THE COMPOSITION AND RICHNESS OF DANUBIAN FLOODPLAIN FOREST LAND SNAIL FAUNAS IN RELATION TO FOREST TYPE AND FLOOD FREQUENCY

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ABSTRACT

The species richness and composition of land snail assemblages in 42 floodplain forest sites along the Danube River in Slovakia were studied to find the main ecological gradients responsible for the variation in the faunas. We found just one, but steep, ecological gradient influencing the variation of snail species composition among different floodplain forest types, reflected in the first detrended correspondence analysis axis, which explained 29.6% of total variation. Site scores on this axis were significantly correlated with site humidity ($r_s = -0.868$; $P < 0.001$). Significant loading on the first axis was also found for flood frequency and several vegetation descriptors. Species composition mainly reflected differences between sites without floods and the others. Species richness as well as total abundances of live individuals were not significantly controlled by any explanatory variable, although some trends could be discerned. Considering vegetation classification, substantial differences were observed between wet softwood floodplain forests and the remaining types, drier softwood forests and different types of hardwood forests, which were impossible to distinguish based on land snail assemblages. The results are discussed in relation to earlier descriptive studies, and in terms of the conservation of these threatened habitats.

INTRODUCTION

Floodplains provide diverse habitats for plants and animals, corridors for their spreading, and a supply of nutrients to aquatic organisms. They are generally of high importance for ecological functions and biodiversity (Jackons *et al.*, 2001; Schnitzler, Hale & Alsum, 2005). The timing, depth and duration of flooding have been found to be the main determinants of structural complexity, species richness, species composition and primary productivity (Trèmoliéres *et al.*, 1998; Oswalt & King, 2005). The loss and degradation of these ecosystems in the temperate zone has been linked with growing human demands, which mostly result in various hydrological changes, e.g. agricultural drainage and river channel modifications (e.g. Tewari *et al.*, 2003; Oswalt & King, 2005). However, efforts have been made in recent years to restore rivers and their systems in order to improve the protection they provide against extreme flooding events (Buijse *et al.*, 2002).

In the past, much attention has been paid to floodplain forest ecology in Europe (Brown, Harper & Peterken, 1997), and especially with respect to vegetation (e.g. Ellenberg, 1988; Schnitzler, 1994; Rodwell, 1998). Although there are many studies dealing with land snail assemblages of floodplain forests (e.g. Ložek, 1955; Vašátko, 1972; Bába, 1974, 1994; Šteffek, 1979, 1986; Frank, 1984, 1985; Beran, 1995; Obrdlik, Falkner & Castella, 1995; Lisický *et al.*, 1997; Horsák, 2000; Čejka, 1997, 1999, 2003), most of them are descriptive, and none analyse community patterns in relation to environmental gradients. By contrast, there are many ecological studies analysing factors influencing species distribution patterns of land snails in other types of European forests (e.g. Wäreborn, 1969; Bishop, 1980; Waldén, 1981; Millar & Waite, 1999; Martin & Sommer, 2004; Cameron & Pokryszko, 2004; Pokryszko & Cameron, 2005; Hylander *et al.*, 2005). Since floodplain forests are very different from other temperate forest communities (Schnitzler *et al.*, 2005) a study dealing with the main ecological predictors of land snail communities in floodplain forests would be useful.

There is a rich pattern of forest units described in the large floodplains of Europe, which can be divided into two main groups: softwood forests composed of willow and poplar trees and hardwood forests composed of oak, elm and ash trees. Softwoods, which are fast-growing pioneer species, are generally located along the main channel, where flooding occurs frequently. Hardwoods are located in more protected areas where rate of flow is reduced by topography or a thick layer of plants (Schnitzler, 1994). Both communities may be connected by various successional stages (Ellenberg, 1988). In this study we investigated shelled land-snail assemblages of different types of floodplain forest communities in the Slovak Danube River basin. Today, Danube floodplain forests cover only a narrow belt along the Danube River and represent only fragments of the original floodplain vegetation. A section of the Slovak Danube River and its floodplain along the Austrian and Hungarian borders have been designated as a Wetland of International Importance under the Ramsar Convention in 1993 and as a Protected Landscape Area in 1998, due to its aquifers as a valuable source of drinking water in Central Europe, its diverse flora and fauna, and the occurrence of many threatened habitats.

The main goals of this study were: (1) to describe and explain patterns of land snail species distribution within a large range of floodplain forest types, from initial stages of softwood forest to old hardwood forests; (2) to find the main factors controlling snail species composition; (3) to test how different flood frequencies influence land snail communities; and (4) to test whether the composition of land snails reflect the forest classification of studied sites.

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MATERIAL AND METHODS

Study area and sites

The study area stretches between Bratislava City and Čilčov Village in SW Slovakia (river km 1,876.0–1,798.0, standard measures from river mouth); along the river line between coordinates 48°09′N 17°01′E; 47°46′N 17°44′E (Fig. 1). The sites belong to three of the most common and easily recognized plant associations (Jurko, 1958): (1) the softwood floodplain forests of the *Salici-Populetum* association, (2) the transitional floodplain forests of the *Fraxino-Populetum* ass., (3) hardwood floodplain forests of the *Fraxino Pannonicae-Ulmetum* ass. (see Table 1 for subassociations and other details).

