

COMPOSITION AND SPECIES RICHNESS OF MOLLUSCAN COMMUNITIES IN RELATION TO VEGETATION AND WATER CHEMISTRY IN THE WESTERN CARPATHIAN SPRING FENS: THE POOR–RICH GRADIENT

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ABSTRACT

Molluscs, vegetation and water chemistry were investigated at 48 spring fens situated in the borderland between the Czech Republic and Slovakia in 1997–2000. The purpose of this study was to test whether the gradient from mineral-poor to mineral-rich fens is reflected in the composition and species richness of mollusc communities, and to determine the importance of vegetation in predicting the mollusc community composition. A cluster analysis of mollusc communities separated the fens studied into five basic clusters which accord well with the results of detrended correspondence analysis (DCA). These clusters are arranged along the first DCA axis following the poor–rich trophic gradient. Ca, Mg, Fe, K, pH and conductivity are strongly correlated with the first DCA axis of the mollusc data. Similarly, Ca, Mg, Fe, pH and conductivity explain a substantial part of species-data variation, as verified by separated canonical correspondence analyses (CCAs) with a single variable. When sites with *Sphagnum* spp. were excluded, no significant correlations with K, pH and conductivity were found, whereas the significance of correlation with Fe increased markedly. Site classifications based on mollusc data are applicable to vegetation data and vice versa. Vegetation composition is a more important factor for explaining the variation in mollusc species than water chemistry when both are included in two separated CCAs as constraining variables. We found a linear correlation between mollusc species richness and water calcium concentration in the poor fens. In the rich fens, such a correlation was not found, and species richness was dependent on other abiotic and biotic factors, namely the Fe concentration and the water regime.

INTRODUCTION

Mire and spring ecosystems have always been of interest to European and North-American plant ecologists and phytosociologists (e.g. Malmer, 1986; Bragazza & Gerdol, 1999; Vitt, 2000; Wheeler & Proctor, 2000; Økland, Økland & Rydgren, 2001). The shared feature of their results is the existence of a gradient from mineral-poor acidic to mineral-rich alkaline sites, called the poor–rich trophic gradient (Malmer, 1986; Gerdol, 1995; Hájek, 2002; Hájek, Hekera & Hájková, 2002), which is responsible for most of the floristic variance. On this gradient, the following divisions are the basis of mire classification: ombrotrophic bogs, poor fens (transitional mires) and rich fens. In several areas, the calcium saturation ratio in the Ca-richest springs results in tufa formation (see Jäger & Ložek, 1968; Pentecost, 1992; Almendinger & Leete, 1998).

In Western Carpathian fens, the poor–rich gradient can be identified based on phytosociological data (vascular plants, bryophytes; Hájek *et al.*, 2002), as well as on algological data (Pouličeková, Bogdanová, Hekera, & Hájková, 2001). It is assumed that this gradient is also reflected by the diversity and composition of mollusc communities, with calcium content and pH as the major factors. Numerous authors (e.g. Wärebörn, 1969, 1970; Waldén, 1981; Pokryszko, 1993; Millar & Waite, 1999) have found a strong positive correlation between the pH value and Ca content of soil or litter and the number of species and/or individuals.

Molluscs not only need calcium for the growth of their shells and other physiological processes (see Wärebörn, 1970), but

lack of calcium may also restrict their reproduction (Wärebörn, 1979). Molluscs are able to assimilate calcite (CaCO_3); Ca and CO_3 ions are utilized to build the shell (Wärebörn, 1969). Therefore, molluscs reach higher abundance and species richness in calcareous areas. However, it is known that many mollusc species live in habitats with no CaCO_3 (e.g. Ložek, 1962; Wärebörn, 1969; Bishop, 1980). Field and laboratory studies showed that in these habitats molluscs are able to obtain the necessary calcium from leaf litter of trees (ash, lime, maple and elm), which contain calcium in the easily soluble citrate form (see Wärebörn, 1969; von Proschwitz, 1993).

There is a long tradition of molluscan studies in the Czech Republic and Slovakia, but spring and fen ecosystems have only rarely been investigated. The purpose of most of the malacological studies was to discover populations of rare and relict snails. Thus, these studies covered only petrifying springs, which are the richest from the malacological point of view (e.g. Ložek, 1971, 1982; Ložek & Šteffek, 1983; Luživjanská, 1992). There are only limited faunistic data available from Western Carpathian petrifying springs (Šteffek, 1992).

In Europe, molluscan ecology with respect to environmental factors (particularly soil chemistry) has been intensively studied mainly in various forest types of oligotrophic areas (e.g. Bishop, 1977; Bishop, 1980; Waldén, 1981; Wärebörn, 1969; Wärebörn, 1992; von Proschwitz, 1993), but no link was made to ecological factors influencing the composition of vegetation. Malacocenoses of three different hydrological fen types in southern Norway, strongly influenced by the boreal species pool, were studied by Pokryszko (1993) with respect to litter pH, Ca content of the litter and altitude. However, these habitats represent

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only a small part of ecological variation in spring fens. Relationships between molluscs and plant communities, and their dependence on spring water chemistry over the entire poor–rich gradient, have never been investigated.

The objective of this paper is to compare malacological and vegetation data along the poor–rich gradient in springs with known water chemistry, and thus to test the existence of a poor–rich mire gradient in the composition of molluscan communities, and also the hypothesis of increasing molluscan species richness towards Ca-rich fens. Our second hypothesis presumes that vegetation composition reflecting major complex environmental gradients explains more of the variation in molluscan data than do purely chemical factors. Thus, we want to test whether or not vegetation composition can predict the quality of molluscan taxocenoses.

METHODS

The majority of fens in the area of study were investigated. Only sites distant from roads and tracks were excluded to avoid long delays between sampling and laboratory analyses. The number of extremely acid *Sphagnum*-fens studied was reduced compared with the previous botanical research (Hájek *et al.*, 2002) due to the total absence of molluscs there. Fieldwork was conducted from 1997 to 2000.

