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A MULTIDIMENSIONAL SCALING STUDY OF NICHE SEPARATION IN TERRESTRIAL SNAIL ASSEMBLAGES

K. Bába[1] & J. Podani[2]

1 Department of Biology, Juhász Gy. Teachers Training College, Szeged, Hungary
2 Department of Plant Taxonomy & Ecology, ELTE, Budapest, Hungary. Email: podani@ludens.elte.hu

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Abstract: The use of Horn's index is extended to express niche separation in multidimensional niche spaces where each axis represents a combination of states of environmental variables of the nominal or ordinal type. Pairwise niche separation coefficients are applied to snail assemblages in three different successional seres of terrestrial plant communities in the Hungarian Great Plain. Matrices of separation coefficients are subjected to metric and nonmetric multidimensional scaling in order to reveal underlying niche relationships in the assemblages. Principal coordinates analysis proved to be more effective in detecting species groups than nonmetric scaling.

Introduction

Niche spaces are generally considered as conceptual spaces with dimensions corresponding to ecological factors (e.g., Hutchinson 1957) or variables related to resource exploitation (e.g., Hurlbert 1978). In both cases, measurements of niche overlap/separation between two or more species are made in a hope that the results reveal potential competitive forces in communities. Although high overlap does not necessarily imply strong competition (cf. Abrams 1980, Shmida & Ellner 1984), niche measurements do provide some information on similarities in resource utilization and ecological requirements. Most studies of this kind are restricted to a single variable and, if more factors have been involved, to their separate analysis. However, individual treatment of niche dimensions is a cumbersome task: a multidimensional situation requires use of multivariate data analytical methods. Multivariate approches to the niche problem, however, are not too common even though multivariate methods themselves are widely applied in ecology. Most often, discriminant analysis is used to distinguish among several species or habitats in several niche dimensions. A classical and relevant example is Green (1971) who analyzed niche separation among freshwater bivalves of Canadian lakes. Similar approaches were taken by Dueser & Shugart (1978) for mammals, and Shugart & Patten (1972) and Conner & Adkisson (1976) for birds. Discriminant analysis requires that variables be measured on the interval scale; not to mention other, more fundamental limitations. If the variables are categorical (nominal or ordinal), discriminant analysis does not apply (although there is a suggestion by Strahler 1978 to avoid this problem).

In this paper we adopt a different approach by using multidimensional scaling for reduction of dimensionality. Multidimensional scaling operates on distance or dissimilarity matrices so the type of measurement scale poses no problems. We emphasize that measurement of niche separation in fact involves calculation of a dissimilarity between populations in the niche space, so the real problem now is to find a dissimilarity function that fits best the actual situation. We shall make an attempt to define potential niche (or milieu) states in terms of combinations of categories for all variables considered. Then, if species performance data (e.g., abundance) are presented in matrices of species by niche states, rather than species by sampling units as in conventional synecological or syntaxonomic studies, multidimensional scaling methods will be the most straightforward techniques to reveal underlying niche relationships among species. For expressing niche separation we suggest to extend the use of the complement of Horn index (Horn 1966) to compare pairs of species based on their performance in the niche states. The methods are applied to the analysis of terrestrial mollusc assemblages of three different successional seres of principal plant communities in the Hungarian Great Plain. These seres provide a great variety of habitats for terrestrial molluscs. However, our present knowledge on the relationships between snail distribution, vegetation types and dominant ecological factors is very limited. Most important is to compare niche separation of generalist species occurring in all the three successional seres, and to reveal species that are decisive in influencing structural relationships in the realized niche space.

Material and methods

Study area and vegetation types

The study sites are located in the Great Hungarian Plain (52,000 km^2 in area); the largest of the six different major geographical regions of the country. Of the 12 landscape sectors distinguished by Somogyi (1961) within this area, nine appear in the so-called Tisza-Plain, whereas the other three belong to the Dráva and Danube watershed (Fig. 1).

The three forest successional seres examined in the Plain include 12 community types (Table 1). In addition, samples from planted poplar and alder stands were added to the sand and organogenic seres, respectively.

The *organogenic sere* develops in areas formerly covered by stagnant water where accumulation of soil transfers swamp forests into gallery forests (see Járai-Komlódi 1959, Simon 1957, for a phytosociological characterization). During succession soil accumulation is intensive, the soil of mires develops into soils of swamp forests, and then into meadow soils. The microclimate becomes drier as succession proceeds. Forests from this sere are characterized by a marked mosaic structure depending on humidity conditions.