Field methods and explanatory variables

Sampling was carried out three times per year (spring, summer, autumn), mostly in 1990–2000, but completed in 2005. Each site was an area of ca. 400 m^2, chosen to represent a typical part of the surrounding vegetation, avoiding edges or transitions to different habitats. Within each site snails were searched by eye. One person searched this way in all appropriate microhabitats for 1 h at each site (see Cameron & Pokryszko, 2005). Slugs were not included because their activity depends largely on weather conditions (Rollo, 1991), and the sampling methods used were not suitable to determine slug abundance (Oggier, Zschokke & Baur, 1998). Four quadrats, each measuring 25 × 25 cm^2, were collected during each sampling period within a site; all litter, twigs, vegetation, and loose soil were sieved (10 mm mesh size) from the quadrats down to a depth where the soil became difficult to remove (app. 4 cm). The coarse fraction was searched by eye in the field and discarded. The residue was bagged and taken to the laboratory. In total, we obtained a set of 12 quadrats and two person hours for each site (spring and autumn: 1-h search was practically impossible during the summer season due to extremely high mosquito density).

Several environmental variables were noted for each site during fieldwork: humidity (as soil moisture), stand age, coverage of herb, shrub and tree layer, amount of litter (five-grade scale), four types of litter (willow, poplar, ash, mixed), age of the site, flood frequency (0, without floods; 1, groundwater floods; 2, irregular floods; 3, regular floods). For each sampling plot, plant species were recorded in order to estimate soil moisture using Ellenberg plant indicator values (Ellenberg *et al.*, 1992). A mean of available Ellenberg indicator values of species recorded on a particular sampling plot was calculated using the JUICE program (Tichy, 2002). As we wanted to reduce both random variation of the mean values and their inaccuracy caused by missing values, we scored the resulting mean indicator values on a scale of 1–7. Age of stand was obtained from regional forest-management plans. Coverage of herb, shrub and tree layers was expressed as a percentage proportion of the layer in the area of 20 × 20 m^2.

As soils of the studied floodplain do not significantly differ in calcium content (Jurko, 1958; Lisický, 1991), which is generally high, we did not expect any significant influence of calcium content on the snail communities. Therefore, we did not measure the calcium content in all of the sites, but to validate this presumption we randomly chose six sites, which varied highly in the number of species (from 7 to 24). In these sites topsoil carbonate calcium content was measured using the procedures of Fiala *et al.* (1999). As we expected, we did not observe any relationship between calcium content and species richness ($r_s = 0.06$, $P = 0.91$) nor with total abundance of live individuals ($r_s = 0.09$, $P = 0.87$).

Extraction of snails from soil samples

The samples were oven dried and washed; the floating fraction (part of the plant material and air-filled shells) was then air-dried and sieved to three fractions. Snails were removed by eye from the larger fractions, and under a binocular microscope from the smaller fractions down to 0.5 mm. The individual shells were identified and classified as alive, fresh or old at time of collection. If the body was seen inside, it was scored as alive, if the shell was empty with the periostracum intact, it was scored as fresh; shells with substantially peeled or missing periostracum were scored as old (Millar & Waite, 1999).

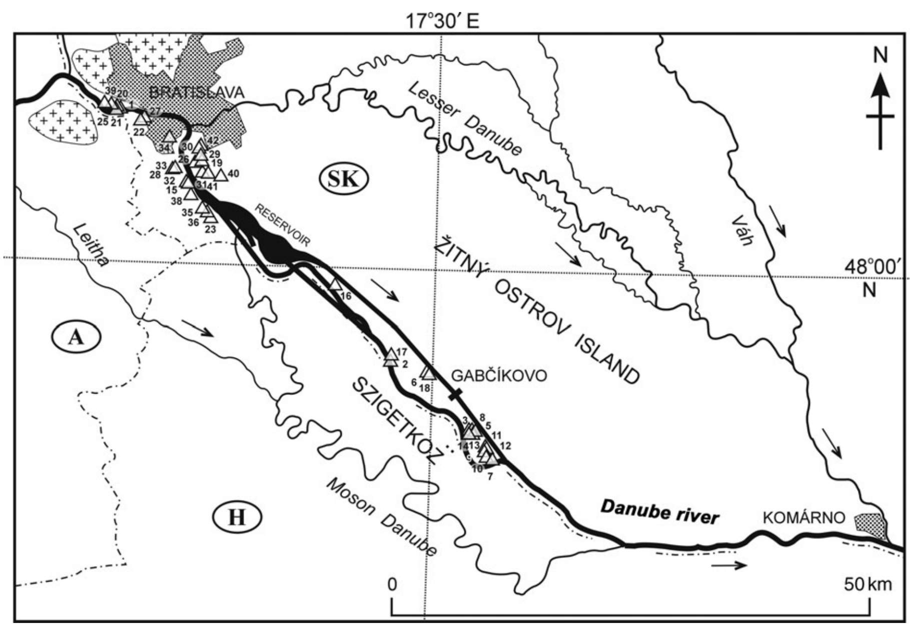

Figure 1. The location of study area with the position of sampling sites (1–42) within Danubian lowland.