Study area

The study of 48 sites was performed in the borderland between the Czech Republic and Slovakia, on the margin of the Western Carpathians (Fig. 1). The bedrock of this area is formed by alternating claystone and sandstone layers (so called Magura and Silesian Flysch). The individual beds are mostly situated in narrow strips running from the south-west to the north-east (Poprawa & Nemčok, 1988). Marls, claystone, limestone and calcareous sandstone prevail in the south-western part of the study area (the White Carpathian Unit), where spring water is extremely mineral-rich. Flysch beds belonging to the Rača Unit (springs were investigated mainly in Vsetín and Solán beds) and Bystrica Unit (springs were investigated in Zlín and LACKO beds) occur towards the north-east and to the eastern edge of the study area. The northern part of the borderland (the Silesian

Unit) is mostly of decalcified, iron-cemented sandstone from Istebna and Godula beds, bordered by very narrow strips of Submenilitic and Krosno beds. Climatic differences in mean precipitation (increasing to the north-east) and temperature values (increasing to the south-west) exist within the study area. The altitudes of the investigated sites vary between 390 m (U Baladů, White Carpathians) and 905 m a.s.l. (Biely Kríž, Moravskoslezské Beskydy Mountains).

We found the westernmost Carpathians to be a suitable model region because of the diverse chemical composition of aquifers, which influence the spring biota composition primarily through their water chemistry (Hájek *et al.*, 2002; Pouličková *et al.*, 2001).

Study sites

According to the indirect ordination of vegetation samples (Hájek *et al.*, 2002), the spring fens under study can be divided along the poor–rich gradient into the following basic types: (1) extremely rich fens with tufa formation (petrifying springs), dominated by the moss *Cratoneuron commutatum*, low sedges and other Cyperaceae—the *Carici flavae-Cratoneuretum* association (two subtypes are distinguishable within this fen: low-productive springs dominated by *Carex* and *Eriophorum* species in the herb layer and medium-productive types with *Cirsium rivulare* and other meadow herbs and grasses)—20 sites; (2) brown-moss rich fens without tufa formation, dominated by the moss *Drepanocladus revolvens* agg. (Hájková & Hájek, 2000)—the *Valeriano simplicifoliae-Caricetum flavae* association—17 sites; (3) rich *Sphagnum*-fens with the occurrence of calcitolerant *Sphagnum* species (*S. warnstorffii*, *S. contortum*, *S. teres*) together with species of mineral-rich fens (*Eriophorum latifolium*, *Eleocharis quinqueflora*, *Parnassia palustris*, *Juncus articulatus*, *Homalothecium nitens*, *Campylium stellatum*)—the *Sphagno warnstorffii-Eriophoretum latifolii* association—three sites, generally a rare habitat in the study area; (4) poor *Sphagnum*-fens, dominated by *Sphagnum recurvum* agg.—the *Carici echinatae-Sphagnetum* association (they can be divided into slightly acidic poor fens dominated by *S. flexuosum* and acidic fens with *S. fallax* and some bog species)—seven sites (see Hájek & Háberová, 2001, 2002). The majority of these spring fens are young; they developed after the settlement-induced deforestation of wooded springs (Rybníček & Rybníčková, 1995; Hájková & Hájek, 2002).

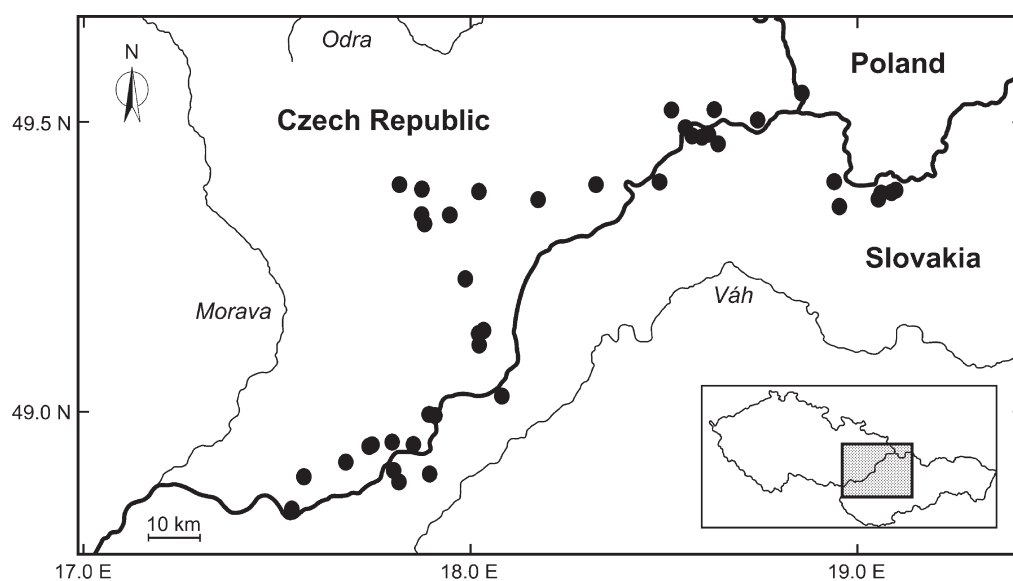


Figure 1. Position of sampling sites in the study area.

Vegetation

At all sites, the occurrence and cover of species were recorded on the nine-grade Braun-Blanquet scale (van der Maarel, 1979) for both vascular plants and bryophytes (i.e. a phytosociological relevé, see Westhoff & van der Maarel, 1978). Only one relevé per spring fen was analysed. The malacological litter samples were taken in the vegetation relevé plots (c. 16 m² each). The names of the plant communities are given according to Valachovič (2001), vascular plants and bryophytes according to Marhold (1998) and Frey, Frahm, Fischer & Lobin (1995).

Molluscs

In each site, one sample of 12 l volume, comprising the upper soil layer including litter and herbaceous vegetation, was collected. The samples were washed through a bowl-shaped sieve (mesh size 0.5 mm) to wash out the fine clay particles (which otherwise would have caused all the material to stick together after drying). The coarse plant matter was also picked out as described in detail by Horsák (2003). After drying, the material was separated by sieving into fractions of different particle size, from which the mollusc shells were extracted by hand-sorting under a binocular microscope. Samples were not collected randomly, as they were meant to reflect the vegetation composition and structure as the vegetation relevé. The primary goal was always to detect the species at the site as exhaustively as possible. Relative abundance was calculated from live specimens, and empty shells with an entire periostracum. The mollusc species names follow Juříčková, Horsák & Beran (2001).