The *mineralogenic sere* develops in floodplains of major rivers on the elevated Pleistocene and Holocene terraces (Kárpáti & Tóth 1961-1962, Simon 1957). Some of the gallery forests studied (*Fraxino-Ulmetum*) appear in flood plains resulted from river regulations in the last century. This sere is characterized by raw and humic alluvial soils that develop first into alluvial forest soils or meadow soils and, less frequently, into clayey brown forest soils. Similarly to the previous sere, the microclimate becomes drier along succession. The mineralogenic sere has been much influenced and perturbed by floods in spring and autumn.

Colonization processes on the moving sand start from open and then closed sand steppe communities, constituting the *sand successional sere.* Plant communities 9-11 (Table 1) are represented by samples taken from slightly humic sand, whereas the *Convallario-Quercetum* community was examined in a wide variety of soils, including meadow/forest soils, rustbrown forest soils and their mixtures with humic sand (classification of soils follows Stefanovits 1967). The phytosociological description of these communities is presented in Papp & Szodtfridt (1967) and Simon & Szerényi (1975). The most influential changes along this sere are humification and increase of soil moisture (Bába 1979).

Table 1. Plant communities from three successional seres sampled for snail data (nomenclature follows Soó 1964-1980).

Organogenic sere

1. *Calamagrosti-Salicetum cinereae* Soó & Zólyomi 1955
2. *Fraxino pannonicae-Alnetum hungaricum* Soó & Komlódi 1960
3. *Salici pentandrae-Betuletum pubescentis* Soó 1955
4. *Dryopteridi-Alnetum* Klika 1940

Mineralogenic sere

5. *Salicetum triandrae* Malcuit 1929
6. *Salicetum albae-fragilis* Soó 1971
7. *Fraxino pannonicae-Ulmetum* Soó 1960
8. *Querco robori-Carpinetum hungaricum* Soó 1967

Sand sere

9. *Brometum tectorum* Soó 1939
10. *Festucetum vaginatae danubiale* Soó 1929
11. *Junipero-Populetum albae* Zólyomi 1950, Szodtfridt 1969
12. *Convallario-Quercetum roboris danubiale* Soó 1957

Malacological data

A total of 247 plant community stands were sampled in 1958-1980 (see Bába 1969, 1977, 1979, 1980, 1983, 1986, for details). In each stand, ten 0.25 m by 0.25 m quadrats were located randomly and all living snails were collected and identified. Species abundances recorded for separate sampling units were then transformed into density per unit area values to yield a species by stands data matrix for each successional sere. Table 2 lists the 39 species found in the study area and indicates their presence/absence in each successional sere. The large sample size for the mineralogenic series (n=178) explains its relatively high richness (35 species were collected), whereas the sand series (n=48) has 23 species, and the organogenic series (n=21) has 22. Because of excessive differences in sample sizes, however, one should not draw far reaching conclusions from the species numbers as to the malacological diversity of the three successional seres.

In addition to presence/absence data, Table 2 gives other useful information on the species occurring in the sample. They have been classified into three trophic groups (O: omnivorous, H: herbivorous, and S: saprophagous), following Frömming (1956). Incremental sum of squares clustering was used in a previous study (unpublished) to establish ecological species groups. These are A: hygrophilous, shade species, B: photophilous species of swamps, C: hygrophilous and photophilous, D: xerophilous species of open areas, and E: riparian ubiquists.

Environmental data

Each of the 247 stands is characterized by 8 environmental variables, all categorical. These are:

1) Humidity level; eight categories were derived from the TWR scale of Zólyomi et al. (1964).

2) Hydrological status with 7 categories, used extensively in forestry (Járó 1971). Six categories were encountered in the study area, 1: excessively drained, 2: with variable water supply, 3: with seepage water, 4: influenced by water temporarily, 5: influenced by water permanently, 6: wet to the surface. The values correspond to the water level as observed in April.

3) Physical soil types: 1: debris, 2: coarse sand, 3: sand, 4: adobe, 5: clay, and 6: hard clay.

Table 2. Presence/absence and some basic characteristics of species appearing in the three successional seres of plant communities. Nomenclature follows Kerney et al. (1983). For abbreviations of trophic type and ecogroups, see text.