Table 1. Vegetation classification and short characterization of studied habitats.

Phytocoenological association	Subassociation	Plant dominants (summer aspect)	No. of sites
Salici-Populetum (SP) (softwood floodplain forest)	**I.** initial successional stage (SPi)	E3 + E2 (0%); E1 (95–100%) *Phalaris arundinacea*, *Aster lanceolatus*, *Phragmites australis*	3
	II. *phragmito-caricetosum* (SPpc)	E3 (30–50%) *Populus alba*, *P. nigra*; E2 (10%) *P. alba*, *Salix fragilis*; E1 (100%) *Rubus caesius*, *Carex gracilis*, *Aster lanceolatus*, *Leucojum aestivum*, *Phragmites australis*	2
	III. *myosotidetosum* (SPm)	E3 (15–60%) *Salix alba*, *Salix fragilis*; E2 (0–10%); E1 (15–100%) *Galium palustre*, *Polygonum mite*, *Oenanthe aquatica*, *Phalaris arundinacea*, *Leucojum aestivum*, *Myosotis palustris*	6
	IV. *typicum* (SPt) var. with *Rubus caesius*	E3 (75%) *Salix alba*, willow or poplar plantation; E2 (0%); E1 (95%) *Rubus caesius*, *Leucojum aestivum*, *Galium palustre*, *Phalaris arundinacea*, *Carex riparia*	1
	V. *typicum* var. with *Urtica dioica*	E3 (50–80%) *Salix alba* or plantation of *Populus* × *canadensis*; E2 (10–60%) *Sambucus nigra*, *Swida sanguinea*, *Padus avium*; E1 (75–100%) *Urtica dioica*, *Galium aparine*, *Impatiens glandulifera*, *Impatiens parviflora*	7
	VI. *typicum* var. with *Swida sanguinea*	E3 (40–70%) *Populus alba* or *Populus* × *canadensis*; E2 (40–60%) *Swida sanguinea*; E1 (90–100%) *Rubus caesius*, *Impatiens parviflora*, *Urtica dioica*, *Swida sanguinea*, *Galium aparine*	4
Fraxino-Populetum (FP) (transitional f. f.)	**VII.**	E3 (50–60%) *Populus alba*, *Fraxinus excelsior* or *Populus* × *canadensis*; E2 (15–50%) *Swida sanguinea*, *Sambucus nigra*, *Acer pseudoplatanus*; E1 (50–100%) *Lamium maculatum*, *Galium aparine. Allium ursinum* in the spring aspect	8
Ulmo-Fraxinetum (UFr) (hardwood f. f.)	**VIII.**	E3 (50–90%) *Fraxinus excelsior,Tilia cordata*, *Quercus robur*; E2 (30–50%) *Sambucus nigra*, *Acer campestre*; E1 (80–100%) *Aegopodium podagraria*, *Viola odorata*, *Geum urbanum*, *Brachypodium silvaticum*, *Stachys sylvatica*. The spring aspect: *Ficaria verna*, *Galanthus nivalis*, *Alliaria officinalis*	5
Ulmo-Quercetum (UQ) (hardwood f. f.)	**IX.**	E3 (30–90%) *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior*; E2 (50–75%) *Cornus mas*, *Coryllus avellana*, *Ligustrum vulgare*, *Crataegus monogyna*; E1 (40–85%) *Convallaria majalis*, *Polygonatum* spp., *Viola* spp., *Cornus mas*, *Acer campestre*, *Ligustrum vulgare*, *Hedera helix*	6

Covers of three vegetation layers are given in parentheses: E3, tree layer; E2, shrub layer; E1, herb layer.

All shells extracted were identified and counted, excluding very old or unidentifiable remains. The species names are given according to Turner *et al*. (1998); for authorities see the Appendix. The samples are kept in the collection of the Institute of Zoology, Bratislava, Slovakia.

Data analysis

Only live specimens and empty shells with entire periostracum were used for the analyses. Of the 41 species found in total, those (7) found only at a single site were omitted from the detrended correspondence analysis (DCA) in order to reduce random noise (see Appendix). The snail abundance data were square-root transformed in order to reduce the influence of dominance. The explanatory variables that did not fit normal distributions (Kolmogorov–Smirnov test) were also square-root transformed. We calculated Spearman rank correlations (r_s) to examine possible correlations among explanatory variables and between explanatory variables and snail species richness, abundance of live individuals, and site scores on the first four ordination axes for all continuous and ordinal variables. The significance of relationships between continuous and ordinal variables and nominal variables was tested using the Mann-Whitney U test. Fisher's exact test was used for the testing of relationships between nominal variables describing the quality of litter and nominal variables describing flood frequency. Sequential Bonferroni corrections of the significance level were used for multiple comparisons of environmental variables (Holm, 1979). The CANOCO 4.5 package (ter Braak and Šmilauer, 2002) was used for DCA techniques and STATISTICA 7 (www.statsoft.com) was used for the other (uni-dimensional) analyses.