Water chemistry

August 2000 was chosen as a suitable month for obtaining representative values for the concentrations of major elements in the spring fens (Hájek *et al.*, 2002). Water samples were taken from the micro-sites best supplied by water in the central parts of the springs. For ion concentration determination, conservants were added to the subdivided samples immediately after the sampling: for metallic elements, 0.5 ml of concentrated HNO₃ per 100 ml of sample; for anions, 3 ml of chloroform per 1000 ml (Hájek *et al.*, 2002). Water conductivity at 20°C, pH at 20°C and redox potential (argentochlorid reference) were measured *in situ* using portable instruments with automatic temperature compensation (CM 101 and PH 119, Snail Instruments). Conductivity caused by H⁺ ions in acid waters was subtracted (Sjörs, 1952).

Statistical analyses

The data for mollusc percentage abundance were transformed into a nine-grade scale corresponding to the scale used in vegetation analyses separately for the two major ecological groups, i.e. terrestrial and aquatic molluscs. Mollusc species found on less than four sites were omitted from the data set used for statistical analyses. These were mostly cases where no live specimens were found and the shells belonged to snails that were considered to inhabit adjacent biotopes, but were not living in the fens [e.g. *Orcula dolium* (Draparnaud)]. All slugs were also omitted (a total of five species), as their occurrence and abundance are most difficult to assess by the method used. Mollusc communities were classified by cluster analysis (Group average) using the Baroni-Urbani-Buser coefficient, which takes the absence of species in some habitats into account. The SYN-TAX package was used for this analysis (Podani, 1993).

The Kolmogorov-Smirnov test confirmed the normal or uniform distribution of all measured variables and, therefore, no transformation was undertaken (cf. Hájek *et al.*, 2002). The

CANOCO 4 package was used for multivariate analyses (ter Braak & Šmilauer, 1998). The species-by-sample matrices (vegetation and mollusc data separately) were subjected to detrended correspondence analysis (DCA), using default options. The ordination site scores obtained were correlated with each other and with environmental factors using Pearson's correlation coefficient. A principal component analysis (PCA) of the chemical data was then carried out. The variation partitioning approach (Borcard, Legendre & Drapeau, 1992; Økland & Eilertsen, 1994; Økland, 1999) was used to determine the relative amount of variation in mollusc data explained by two different constraining variables (vegetation, water chemistry) in single-variable CCAs. The vegetation composition was expressed as DCA ordination scores for each site (axes 1–4). Covariables (vegetation and water chemistry) were used to separate variation caused by both constraining variables together, from variation explained by only one constraining variable. The relative amount of variation caused by both variables together, by vegetation only and by water chemistry only, were compared. The Monte Carlo test (ter Braak & Šmilauer, 1998) was used for testing the significance of the canonical axes.

RESULTS

A total of 57 mollusc species were found; of these, 51 were terrestrial and six aquatic (four snails and two bivalves). In total, more than 35,000 specimens were collected.

Classification of investigated sites based on mollusc communities

Cluster analyses of mollusc communities, based on presence/absence data, separated the investigated sites into five basic clusters (Fig. 2).

The first cluster consists exclusively of extremely rich fens with tufa formation (petrifying springs). Water chemistry favourable for molluscs (high calcium concentration and pH) and readily available supply of calcium from tufa are the main reasons for the high species richness [maximum 32 species, median 24 (21 terrestrial and three aquatic mollusc species)]. Due to precipitated tufa there are small dry patches within the fen, which support xerophilous snails [e.g. *Cochlicopa lubricella* (Rossmässler) and *Truncatellina cylindrica* (A. Férussac)]. These have not been found in the other fens. Eleven snail species were recorded only in the rich fens. Besides the xerophilous species mentioned above, these were species with high requirement for calcium, some of them critically endangered [e.g. *Vertigo moulinsiana* (Dupuy)].

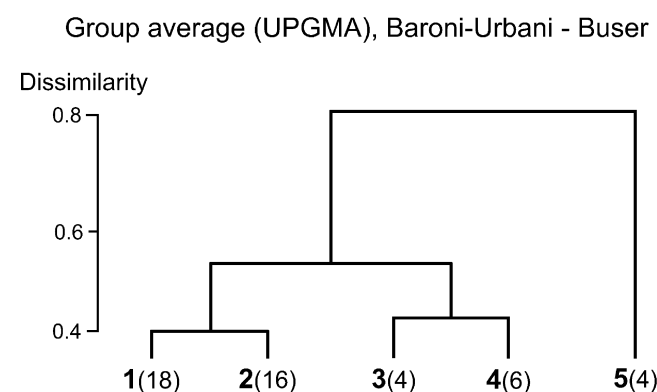


Figure 2. Cluster analysis of mollusc communities based on presence/absence data (Baroni-Urbani-Buser coefficient). Number of sites included in each cluster given in parentheses. For definition of clusters see text.

The second cluster includes brown-moss rich fens without tufa formation. Two sites with some tufa formation fell into this cluster. The mollusc communities in most of these sites were species-rich (maximum 19 species), due particularly to the high calcium concentrations in the water. The median species richness of these fens was 17 (14 terrestrial and three aquatic) species. A high share of meadow species [*Cochlicopa lubrica* (O.F. Müller) and *Perpolita hammonis* (Ström)] and a rather high percentage of *Vertigo substriata* (Jeffreys) were characteristic of this cluster.

The third cluster includes brown-moss rich fens with very low inclination, mostly located in brook alluvia, extremely water-soaked and with high iron content (mainly precipitated but also dissolved). Thirteen (eight terrestrial and five aquatic) mollusc species were recorded in each of the sites included in this cluster. The communities differed from those of the other clusters by the high percentage of aquatic species and of highly hygrophilous terrestrial snails [e.g. *Vertigo antivertigo* (Draparnaud)].