Code	Name	Successional sere			Trophic type	Ecogroup
		Sand	Mineralogenic	Organogenic		
AEGMIN	*Aegopinella minor*	+	+	+	O	C
ARICIR	*Arion circumscriptus*	-	+	-	O	B
ARISUB	*Arion subfuscus*	-	+	-	O	C
BRAFRU	*Bradybaena fruticum*	+	+	+	O	C
CARMIN	*Carychium minimum*	-	+	+	S	A
CARTRI	*Carychium tridentatum*	-	+	+	S	A
CEPVIN	*Cepaea vindobonensis*	+	+	+	H	D
CHIBAN	*Chilostoma banaticum*	-	+	-	H	A
CHOTRI	*Chondrula tridens*	+	+	-	S	D
COCLAM	*Cochlodina laminata*	-	+	-	S	H
COCLUB	*Cochlicopa lubrica*	+	+	+	O	E
COCLLA	*Cochlicopa lubricella*	+	+	+	O	D
COLEDE	*Columella edentula*	+	+	+	H	A
DERAGR	*Deroceras agreste*	+	+	+	O	E
EUCFUL	*Euconulus fulvus*	+	+	+	O	D
EUOSTR	*Euomphalia strigella*	+	+	-	H	A
GRAFRU	*Granaria frumentum*	+	-	-	H	D
HELOBV	*Helicella obvia*	+	-	-	H	D
HELSTR	*Helicopsis striata*	+	-	-	S	D
HELPOM	*Helix pomatia*	+	+	-	H	C
HYGKOV	*Hygromia kovacsi*	-	+	-	S	B
MONCAR	*Monacha cartusiana*	+	+	+	H	B
NESHAM	*Nesovitrea hammonis*	+	+	-	O	A
PERBID	*Perforatella bidentata*	-	+	-	O	B
PERINC	*Perforatella incarnata*	-	+	+	H	A
PERRUB	*Perforatella rubignosa*	-	+	+	H	E
PERVIC	*Perforatella vicina*	-	+	-	O	C
PUNPYG	*Punctum pygmaeum*	+	+	+	S	A
PUPMUS	*Pupilla muscorum*	+	+	-	H	D
SUCELE	*Succinea elegans*	-	+	+	O	B
SUCOBL	*Succinea oblonga*	+	+	+	O	E
SUCPUT	*Succinea putris*	-	+	-	O	B
TRUCYL	*Truncatellina cylindrica*	+	+	-	S	D
VALCOS	*Vallonia costata*	+	+	+	O	D
VALPUL	*Vallonia pulchella*	+	+	+	S	E
VERANT	*Vertigo antivertigo*	-	-	+	S	E
VITCRY	*Vitrea crystallina*	-	+	+	S	A
VITPEL	*Vitrina pellucida*	+	+	+	O	D
ZONNIT	*Zonitoides nitidus*	-	+	+	O	E

4) Forest age derived from forest inventories. 1: young (5-40 years), 2: medium aged (41-60 years), 3: old (61-130 years), 4: medium aged and old combined, 5: mixed, from young to old.

5) Canopy closure, five categories corresponding to 0% (in grasslands), 10-39%, 40-59%, 60-79%, and 80-100%. Estimated by eye in the field.

6) Genetic soil type. 1: entisol, moving sand, 2: alluvial soil, 3: humic alluvial soil, 4: rustbrown forest soil, 5: chernozem, 6: alkali soil, 7: meadow soil, 8: soil of mires, 9: forest soil of swamps and floodplains, 10: humic sand, 11: mixtures of humic sand (the last two appearing only in the sand sere).

7) Soil pH. 1: <5.5, 2: 5.5-6.5, 3: 6.6-7.0, 4: 7.0-7.3, 5: 7.4-7.8, and 6: >7.8. The measurements were made in laboratories of local forestry authorities.