RESULTS

Species richness and abundance

Totals of 41 shelled land snail species (530 records) and 10,970 individuals were found in the 42 sites (Appendix). Species richness varied from 4 to 26 snail species with a median value of 11 species. The studied vegetation types of floodplain forests did not differ from one another in species richness except for the sites of initial successional stages (Fig. 2), which were poorer than the rest. By contrast, the richest sites belonged to softwood willow-poplar floodplain forests of the *Salici-Populetum typicum* association (groups V and VI, see Fig. 2 and Appendix). All the tested relationships among explanatory variables and with richness and abundance are shown in Table 2. Using the Bonferroni correction, neither species richness nor total abundance of live individuals were significantly controlled by any explanatory variable. However, regular flooding had a marginally negative effect on abundances of live individuals.

Species composition and environmental variables

Using DCA we found just one main gradient, which explained 29.6% of total variation in species composition (Fig. 3). The species turnover was well explained by several environmental variables (Table 3), which were mostly correlated with one another, except for the amount of ash litter (Table 2). The factor with the highest loading on the first axis, reflecting

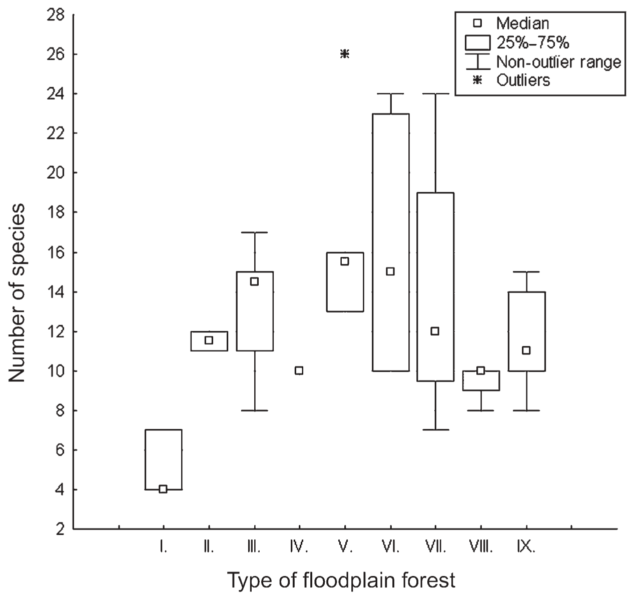

Figure 2. Variation of species richness among different types of floodplain forests (I–IX). For abbreviations see Table 1.

correlations with the site scores, was humidity (estimated from Ellenberg values) ($r_s = -0.868$, $P < 0.001$). Significant, but weaker, correlations were also found for variables related to humidity, e.g. different parameters of floods. Another group of variables significantly related to the first DCA axis consisted of several vegetation characteristics (amount of willow litter, stand age, shrub cover, and amount of ash litter), where the amounts of willow litter had the highest fit ($P < 0.001$, Table 3). Considering vegetation classification of the sites, they can be divided along the first ordination axis into two main groups: (1) wet softwood forests and (2) drier softwood forests and different types of hardwood forests (Fig. 3). Towards drier sites, it was impossible to separate individual vegetation types of alluvial forests on the basis of land snail assemblages. We found almost a complete overlap of dry softwood forest sites (*Salici-Populetum typicum* var. with *Swida sanguinea*) and different types of hardwood forest sites (Fig. 4, types VI–IX). By contrast, particular types of wet softwood forests harboured rather distinct assemblages.

The main pattern of species turnover was characterized by the dichotomy between assemblages consisting mostly of hygrophilous species and assemblages with the dominance of typical woodland species (Fig. 4). Snail assemblages of wet softwood forests (Fig. 3, circles) included a high proportion of hygrophilous snails, e.g. *Carychium minimum* Müller, 1774, *Zonitoides nitidus* (Müller, 1774), *Succinea putris* Linné, 1758, *Oxyloma elegans* (Risso, 1826) and *Pseudotrichia rubiginosa* (Schmidt, 1853); the first three species were abundant and frequent (see Appendix). The remaining types of studied forests harboured assemblages consisting predominantly of typical woodland species, e.g. *Aegopinella nitens* (Michaud, 1831), *Petasina unidentata* (Draparnaud, 1805), *Monachoides incarnatus* (Müller, 1774), *Cochlodina laminata* (Montagu, 1803), *Helix pomatia* Linné, 1758. The first three mentioned species were the dominants of the assemblages, especially *A. nitens* (see Appendix).

Table 2. Relationships between all explanatory variables.