The fourth cluster includes both rich and poor *Sphagnum*-fens. In the latter, water calcium concentration does not decrease below 10 mg/l. The site with the highest species richness hosted nine species (four terrestrial and five aquatic). Only four aquatic molluscs occurred in the most unfavourable site. At most of the sites, three terrestrial [*Vertigo substriata*, *Succinea putris* (Linnaeus), and *Perpolita hammonis*] and three aquatic molluscs [*Galba truncatula* (O.F. Müller), *Pisidium casertanum* (Poli), and *P. personatum* Malm] were encountered.

The fifth cluster includes poor *Sphagnum*-fens, where very low water calcium concentration was measured (less than 4 mg/l). Only a single aquatic bivalve, *Pisidium casertanum*, was able to exist there. Therefore, this cluster is the most dissimilar to the others (Fig. 2). These fens with small water pools present a favourable environment for *Pisidium casertanum*, which may reach high population densities.

The mollusc species used in statistical analyses and recorded in all sites belonging to a given cluster were combined to give a comparison of the mollusc communities found in the above-mentioned five clusters; a total number of individuals, percentage of individuals, and number of sites in which the species was found (in that cluster) is given for each species (Table 1).

The clusters 1 and 2 from rich sites are the most similar, and the transition between them is gradual; hence, two sites on

which tufa precipitated were included in cluster 2. These were initial successional stages of petrifying springs (cluster 1), but the communities were closer to the others of cluster 2, especially in the absence of species strictly linked to the petrifying springs. The species composition of the fens belonging to cluster 3 is very similar to that of cluster 2. The mollusc communities of these sites (cluster 3) are distinctly affected by the water regime and probably also by the higher Fe content.

Data were processed by indirect unimodal analysis—detrended correspondence analysis (DCA). The sum of all eigenvalues is 1.326. The eigenvalue of the first ordination axis is 0.289, that of the second axis is 0.131. Cumulative percentage variance of the species data explained on the first axis is 21.8%, that on the second axis is 31.7%. The result of the DCA analysis is in very good accordance with the result of the cluster analysis (Fig. 3). The sites, classified according to species composition, are arranged along the 1st axis in the DCA diagram following the poor–rich trophic gradient. This is also in compliance with the correlation between DCA site score and the major chemical factors measured (Table 2, Fig. 4).

Molluscs and vegetation

The vegetation data accord well with the mollusc data. The site classification based on molluscs reflects differences in vegetation and vice versa, with the exception of mollusc cluster 3, which has poor relationship with vegetation composition (see Fig. 5). The general trend suggested by visual comparison of both DCA ordination plots is the existence of two major gradients in mollusc species data, of which only the main gradient (first axis) corresponds with the main gradient in vegetation data (Figs 3 and 5). In the ordination plot of vegetation data, the ordination scores of the sites belonging to the clusters 1–3 are close to each other on the second axis (Fig. 5). This composition is verified by Pearson's correlation. The site scores along the 1st DCA axes of plants and molluscs correlate strongly (Table 2), whereas the second axis does not correlate significantly ($P > 0.05$).

The concentrations of potassium and iron seem to be correlated more with mollusc community composition than with vegetation composition when the total gradient is analysed (Table 2). Water pH and conductivity still correlate with first DCA 'vegetation' axis when *Sphagnum*-fens are excluded. This

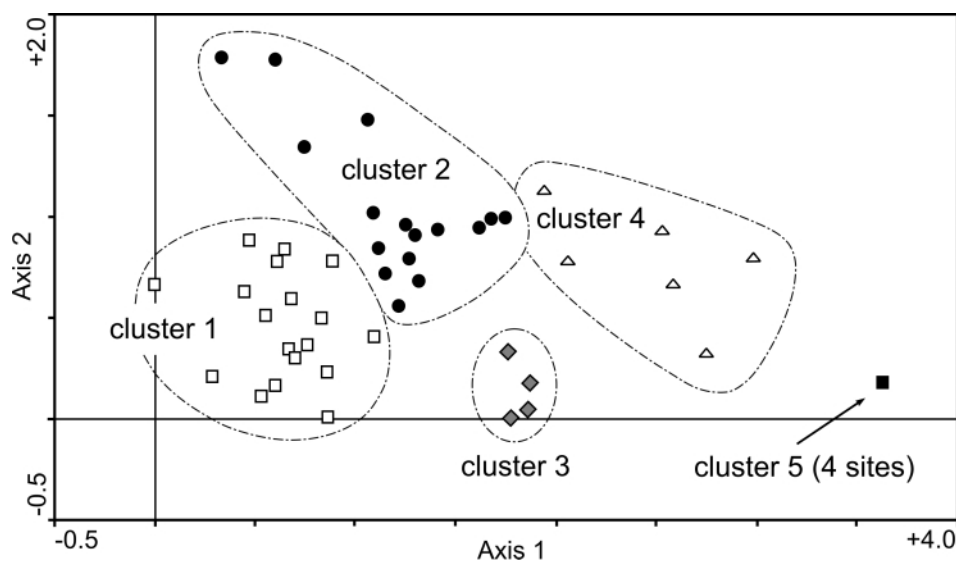


Figure 3. Detrended correspondence analysis (DCA) of mollusc communities: ordination plot of sites on the first two DCA axes. Classification of investigated sites based on cluster analysis (see Fig. 2).