8) Macroclimatic region, following the classification suggested by Kakas (1960 a,b). (See Bába 1983 for evidence that such macroclimatic divisions correlate with snail fanua.) Major districts were distinguished according to the number of summer days (A:<50, B:50-75, C:>75). Subdivisions were made in these districts using Koncek's (see, e.g., Kakas 1960b) evapotranspiration indices (1: warm-semiarid, A_1 and A_2, with evapotranspiration index of 60; 2: moderately warm-semiarid with dry, cold winter, B_2, index of –60; 3: dry-subhumid, denoted by $A_{3\text{-}5}$, and $B_{3\text{-}4}$ with index ranging

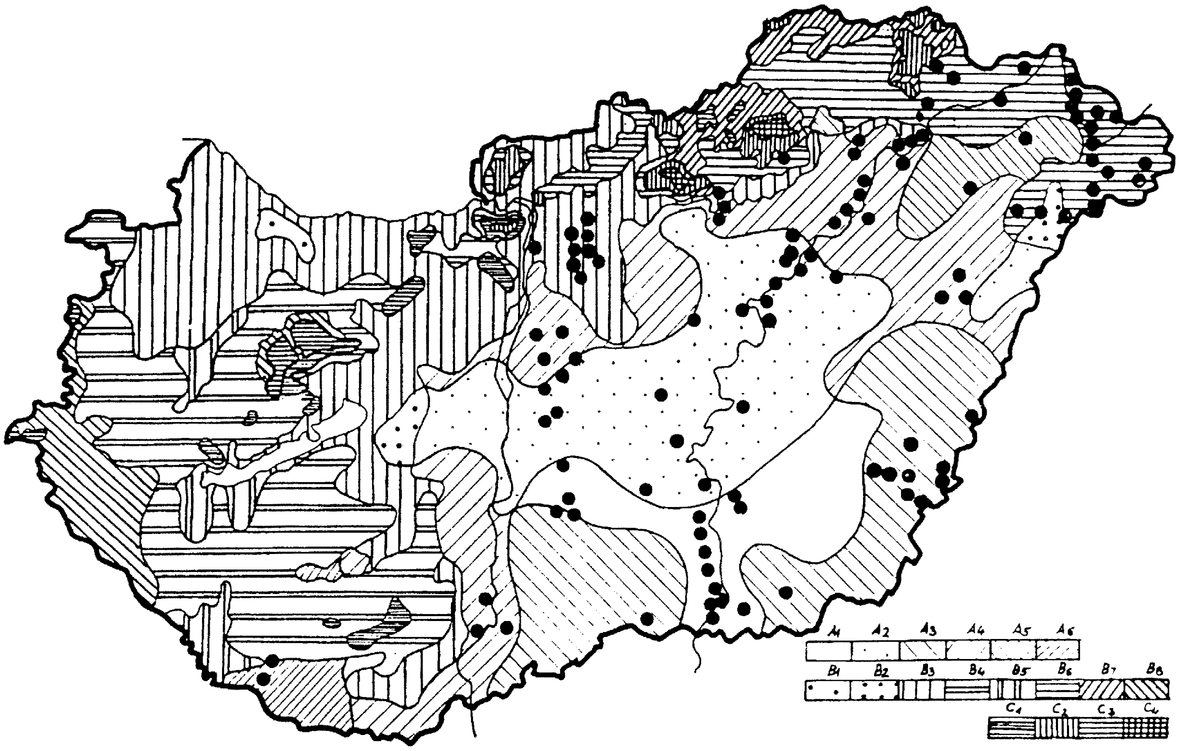

Figure 1. Geographic localization of sampling sites (●) and the climatic regions of Kakas (1960b) in Hungary. Note that a symbol may correspond to several closely located forest stands. See text for abbreviations.

from –60 to 0; and 4: wet-subhumid with an index ranging from 0 to 60, and wet, mild winter, A_6 (cf. Fig. 1).

Measurement of multivariate niche separation

Given s different environmental variables (s=8 in this study), each with k_i categories, the total number of combinations of categories (i.e., possible milieus) is the product

$$m = \prod_{i=1}^{s} k_i \qquad (1)$$

Each of these combinations, denoted by a_j, j=1,...,m, will be defined as a potential *niche* (or *milieu*) *state*. It is necessary to point out here that only a very limited number of states will actually manifest themselves. In fact, the higher the correlations among variables the lower number of combinations are likely to appear in nature. The niche state as specified above is analogous to the *florula* (defined as a particular combination of p plant species, cf. Juhász-Nagy & Podani 1983) and to the *faunula* (combination of p animal species, as in Dévai et al. 1972). Consequently, information theory functions applied to sets of florulas and faunulas may be extended to the niche states as well. In particular, this niche state diversity seems a promising concept for habitat characterization, especially in small-scale surveys.