Part 1	H	TC	SC	HC	LA	SA	FF	SR	TA
Humidity		0.394	**< 0.001**	**0.002**	0.065	**< 0.001**	**< 0.001**	0.377	0.438
Tree cover	−0.135		0.568	0.424	0.104	0.490	0.932	0.123	0.802
Shrub cover	**−0.626**	−0.091		0.009	0.268	**< 0.001**	**< 0.001**	0.382	0.554
Herb cover	**0.464**	−0.127	−0.397		0.658	0.023	0.115	0.383	0.581
Litter amount	−0.288	0.254	0.175	0.070		0.015	0.039	0.356	0.795
Stand age	**−0.601**	0.109	**0.520**	−0.349	0.372		**0.001**	0.608	0.538
Flood frequency	**0.758**	−0.014	**−0.645**	0.247	−0.320	**−0.480**		0.699	0.298
Species richness	0.140	0.241	−0.138	0.138	0.146	−0.081	0.061		**0.002**
Total abundance	0.123	−0.040	0.094	0.088	−0.041	0.098	−0.165	**0.474**	
Part 2	H	TC	SC	HC	LA	SA	FF	SR	TA
Poplar litter	0.826	0.235	0.743	0.028	0.042	0.064	0.472	0.020	0.817
Willow litter	***< 0.001***	0.748	**0.001**	0.315	0.003	0.106	***< 0.001***	0.979	0.612
Ash litter	0.022	0.027	0.415	0.091	0.986	0.389	0.050	0.059	0.258
Mixed litter	**0.002**	0.748	0.005	0.028	0.228	***0.001***	0.042	0.358	0.461
Without floods	**< 0.001**	0.949	***< 0.001***	0.041	0.140	0.006	***< 0.001***	0.451	0.889
Groundwater floods	0.680	0.562	0.829	0.774	0.433	0.813	0.856	0.666	0.346
Irregular floods	0.026	0.514	0.047	0.040	0.841	0.756	0.061	0.373	0.029
Regular floods	***0.002***	0.859	0.006	0.903	0.040	0.007	***< 0.001***	0.755	0.008
Part 3	WF	GF	IF	RF					
Poplar litter	0.197	0.637	0.330	0.633					
Willow litter	**< 0.001**	0.407	0.184	0.009					
Ash litter	0.105	0.532	0.461	0.125					
Mixed litter	0.050	0.414	0.626	0.089					

Spearman correlation coefficients (lower left) and their significance probabilities (upper right) are given for continuous and ordinal variables (part 1), Mann-Whitney *U* test was used for testing relationships between continuous and ordinal variables and nominal variables (part 2), and the significance of relationships between two groups of nominal variables were tested using Fisher's exact two-tailed test (part 3). Significant correlations after Bonferroni correction are in bold (the cut level was $P = 0.003$). Significant and positive relationships within parts 2 and 3 are given in italics.

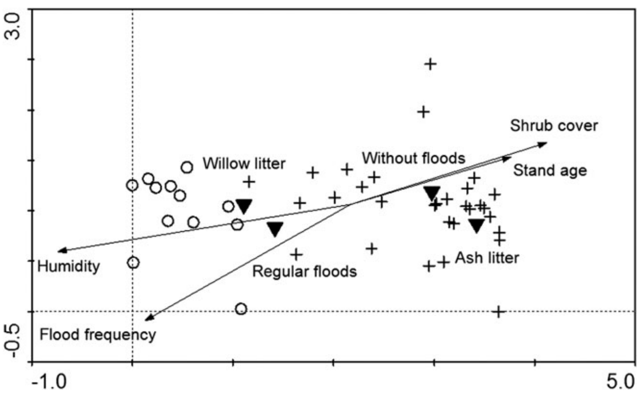

Figure 3. DCA diagram of sites on the first two ordination axes with posteriori plotted explanatory variables (full triangles show position of centroids for nominal variables); only those significantly correlated with the first ordination axis were used (see Table 3). Eigenvalues: first axis 0.615, second axis 0.146. Percentage variance of the species data explained: first axis 29.6%, second axis 7.0%. Species-environment relation: first axis 60.1%, second axis 4.8%. The classification of sites into two groups was based on vegetation types: circles, wet softwood sites (I–III, Table 1); crosses, drier softwood sites and hardwood sites (IV–IX, Table 1).

