truncatellina claustralis (GREDLER, 1856)	1, 2, 3, 4	68.9	*	M	1	2
Truncatellina callicratis (SCACCHI, 1833)	3, 4	66.7	*	M	4	2
Zebrina detrita (O. F. MÜLLER, 1774)	1, 2, 3, 4, 5, 6	61.2	*	M	1	2
Orcula doliolum (BRUGUIÉRE, 1792)	1, 2, 3, 4, 5, 6	67.3	*	N	3	2
Discus rotundatus (O. F. MÜLLER, 1774)	1, 2, 3	65.4	*	N	N	2
Orcula dolium (DRAPARNAUD, 1801)	2, 3, 4, 5, 6	40	*	N	3	2
Acicula polita (HARTMANN, 1840)	1, 2, 3	64	*	O	3	2
Macrogastra plicatula (DRAPARNAUD, 1801)	1, 2, 3	61.3	*	O	N	2
Pyramidula rupestris (DRAPARNAUD, 1801)	2, 3	58.5	*	O	3	2
Vertigo alpestris ALDER, 1838	2, 3, 4	52.6	*	O	3	2
Bulgarica vetusta (ROSSMÄSSLER, 1836)	2, 3	51.1	*	O	3	2
Cepaea nemoralis (LINNÉ, 1758)	1, 3, 4, 5, 6	49.9	*	O	4	2
Clausilia parvula (FÉRUSSAC, 1807)	1, 3	46.7	*	O	N	2
Balea perversa (LINNÉ, 1758)	2, 3	53.3	ns	P	3	2

Species names follow (PINTÉR 1984)	Cluster	IndVal	E	R	%	P
Trichia filicina (L. PFEIFFER, 1841)	1, 2, 3	62.9	*	Q	N	2
Acicula banatica (ROSSMÄSSLER, 1842)	3	50	ns	Q	4	3
Trichia erjaveci (BRUSINA, 1870)	1, 3, 4, 5, 6	38.9	ns	Q	N	2
Cecilioides petitiana (BENOIT, 1862)	1, 2, 3, 4, 6	39.6	ns	R	4	2
Vestia gulo (E. A. BIELZ, 1859)	2, 4	59.3	ns	S	N	3
Helicigona banatica (ROSSMÄSSLER, 1838)	2, 5, 6	35.3	ns	T	N	3
Hygromia kovacsi VARGA et L. PINTÉR, 1972	6	35	ns	U	N	4
Oxychilus hydatinus (ROSSMÄSSLER, 1838)	4, 5, 6	27.8	ns	U	N	2