The Horn formula (Horn 1966) originally suggested for expressing niche overlap between species h and i for one environmental variable with k_1 categories, extends to this more general case as

$$H_{hi} = \frac{\sum_{j=1}^{m}(x_{hj} + x_{ij}) \log (x_{hj} + x_{ij}) - \sum_{j=1}^{m} x_{hj} \log x_{hj} - \sum_{j=1}^{m} x_{ij} \log x_{ij}}{(x_{h.}+x_{i.}) \log (x_{h.}+x_{i.}) - x_{h.} \log x_{h.} - x_{i.} \log x_{i.}} \qquad (2)$$

The complement of (2) is a dissimilarity and will serve as a *measure of niche separation* in the multidimensional niche space:

$$d_{hi} = 1 - H_{hi} \qquad (3)$$

We note that formula (3) is not the only possibility for expressing niche separation between species. In practice, many dissimilarity functions would also apply to this situation. We selected the Horn index because of its wide popularity in niche studies, and because its complement is easily interpretable as a measure of dissimilarity between two frequency distributions. Ganis (1991) lists other possibilities (including distance measures based on hypervolume), but many of them are virtually restricted either to variables of the resource type, or to variables measured on the interval scale. Colwell & Futuyma's (1971) index, an algebraic equivalent of the Czekanowski coefficient, is an exception. It has received application, for example, in a cluster analytic study of plant niches by Yu & Orlóci (1990).

Multivariate analysis

By amalgamating scores for stands which have the same niche state, the original species by stands matrix $\mathbf{Y}_{p,n}$ is transformed to a secondary data matrix $\mathbf{X}_{p,m}$ with realized niche states as columns and species as rows. In agreement with the attribute duality principle, the realized niche states are considered as variables in the analysis of species. Pairwise niche separation measures calculated according to eq. (3) are summarized in a dissimilarity matrix **D**, which is subjected to multidimensional scaling to reduce dimensionality of data. Niche relationships among the species are portrayed in few dimensions, the efficiency of this reduction being case-dependent. We selected a standard metric method (principal coordinates analysis, PCoA, Gower 1971) and nonmetric multidimensional scaling (NMDS, Kruskal 1964) for the evaluation of niche overlaps in the snail assemblages. This strategy allows for a subsequent comparative evaluation of ordination methods. Computations were performed using the SYN-TAX 5.02 package (Podani 1993, 1994).

Species groups ("guilds") were identified on the ordination diagrams by establishing dissimilarity thresholds, connecting points whose dissimilarity is lower than that threshold, and forming isolated, not necessarily complete subgraphs. The threshold was the dissimilarity value in the matrix below which only 5.0% of all the values in **D** fell. Since the dissimilarities in **D** are not independent (they are not taken from a random sample separately for each species pair) and sample size effects are ignored, this selection of values cannot be considered as a basis for a formal significance test, of course. Resampling the dissimilarity matrix and establishing a distribution of minimum dissimilarities in the samples would lead to a meaningful test. In the present case, however, we are not concerned with significance tests *per se*, and the selection of the lowest dissimilarities is satisfactory for identifying relatively compact species groups.

Results and their discussion

Combined ordination of species for all seres

To obtain a general picture on niche relationships for the entire study area, all the 39 species were analyzed based on milieu states derived from all the 247 forest samples. In the result of PCoA (Fig. 2) four groups can be distinguished (the dissimilarity threshold is 0.58 in this case). All species included in cluster 1 are xerophilous species of open areas (ecogroup D). Axis 1 (12%) clearly separates these groups from the other ecogroups (with some intermediate species of ecogroup D which are only loosely associated with group 1), suggesting that closure of vegetation and humidity are the principal ecological factors determining snail distribution. The second axis (accounting for 8% of the variance) separates the other three groups, but they are not so uniform as to the ecogroups of constituting species. Group 2 includes species from ecogroups B and E, whereas the other two groups are formed by species from ecogroups A and C. This distinction allows for an ecological interpretation of the second axis as well. Along this axis the quantity of water and shading are the most influential: ecogroups B and E are found in swamps and along watercourses, thus requiring freshwater, whereas species of ecogroups A and C require high humidity but not excess water on the surface. To allow for some biogeogaphical interpretation, we point out that group 4 contains species of gallery forests which migrate from Transylvania. Trophic categories (Table 2) do not coincide with these groups.