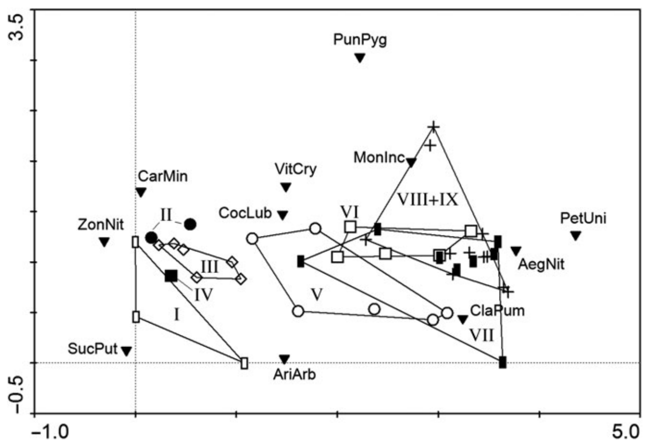

Figure 4. DCA diagram of sites and snail species on the first two ordination axes. The sites are classified based on vegetation type: I, initial successional stage of *Salici-Populetum* association; II, *Salici-Populetum phragmito-caricetosum* subass.; III, *Salici-Populetum myosotidetosum* subass.; IV, *Salici-Populetum typicum* variant with *Rubus caesius*; V, *Salici-Populetum typicum* var. with *Urtica dioica*; VI, *Salici-Populetum typicum* var. with *Swida sanguinea*; VII, *Fraxino-Populetum* ass.; VIII, *Ulmo fraxinetum* ass.; IX, *Ulmo-Quercetum* ass. (for details see Table 1). Only the species with highest fit to ordination axes are shown. Species list in alphabetic order: *Aegopinella nitens*, *Arianta arbustorum*, *Carychium minimum*, *Clausilia pumila*, *Cochlicopa lubrica*, *Monachoides incarnatus*, *Petasina unidentata*, *Punctum pygmaeum*, *Succinea putris*, *Vitrea crystallina*, *Zonitoides nitidus*. For detailed results of the analysis see Figure 3.

Table 3. Correlations among explanatory variables and DCA ordination site scores on the first ordination axis.

Continuous and ordinal variables	First DCA axis	
	r_s	P
Humidity	**− 0.868**	**< 0.001**
Flood frequency	**− 0.665**	**< 0.001**
Stand age	**0.565**	**< 0.001**
Shrub cover	**0.501**	**0.001**
Litter amount	0.349	0.023
Herb cover	− 0.332	0.032
Tree cover	0.224	0.153
Species richness	− 0.125	0.429
Total abundance	− 0.092	0.562
Nominal variables	P	
Without floods	**< 0.001**	
Willow litter	**< 0.001**	
Ash litter	**0.002**	
Regular floods	**0.002**	
Irregular floods	0.076	
Mixed litter	0.124	
Groundwater floods	0.518	
Poplar litter	0.754	

Values of Spearman correlation coefficient (r_s) and significance probabilities (P) are shown for continuous and ordinal variables, for nominal variables only significance of Mann-Whitney U test is given. Significant values are in bold (using Bonferroni correction the cut level was $P = 0.003$). Correlations with the other three DCA axes were not significant for any tested variables.

DISCUSSION

Ecological gradients and variation of species composition

There appears to be just one steep ecological gradient influencing the variation of snail species composition among different floodplain forest types. Nearly one-third of total variation was explained on the first DCA axis, whereas the other axes explained only very small portions of the remaining variation (only 7% was explained on the second axis). Since we found significant correlations between several explanatory variables and the site scores on the first axis, we are able describe ecological factors controlling land snail composition of the studied habitats. The factor with the highest influence was humidity (Table 3), which was partly linked to flood frequency (Table 2). The environments without floods or with regular floods appeared to influence land snail assemblages the most, because they led to very different snail communities. The second group of important predictors of species composition, connected with humidity as well as flood frequency, included variables describing vegetation. Some of them (at least willow litter) were obviously conditioned by site humidity, whereas the others probably represented more or less different site conditions (i.e. stand age, shrub cover). The amount of ash litter can be considered as a distinct variable. This factor was positively and significantly related to the first axis, but it was not related to any of the other measured variables (Tables 2, 3). It is known that litter of trees (e.g. ash, lime), which contain calcium in an easily soluble citrate form have a positive effect on land snail communities (Wäreborn, 1970). Therefore the presence of ash litter could favour species with higher calcium demands and thus alter the composition and/or structure of studied communities.

In conclusion, all the factors related to moisture are linked to the same ecological pattern; nevertheless, they can possess a part of exclusive uncorrelated variation. In particular, flood frequency and humidity need not always be strongly correlated. In our dataset these were strongly correlated, but it should be stressed that a substantial part of the correlation was caused by differences between non-flooded sites and the others. This means that the composition of snail faunas primarily reflected differences between the sites without floods and all other sites. This corresponds with general knowledge of floodplain ecology. The frequency, strength, and timing of flooding are considered as probably the most important determinants of the biota within riparian corridors (Pollock, 1998; Siebel & Blom, 1998).

Species richness and abundance

Generally speaking, the composition and richness of land snail communities is linked with available calcium content (Wäreborn, 1969; Dallinger *et al*., 2001). Close positive relationships between the number of mollusc species and/or individuals and calcium content have been found frequently (e.g. Wäreborn, 1970; Hylander *et al*., 2005; Horsák, 2006). A different situation was found for the Danube floodplain forests where calcium content was no longer the key factor, probably due to its low variation and high level among the sites. By contrast, sites studied here did differ greatly in humidity and flood quality, two of the most important environmental variables responsible for the variation of floodplain communities (Schnitzler, 1994), and this correlated best with the species composition of land snail assemblages in the Slovak Danube River. An important finding was that species richness and abundance seemed to be less affected by this ecological gradient. However, previous studies show that humidity can cause significant differences between snail species richness and abundance of drier and moister forest sites (Martin & Sommer, 2004) or can overtop the importance of calcium content in dry meadow wood sites (Wäreborn, 1969). It seems that the result depends on individual site conditions and whether their values are under ecological thresholds of a majority of species of the assemblage. Briefly, the driest studied sites were probably still wet enough for most of the species pool, therefore no significant decrease of species richness was found. At the opposite end of the humidity gradient, only initial stages of regularly flooded sites hosted significantly lower numbers of snail species. At the regularly flooded sites snails and their substrates can also be regularly washed away in floods. On the basis of our results it seemed that snail abundances are affected, since a marginally negative effect of frequent floods on abundances of live individuals was found.