MOLLUSCS IN CARPATHIAN SPRING FENS

Table 1. List of mollusc species found in all sites belonging to a given cluster and used in statistic analyses.

| | Clusters | | | | | | | | | | | | |
|---|----------|-------|----|------|-------|----|------|-------|---|------|-------|---|-----|
| | 1 | | 2 | | 3 | | 4 | | 5 | | | | |
| Terrestrial species | | | | | | | | | | | | | |
| <i>Platyla polita</i> (Hartmann, 1840) | 15 | 0.12 | 4 | 14 | 0.50 | 3 | – | – | – | – | – | – | – |
| <i>Carychium minimum</i> Müll., 1774 | 3291 | 27.12 | 18 | 258 | 9.29 | 13 | 54 | 29.19 | 4 | – | – | – | – |
| <i>Carychium tridentatum</i> (Risso, 1826) | 1090 | 8.98 | 15 | 589 | 21.20 | 15 | – | – | 2 | 4.44 | 1 | – | – |
| <i>Cochlicopa lubrica</i> (Müll., 1774) | 677 | 5.58 | 18 | 409 | 14.72 | 16 | 9 | 4.86 | 3 | – | – | – | – |
| <i>Cochlicopa lubricella</i> (Rssm., 1835) | 5 | 0.04 | 4 | – | – | – | – | – | – | – | – | – | – |
| <i>Vallonia costata</i> (Müll., 1774) | 121 | 1.00 | 11 | – | – | – | – | – | – | – | – | – | – |
| <i>Vallonia pulchella</i> (Müll., 1774) | 281 | 2.32 | 18 | 96 | 3.46 | 12 | 10 | 5.41 | 2 | – | – | – | – |
| <i>Acanthinula aculeata</i> (Müll., 1774) | 46 | 0.38 | 6 | – | – | – | – | – | – | – | – | – | – |
| <i>Columella edentula</i> (Drap., 1805) | 57 | 0.47 | 7 | 51 | 1.84 | 6 | – | – | – | – | – | – | – |
| <i>Truncatellina cylindrica</i> (Fér., 1807) | 10 | 0.08 | 4 | – | – | – | – | – | – | – | – | – | – |
| <i>Vertigo angustior</i> Jeffreys, 1830 | 1285 | 10.59 | 14 | – | – | – | – | – | – | – | – | – | – |
| <i>Vertigo antivertigo</i> (Drap., 1801) | 692 | 5.70 | 17 | 160 | 5.76 | 10 | 51 | 27.57 | 4 | 1 | 2.22 | 1 | – |
| <i>Vertigo moulinsiana</i> (Dupuy, 1849) | 155 | 1.28 | 6 | – | – | – | – | – | – | – | – | – | – |
| <i>Vertigo pygmaea</i> (Drap., 1801) | 801 | 6.60 | 18 | 180 | 6.48 | 12 | 3 | 1.62 | 2 | – | – | – | – |
| <i>Vertigo substriata</i> (Jeffreys, 1833) | 442 | 3.64 | 12 | 126 | 4.54 | 15 | 4 | 2.16 | 2 | 5 | 11.11 | 4 | – |
| <i>Succinella oblonga</i> (Drap., 1801) | 305 | 2.51 | 11 | – | – | – | 1 | 0.54 | 1 | – | – | – | – |
| <i>Succinea putris</i> (L., 1758) | 146 | 1.20 | 8 | 261 | 9.40 | 12 | 21 | 11.35 | 4 | 23 | 51.11 | 5 | – |
| <i>Oxyloma elegans</i> (Risso, 1826) | 151 | 1.24 | 7 | 10 | 0.36 | 1 | 9 | 4.86 | 1 | – | – | – | – |
| <i>Punctum pygmaeum</i> (Drap., 1801) | 619 | 5.10 | 18 | 96 | 3.46 | 12 | – | – | – | – | – | – | – |
| <i>Zonitoides nitidus</i> (Müll., 1774) | 339 | 2.79 | 4 | 12 | 0.43 | 1 | 13 | 7.03 | 4 | – | – | – | – |
| <i>Euconulus fulvus</i> (Müll., 1774) | 580 | 4.78 | 17 | 166 | 5.98 | 14 | 1 | 0.54 | 1 | 2 | 4.44 | 1 | – |
| <i>Vitrina pellucida</i> (Müll., 1774) | 29 | 0.24 | 9 | 21 | 0.76 | 7 | 1 | 0.54 | 1 | – | – | – | – |
| <i>Vitrea contracta</i> (West., 1871) | 52 | 0.43 | 7 | – | – | – | – | – | – | – | – | – | – |
| <i>Vitrea crystallina</i> (Müll., 1774) | 69 | 0.57 | 6 | 3 | 0.11 | 1 | – | – | 1 | 2.22 | 1 | – | – |
| <i>Vitrea diaphana</i> (Studer, 1820) | 29 | 0.24 | 4 | 4 | 0.14 | 2 | – | – | – | – | – | – | – |
| <i>Aegopinella minor</i> (Stabile, 1864) | 11 | 0.09 | 5 | – | – | – | – | – | – | – | – | – | – |
| <i>Aegopinella pura</i> (Alder, 1830) | 141 | 1.16 | 10 | 46 | 1.66 | 7 | – | – | – | – | – | – | – |
| <i>Perpolita hammonis</i> (Ström, 1765) | 356 | 2.93 | 10 | 236 | 8.50 | 16 | 2 | 1.08 | 1 | 11 | 24.44 | 5 | – |
| <i>Oxychilus glaber</i> (Rssm., 1835) | 7 | 0.06 | 4 | – | – | – | – | – | – | – | – | – | – |
| <i>Daudebardia brevipes</i> (Drap., 1805) | 52 | 0.43 | 10 | 5 | 0.18 | 3 | – | – | – | – | – | – | – |
| <i>Daudebardia rufa</i> (Drap., 1805) | 28 | 0.23 | 6 | 9 | 0.32 | 5 | – | – | – | – | – | – | – |
| <i>Euomphalia strigella</i> (Drap., 1801) | 4 | 0.03 | 4 | – | – | – | – | – | – | – | – | – | – |
| <i>Plicutera lubomirskii</i> (Ślósarskii, 1881) | 82 | 0.68 | 12 | 2 | 0.07 | 1 | – | – | – | – | – | – | – |
| <i>Perforatella bidentata</i> (Gmelin, 1791) | 100 | 0.82 | 4 | 1 | 0.04 | 1 | – | – | – | – | – | – | – |
| <i>Monachoides incarnatus</i> (Müll., 1774) | 47 | 0.39 | 13 | 19 | 0.68 | 9 | – | – | – | – | – | – | – |
| <i>Monachoides vicinus</i> (Rssm., 1842) | 7 | 0.06 | 3 | 3 | 0.11 | 1 | – | – | – | – | – | – | – |
| <i>Arianta arbustorum</i> (L., 1758) | 6 | 0.05 | 3 | 1 | 0.04 | 1 | 6 | 3.24 | 1 | – | – | – | – |
| <i>Cepaea vindobonensis</i> (Fér., 1821) | 8 | 0.07 | 4 | – | – | – | – | – | – | – | – | – | – |
| Total no. of individuals for each cluster | 12136 | | | 2778 | | | 185 | | | 45 | | | 0 |
| Aquatic species | | | | | | | | | | | | | |
| <i>Bythinella austriaca</i> s.lat. (Fröld., 1857) | 3783 | 62.51 | 16 | 3583 | 55.23 | 9 | 394 | 7.75 | 3 | 624 | 26.78 | 1 | – |
| <i>Galba truncatula</i> (Müll., 1774) | 299 | 4.94 | 16 | 180 | 2.77 | 12 | 70 | 1.38 | 4 | 38 | 1.63 | 5 | – |
| <i>Radix peregra</i> (Müll., 1774) | 4 | 0.07 | 2 | 36 | 0.55 | 3 | 49 | 0.96 | 4 | 35 | 1.50 | 3 | – |
| <i>Anisus leucostoma</i> (Millet, 1813) | 121 | 2.00 | 1 | 1 | 0.02 | 1 | 13 | 0.26 | 2 | – | – | – | – |
| <i>Pisidium casertanum</i> (Poli, 1791) | 258 | 4.26 | 7 | 374 | 5.76 | 9 | 1139 | 22.39 | 4 | 970 | 41.63 | 5 | 216 |
| <i>Pisidium personatum</i> Malm, 1855 | 1587 | 26.22 | 15 | 2314 | 35.67 | 14 | 3421 | 67.26 | 4 | 663 | 28.45 | 5 | – |
| Total no. of individuals for each cluster | 6052 | | | 6488 | | | 5086 | | | 2330 | | | 216 |