The results of non-metric multidimensional scaling (not shown) provide a less clear separation of the four groups of species. Although clusters 1 and 4 are well-separated, the species of the other two groups are mixed. Compared to the

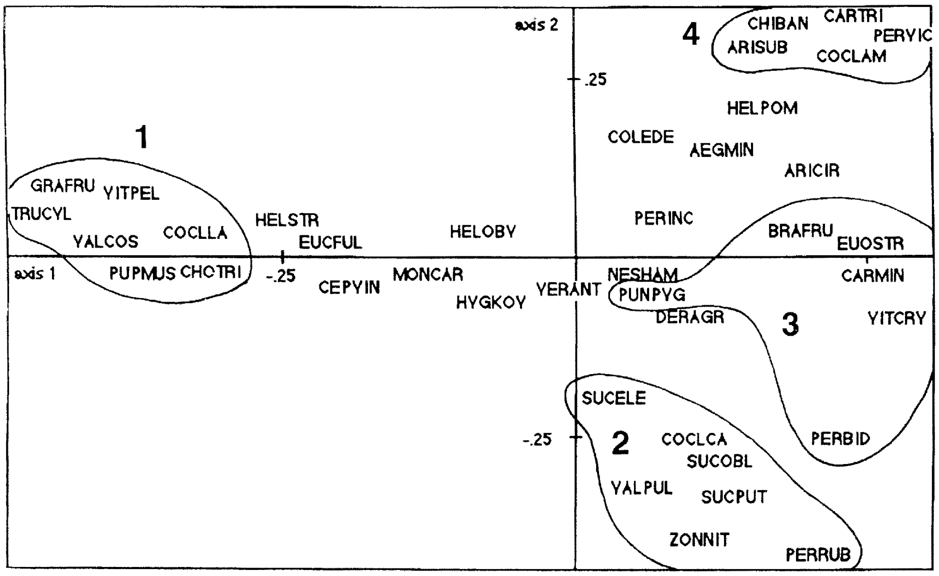

Figure 2. Principal coordinates ordination of all species based on the full data set. Species groups are delimited on the basis of the dissimilarity threshold.

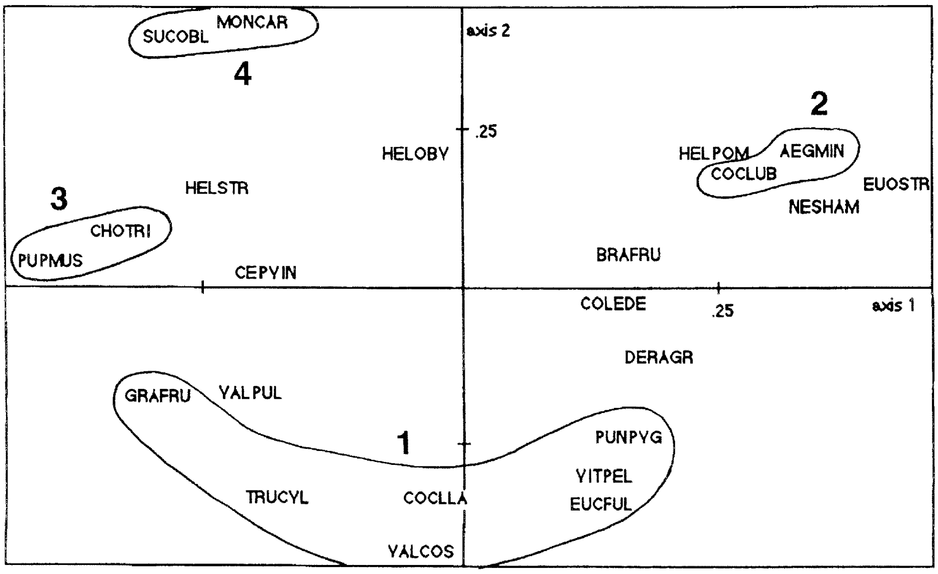

Figure 3. Principal coordinates ordination of 23 snail species appearing in the sand successional sere.