There are some molluscan studies where species richness is closely related to the pattern of species composition (e.g. Horsák, 2005; Hylander *et al*., 2005). However, it seems that this pattern can be found only when the calcium content is an overriding factor, i.e. at sites with lower amounts of calcium where this element is limiting for the majority of the species (Horsák & Hájek, 2003; Horsák, 2006). This feature of land snail ecology is connected with a low degree of interspecific competition (Waldén, 1981) and with the predominance of species favoured by calcium-rich conditions (Hylander *et al*., 2005; Horsák *et al*., 2007a, b). Species richness in our forests was not significantly related to any of the explanatory variables (Table 2), although we observed two possible trends of the species richness pattern. Significantly low numbers of species were observed only at sites in the earliest stages of succession, which is, perhaps, to be expected; however, because of the low numbers of recorded individuals at these sites it is possible that species richness could be influenced by an insufficient sampling size (Cameron & Pokryszko, 2005). The second, worthy of further research, is a unimodal response of species richness to humidity with its maximum in the middle values (unfortunately not significant in our dataset). The highest numbers of species were found at irregularly flooded sites (i.e. *Salici-Populetum typicum*). These sites were transitions between often-flooded wet softwood forest sites and relatively dry hardwood forest sites. They can harbour species with high demand for humidity as well as typical forest species, especially those that cannot dwell under extremely wet and unstable conditions of regularly flooded sites. A similar pattern of species richness with a peak in the intermediate moist sites was found in the Great Smoky Mountains forest habitats (Getz & Uetz, 1994), and is suggested by the results of Cameron & Pokryszko (2004) in the Białowieża Forest in eastern Poland.

Previous studies and conservation implications

Although there are a number of studies dealing with land snail communities of floodplains, most are regionally focussed, highly descriptive accounts without advanced statistical assessment and general conclusions. In the study area, the most recent and detailed description of land snail faunas of 24 Slovak Danube floodplain sites was published by Čejka (1999). This gives more detailed information about individual site faunas in the study area. Two important inventory studies were carried out in the past. Ložek (1955) investigated the land snail fauna of the area because of the upcoming construction of the Gabčíkovo–Nagymaros Waterworks. Without statistical analysis, he was able to divide snail assemblages of the surveyed floodplain forests into two types. His empirical classification perfectly corresponds with our results. He considered snail faunas of regularly flooded softwood forests located on the riverside of dykes and their drier varieties situated beyond the dykes as distinct communities (see classification in Fig. 3). Šteffek (1979, 1986) briefly characterized the molluscan communities on the basis of vegetation typology. His classification corresponds to our results for wet softwood forests and hardwood forests, but his conclusions for snail fauna inhabiting forest types in the middle of the humidity gradient are different (i.e. groups V–VII, Table 1). His characterization of these floodplain forest types comprises snail species typical for wet softwood forests (e.g. *Carychium minimum*) and those preferring hardwood forests (e.g. *Petasina unidentata*). This discrepancy is hard to explain without having detailed information about the sites he had sampled. It might be, for example, caused by his effort to distinguish forests of ass. *Salici-Populetum* from those of ass. *Fraxino-Populetum*. As shown by our results (see Fig. 4) these vegetation types (groups V–VII) hosted indistinguishable land snail assemblages. This case shows the necessity of multidimensional and ordinal statistical treatment for verifying the researcher's field experience; purely classificatory vegetation analysis may be misleading.

Snail assemblages were also studied in the Austrian Danube floodplain (Frank, 1984, 1985) and in the Tisza River floodplain (Bába, 1977). Although these papers are descriptive, they provide detailed characteristics of mollusc assemblages along a moisture and successional gradient. To our knowledge, just one comprehensive study dealing with floodplain gastropod communities has been published (Obrdlik *et al*., 1995). This paper analysed the geographical pattern of gastropods in twelve European floodplains. It served as an important survey of species spectra and diversity in terms of regional species pools and human impact. Unfortunately, no analysis of the variability of species spectra within each studied floodplain was done or even possible, mainly due to constraints linked with the character of data collecting. Thus it seems that our study is the first attempt to assess the ecology of floodplain land snail assemblages.