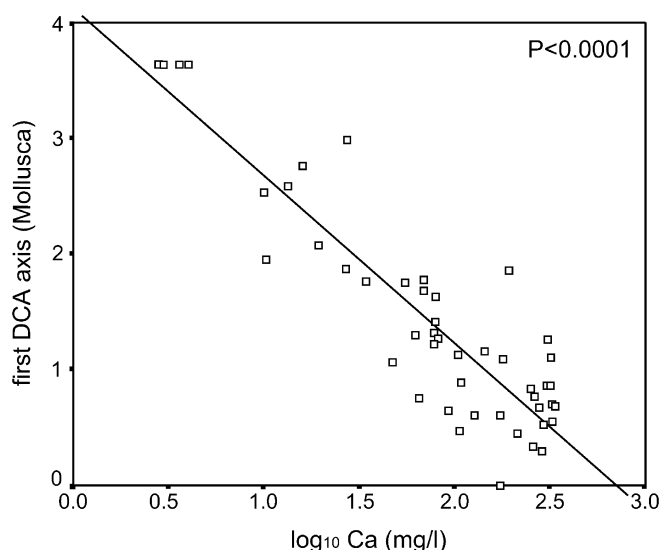
Column 1 gives the total number of collected individuals; column 2 gives their dominance (%); column 3 gives the number of sites with the occurrence of the species for each cluster.

Clusters: **1**, rich fens with tufa formation (18 sites); **2**, brown-moss rich fens without tufa formation (16 sites); **3**, brown-moss rich fens with very low inclination, mostly located in brook alluvia, and extremely water-soaked (four sites); **4**, rich *Sphagnum*-fens (six sites); **5**, poor *Sphagnum*-fens (four sites).

Table 2. Pearson's correlation coefficients between DCA site score on the first axis (for molluscs, DCA M.1 and vegetation, DCA V.1) and measured chemical variables and their significance values.

| | A (entire gradient) | | | | B (short gradient) | | | |
|-----------------|---------------------|------------------------|----------|-------------------------|--------------------|--------|---------|-----------------------|
| | DCA.M.1 | P | DCA.V.1 | P | DCA.M.1 | P | DCA.V.1 | P |
| DCA.M.2 | – | – | –0.019 | 0.899 | – | – | 0.506 | 0.002* |
| DCA.V.1 | 0.905 | <1.10 ⁻¹⁶ * | – | – | 0.556 | <0.01* | – | – |
| DCA.V.2 | –0.132 | 0.373 | – | – | –0.310 | 0.074 | – | – |
| Ca | –0.687 | <1.10 ⁻⁷ * | –0.785 | <1.10 ⁻¹² * | –0.433 | 0.011* | –0.667 | <1.10 ⁻⁴ * |
| Mg | –0.655 | <1.10 ⁻⁶ * | –0.67427 | <0.1.10 ⁻⁶ * | –0.393 | 0.021* | –0.347 | 0.045* |
| Fe | 0.333 | 0.021* | 0.295 | 0.041* | 0.442 | 0.009* | 0.562 | <0.01* |
| K | –0.347 | 0.016* | –0.278 | 0.056 | 0.042 | 0.813 | 0.254 | 0.147 |
| Na | –0.416 | 0.003* | –0.425 | 0.003* | 0.109 | 0.54 | 0.145 | 0.414 |
| Si | –0.252 | 0.084 | –0.17 | 0.249 | 0.026 | 0.885 | 0.269 | 0.124 |
| SO ₄ | –0.149 | 0.312 | –0.267 | 0.066 | –0.023 | 0.897 | –0.393 | 0.021* |
| Cl | 0.060 | 0.686 | –0.015 | 0.917 | 0.026 | 0.883 | –0.230 | 0.191 |
| pH | –0.618 | <1.10 ⁻⁵ * | –0.73 | <1.10 ⁻⁸ * | –0.141 | 0.425 | –0.484 | 0.004* |
| Conduct. | –0.658 | <1.10 ⁻⁶ * | –0.787 | <1.10 ⁻¹² * | –0.176 | 0.320 | –0.615 | <0.01* |
| Redox | –0.022 | 0.880 | –0.124 | 0.400 | –0.151 | 0.393 | –0.213 | 0.226 |

A, the entire poor–rich gradient (all sites, $N = 48$), B, short gradient (without sites with occurrence of *Sphagnum* spp., $N = 34$). Asterisk indicates significant probability values (<0.05).