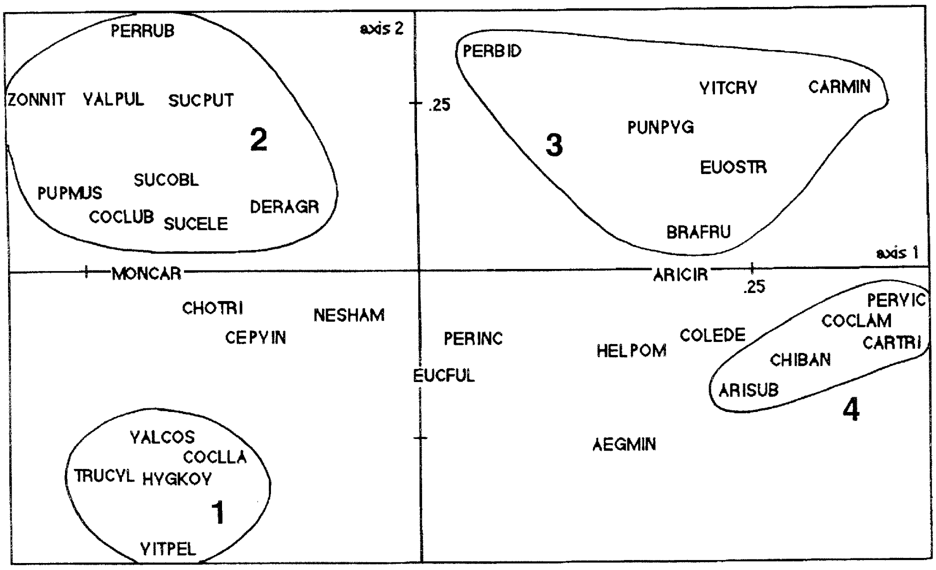

Figure 4. Principal coordinates ordination of the 35 species appearing in the forests of the mineralogic sere.

PCoA configuration, the NMDS solution forces a more even distribution of points in the two dimensions arbitrarily requested.

Ordination of species from the sand sere

The first two axes explain 30% of the variation in the PCoA ordination of 23 species appearing in the plant communities of the sand sere (Fig. 3). The application of the threshold ($d_{\max} = 0.39$) leads to a large cluster and three pairs of species. The large cluster and the pair of *Pupilla muscorum* - *Chondrula tridens* correspond to ecogroup D (xerophilous species) except that *Punctum pygmaeum* (from ecogroup A) also appears here. Its appearance among the xerophilous species is due to its presence in partly shaded grassland patches among scattered trees. *Pupilla muscorum* and *Chondrula tridens* appear in all stands of the *Festucetum* community type, as well as in the *Junipero-Populetum* (#10-11, Table 1), hence their closeness. The pair of *Succinea oblonga* and *Monacha cartusiana* characterizes poplar stands planted in temporarily wet depressions. *Aegopinella minor* and *Cochlicopa lubrica*, the third separate species pair is typical of the most humid part of the sand sere, i.e., the wettest stands of the *Convallario-Quercetum*. The axes cannot be interpreted so easily as in case of the total data set. There is, however, an obvious humidity gradient from the lower left to the upper right. The points are quite evenly positioned in the plane, which is even more so in the two-dimensional NMDS solution. The same observation holds true for the ordinations of species based on data from the other two seres.

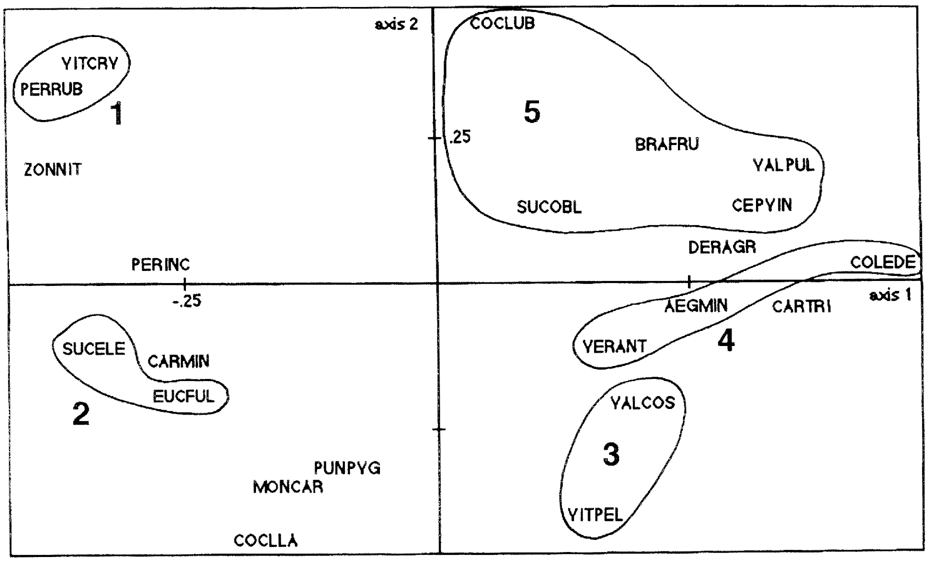

Figure 5. Principal coordinates ordination of 22 snail species present in the organogenic successional sere.