**Figure 4.** The linear regression of DCA site scores (first axis of mollusc data) on water calcium concentration (logarithmically transformed $Y = \log_{10}$).

correlation has not been, however, found for mollusc data (Table 2).

Separated CCAs with a single variable confirm that vegetation composition is the factor explains the highest percentage of variation in mollusc species data (26% of variance, see Table 3). Vegetation and water chemistry together explain 35 % of mollusc data variation. The remaining 65% represent unexplained variation, which involves also lack-of-fit of data to the unimodal model used (Økland, 1999). When the influence of total chemistry is eliminated as a co-variable, vegetation composition still significantly explains 13% of the variation in mollusc data. Water chemistry data explain less variation in both cases, i.e. when evaluated separately and when evaluated with vegetation composition as a co-variable (see Table 3). Thus, vegetation can reliably predict the composition of the mollusc community, and do so better than those water chemistry parameters that are traditionally used in ecology.

Table 3. Percentage variance of mollusc species data explained by each variable in separated CCAs.

| | Without co-variable | Co-variable(s) | | |
|--------------|---------------------|----------------|------------------------|-----------------------|
| | | Ca | Vegetation site scores | Chemistry site scores |
| Ca | 10.2%*** | – | NS | – |
| Fe | 4.3%** | NS | NS | – |
| Mg | 8.5%*** | NS | NS | – |
| Sulphates | NS | NS | NS* | – |
| K | NS* | 3.7%** | NS* | – |
| Na | NS | NS | NS | – |
| pH | 11.8%*** | 6.7%*** | NS* | – |
| Redox | NS | NS | NS | – |
| Si | NS | NS | NS | – |
| Conductivity | 10.6%*** | 5%*** | NS | – |
| Vegetation | 26.1%*** | 13.4%*** | – | 13%*** |
| Chemistry | 22.2%*** | 9.7%** | (8.4%) NS | – |

Significance of the Monte Carlo test of first or all canonical axes: * $P < 0.1$; ** $P < 0.05$; *** $P < 0.005$; NS, not significant.

Relations between water chemistry and mollusc community composition

Ca, Mg, Fe, K, pH and conductivity are strongly correlated with the 1st DCA axis of mollusc data (Tables 2, 3), while Fe is negatively correlated with Ca, Mg, K, pH and conductivity. However, when *Sphagnum* sites, the least favourable for molluscs ($n = 14$) are excluded, there are no significant correlations with K, pH and conductivity whereas significance of correlation with Fe increased markedly (Table 2).

According to the results of separated CACs, a large part of entire species composition variability of mollusc communities is explained by the following variables, in this order: pH, conductivity, Ca, Mg and Fe (Table 3). The importance of other measured ion concentrations is not significant, as indicated by non-significant Monte Carlo test. CCA with a single variable, and Ca as a covariable also showed that K, pH and conductivity

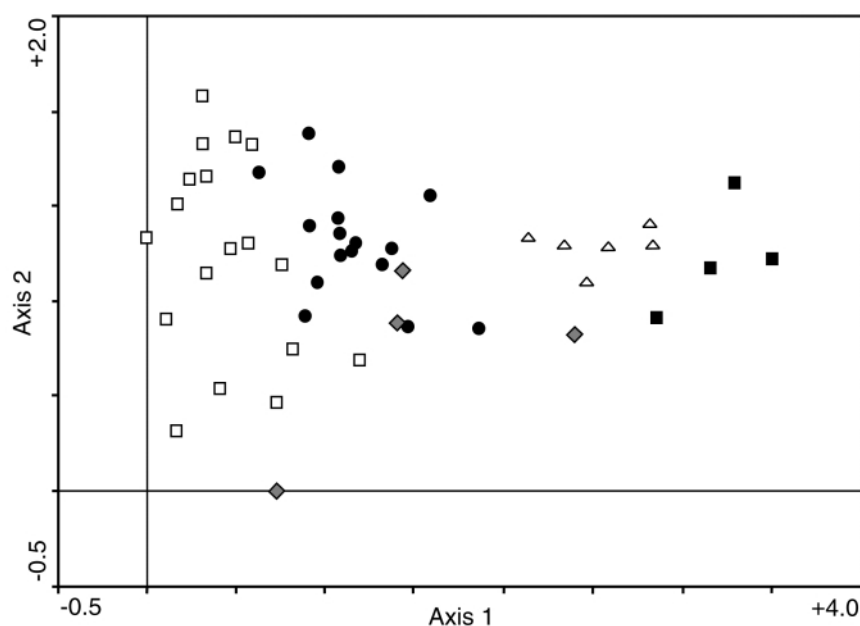


Figure 5. Detrended correspondence analysis (DCA) of vegetation relevés: ordination plot of sites on the first two DCA axes. Classification of investigated sites based on classification of mollusc communities (see Fig. 2), cluster symbols as in Figure 3.

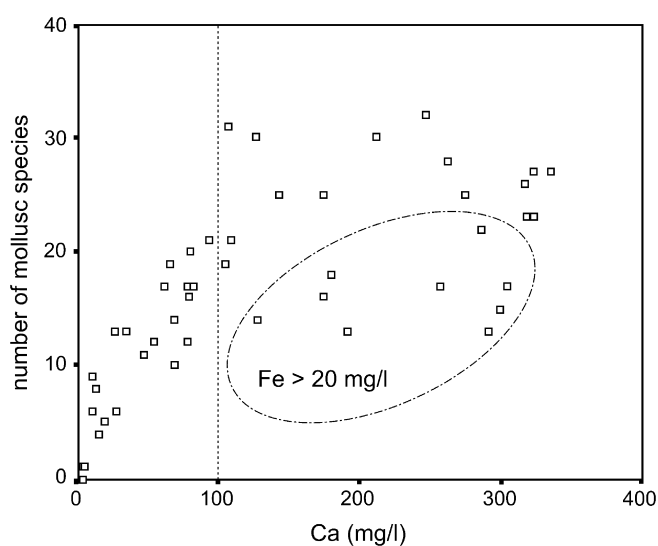


Figure 6. Relationship between water–calcium concentration and mollusc species richness. The encircled sites have a water iron concentration above 20 mg/l. For further annotation see Results.

significantly explain a part of the remaining variation, not explained by Ca concentration.