Ordination of species from the mineralogenic sere

The distance threshold used for creating the groups is in this case is 0.53; the percentage accounted for by the first two PCoA axes is 22% (Fig. 4). The four groups recognized here and the interpretation of axes are largely the same as in Fig. 2. The explanation is that sample size in the mineralogenic sere is 178, 72% of the total, and almost all species occur here. Nevertheless, there are some differences. Note, for example, the close association of *Hygromia kovacsi* (from ecogroup B) with the xerophilous species (group 1). In the analysis of the total data set this species was closer to group 2 (see also Fig. 2). Also, group 1 includes only four xerophilous species, the others being associated with different groups (e.g., *Pupilla muscorum* and *Cochlicopa lubricella* appear in group 2). Group 1 is a set of more hygrophilous species (ecogroups E and B), appearing mostly in willow stands, willow-poplar forests and degraded gallery forests. Species groups 3 and 4 characterize the gallery forests. The latter group reflects fauna transport by the rivers (Szamos, Upper Tisza) from Transylvania.

In the first stages of this plant community successional sere, species group 2 is dominant. Then, succession proceeds into two directions: habitat desiccation favours group 1, whereas under more hygrophilous conditions group 4 and subsequently group 3 become dominant.

Ordination of species from the organogenic sere

The first two PCoA axes (Fig. 5), accounting for 41% of the total variation, are the most efficient among all seres, although the number of species is only one less than in the sand sere. The dissimilarity threshold applied here is the lowest of all cases ($d_{\max}$=0.28). This produces groups of species with very high niche overlap. Only one cluster contains more than three species, this incorporates species of various ecogroups (C, D and E), thus providing counter-evidence about the ecological categorization. (Nevertheless, these species are typical of *Fraxino-Alnetum* communities of moderately wet habitats.) The other, smaller groups (for example, *Perforatella rubiginosa - Vitrea crystallina*) are also heterogeneous in this regard. The separation of the *Salici-Betuletum* and *Dryopteridi-Alnetum* communities is explained by the contrast between this pair, and that of *Succinea elegans - Euconulus fulvus*. Species of the remaining two clusters prefer drier microclimates. Identification of PCoA axes with environmental factors is difficult in this case.

Concluding remarks

We reported on a novel approach to the measurement of niche separation in milieu space in which axes correspond with combinations of categorical environmental variables, called milieu states. The fusion of original stands that have identical niche state leads to a reduced data matrix in which common milieu states receive higher weight than when the original data are subjected to analysis. The question of whether this implicit weighting is always meaningful merits future investigations, however. When dissimilarities among species in this milieu space are subjected to metric scaling, the milieu states are replaced by new orthogonal dimensions. These new axes express more efficiently the between-species relationships than any milieu state. Since they are in some sense "compound" factors, it is not expected that ordination axes can easily be interpreted as single environmental variables. It should also be also pointed out that our approach is not aimed at eliminating correlations between ecological factors: they remain in force when data are transformed into milieu states.

Ordination results suggest that the ecological categorization of species obtained previously by clustering (Table 2) does not explain sufficiently the interspecific relationships disclosed. This is even more so with the trophic categories which give very little complementary information in evaluating the species groups.

Further methodological observations concern the relative merits of PCoA and NMDS, when groups of points are delineated using dissimilarity thresholds. These groups are always more compact in the PCoA space than in the two-dimensional NMDS solutions, regardless of the efficiency of the PCoA ordination. The explanation is that NMDS considers only ordinal information conveyed by the dissimilarities, thus forcing a somewhat less clear-cut group structure upon the data. The low cumulative percentages of the variance on the first two PCoA axes indicate high stochastic variation in the data, which NMDS attempts to explain fully – even though in ordinal terms. Consequently, when meaningful information is responsible for a relatively low amount of variance in the data, NMDS is less efficient than PCoA. We used only a single measure of niche separation in the multivariate space, however. The comparison of various measures of multivariate niche separation under different circumstances remains a future task to further clarify relationships between PCoA and NMDS.

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