Relations between water chemistry and mollusc species richness

The dependence of mollusc species richness on the factors measured is not the same along the entire gradient. On sites with calcium concentration of less than 100 mg/l the number of species shows a linear increase, with the increase in concentration of Ca, Mg, Na and with growing pH and conductivity ($P < 0.01$; Fig. 6). The total species number is heavily correlated with the number of terrestrial gastropods ($P < 0.01$). The number of aquatic species shows no dependence on the measured factors. On sites where we measured a Ca concentration in water

above 100 mg/l, the number of species does not correlate with the increasing calcium concentration (Fig. 6). On the contrary, mollusc species richness significantly decreases with increasing K and Fe concentrations ($P = 0.025$). The number of aquatic species decreases significantly with the increase in the slope of the fen ($P = 0.001$).

The rich *Sphagnum*-fens are the most extreme sites hosting terrestrial snails; mostly only the same three most tolerant snail species were found here (see Table 1). The calcium concentrations in water vary between 10 and 25 mg/l, and pH values are between 5.5 and 6. The limiting calcium concentration and acidity in water for any mollusc occurrence at all is somewhere between 2.7 and 4 mg/l, and pH 4.8 and 5.5, respectively. Only the bivalve *Pisidium casertanum* is able to dwell in such poor *Sphagnum*-fens. In *Sphagnum*-fens with lower values of the above-mentioned factors, no molluscs were found in the samples.

DISCUSSION

Choice of method

As there are no molluscs strictly dependent on acidic mineral-poor fens, such habitats can only be colonized by stress-tolerant species, which do not require higher calcium content and pH. These species [e.g. *Vertigo substriata*, *Succinea putris*, *Perpolita hammonis*, *Radix peregra* (O.F. Müller), *Pisidium personatum*, *P. casertanum*] occur along the entire poor–rich gradient. With gradually decreasing calcium concentration, we can observe a gradual decrease in the species with higher requirements. Therefore, we have chosen a classification method that takes the absence of a species into account (Baroni-Urbani–Buser coefficient). This method proved to be very suitable, particularly because the divisions reflect the entire poor–rich gradient. The agreement between classification and DCA ordination suggests that the absence of a species group confined to acidic fens does not result in misleading site scores. On the other hand, it is necessary to take into account the shift of optima of indifferent species to the poor end of the first axis.

Influence of the vegetation

The strong predictive value of vegetation for the composition and species richness of mollusc communities probably occurs for the following reasons.

First, vegetation explains more variability than chemistry, as the mollusc community composition and species richness accords well with the poor–rich trophic gradient. The vegetation also reflects other abiotic and biotic factors affecting the molluscs, such as the effects of geographical position, geomorphology, climate and individual site histories. The abundance and structure of tufa plays a role in the case of petrifying springs. The vegetation and molluscs respond to the same main complex-gradients, which is clearly indicated by the composition of fen communities.

Secondly, most of the terrestrial snails are herbivorous. However, some, such as *Daudebardia* spp., are carnivorous, and some feed on the microflora (bacteria and fungi), for example, *Vetrigo moulinsiana*, which feeds on fungi which are parasites of wetland plants (Steusloff, 1937). It is known that molluscs occurring in oligotrophic biotopes are able to obtain the necessary calcium from tree-leaf litter, which contains calcium in the form of citrate (Wäreborn, 1969). In these cases, analyses of Ca contents and pH measurements should be based on the litter layer. This is obviously of little importance in the case of the extremely rich fens, with abundant calcium available in the tufa or in the case of poor *Sphagnum*-fens, which are only colonized by aquatic species. However, on the less waterlogged sites, particularly of cluster 2, where the community of terrestrial molluscs is less affected by water chemistry, differences in calcium citrate content in the plant biomass could be of greater importance. We have found no molluscs in homogenous patches of *Sphagnum*, while there were several species on patches at the same sites with less cover of *Sphagnum*. This is probably due to the very slow decomposition rate of *Sphagnum*, caused particularly by the production of secondary metabolites, such as sphagnum acid, which may inhibit the activity of micro-organisms involved in the decomposition process (see Scheffer, Logtestijn & Verhoeven, 2001). The accumulation of dead organic matter further substantially limits the contacts with the mineral soil (Glime, Wetzel & Kennedy, 1982; Dierssen & Dierssen, 2001), while minerals are leached by rainfall. As a result, the chemistry in the homogeneous patches of *Sphagnum* is entirely different and much less favourable for molluscs than in places without *Sphagnum* carpets.

Chemistry

In sites with high Ca concentrations, this element is not the major factor affecting the mollusc species composition or species richness. Instead, other abiotic and biotic factors that are much harder to measure are of importance. For this reason, the significant impact of Fe in the extremely Ca-rich fens is a very interesting finding. Many authors have studied the toxicity of Fe on organisms (for references, see Vuori, 1995). The direct toxic effect of dissolved Fe^{2+} is important, since it is considered to be more toxic to aquatic animals than Fe^{3+} (Gerhart, 1992). In the fens, the terrestrial fauna is in direct contact with the aquatic environment and is thus affected by water chemistry. Iron dissolves only very poorly on calcareous substrates (Tyler, 1996) and plants can only utilize it as Fe^{2+} . Therefore, plant species growing on calcareous substrates have developed various mechanisms to transform iron into the Fe^{2+} form (see Marschner, Roemheld & Kissel, 1986). This is important with respect to the prevailing herbivory in gastropods. It seems that the ability of some plants to transform insoluble forms of Fe into the metabolically active form, which determines the calcicole-calcifuge behaviour of plants (Zohlen & Tyler, 2000), can also affect the

composition and species richness of mollusc communities in petrifying springs.

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