Finally, it should be stressed that floodplains are important components of local diversity and have a high ecological and economical importance. In the second half of the 20th century, intensification of agriculture, urban and rural demands, river regulations, and other negative human impacts on lowland floodplains increased dramatically. River channel modifications have probably the most negative impact on floodplain communities. Channelization affects the hydrology of the adjacent floodplain forests at multiple spatial and temporal scales (Shankman, 1996). The decrease of groundwater level is linked to rapid successional changes and especially to a loss of typical softwood communities. This fact is important also in terms of land snail conservation. Three out of the 41 species recorded are considered as rare and endangered [i.e. *Cochlicopa nitens* (Gallenstein, 1848), *Euconulus praticola* (Reinhardt, 1883), and *Pseudotrichia rubiginosa*]. These snails almost exclusively inhabited wet softwood sites. *Cochlicopa nitens* was listed in the Red Book of Endangered plant and animal species of former Czechoslovakia and is considered as a relict species of lowland wetlands (Ložek, 1992). After the channelization of the lower Dyje and Morava River (Danube tributary) it disappeared from almost all the previously known sites.

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REFERENCES

BÁBA, K. 1974. Quantitative conditions of the molluscs in the oak woods of various states of succession at Csévharaszt. *Abstracta Botanica*, **2**: 71–76.

BÁBA, K. 1977. Die kontinentalen Schneckenbestände der Eichen-Ulmen- Eschen-Auwäldern (*Fraxino pannonicae-Ulmetum pannonicum* Soó) in der Ungarischen Tiefebene. *Malacologia*, **16**: 51–57.

BÁBA, K. 1994. Die Verbreitung der Landschnecken im ungarischen Teil des Alföld. III. Bildung der Artengruppen. *Soósiana*, **21/22**: 64–79.

BERAN, L. 1995. [Molluscs of the Elge lowland between Poděbrady and Kolín]. *Muzeum a součastnost, řada přírodovědná, Roztoky*, **9**: 3–39. [In Czech, English summary]

BISHOP, M.J. 1980. The Mollusca of acid woodland in the Italian province of Novara. *Journal of Conchology*, **30**: 181–188.

BROWN, A.G., HARPER, D. & PETERKEN, G.F. 1997. European floodplain forests: structure, functioning and management. *Global Ecology and Biogeography Letters*, **6**: 169–178.

BUIJSE, A.D., COOPS, H., STARAS, M., JANS, L.H., GEEST, G.J.V., GRIFTS, R.E., IBELINGS, B.W., OOSTERBERG, W. & ROOZEN, F.C.J.M. 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology*, **47**: 889–907.

CAMERON, R.A.D. & POKRYSZKO, B.M. 2004. Land mollusc faunas of Białowieża forest (Poland), and the character and survival of forest faunas in the North European Plain. *Journal of Molluscan Studies*, **70**: 149–164.

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**: 529–548.

ČEJKA, T. 1997. Adaptive successional changes in malacocoenoses as a reaction to the changed hydrological conditions in the diversion area of the Gabčíkovo power plant (Slovakia, the Danube river). *Biologia*, **52**: 615–623.

ČEJKA, T. 1999. The terrestrial molluscan fauna of the Danubian floodplain (Slovakia). *Biologia*, **54**: 489–500.

ČEJKA, T. 2003. Molluscs (Mollusca). In: *Biodiversity of Abrod – state, changes and restoration* (V. Stanová & A. Viceníková, eds), 187–190. Daphne – Institute of Applied Ecology, Bratislava.

DALLINGER, R., BERGER, B., TRIEBSKORN-KÖHLER, R. & KÖHLER, H. 2001. Soil biology and ecotoxicology. In: *The Biology of terrestrial molluscs* (G.M. Barker, ed.), 489–525. CABI Publishing, Wallingford.

ELLENBERG, H. 1988. *Vegetation ecology of Central Europe, Edn 4*. Cambridge University Press, Cambridge.

ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, V., WERNER, W. & PAULIßEN, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. second ed. *Scripta Geobotanica*, **18**: 1–258.

FIALA, K., KOBZA, J., MATÚŠKOVÁ, L., MAKOVNÍKOVÁ, J., BARANČÍKOVÁ, G., HOUŠKOVÁ, B., PECHOVÁ, B., BÚRIK, V., BREČKOVÁ, V., LITAVEC, T., CHROMANIČOVÁ, A. & VÁRADIOVÁ, D. 1999. [*Standard methods of soil analyses*]. Soil Fertility Research Institute, Bratislava. [In Slovak]

FRANK, C. 1984. Aquatische und terrestrische Mollusken der niederösterreichischen Donau – Auengebiete und der angrenzenden Biotope. VI. Die Donau von Wien bis zur Staatsgrenze. Teil. 1. *Zeitschrift für angewandte Zoologie*, **3**: 257–303.

FRANK, C. 1985. Aquatische und terrestrische Mollusken der niederösterreichischen Donau – Auengebiete und der angrenzenden Biotope. VI. Die Donau von Wien bis zur Staatsgrenze. Teil 2. *Zeitschrift für angewandte Zoologie*, **4**: 405–457.

GETZ, L.L. & UETZ, G.W. 1994. Species diversity of terrestrial snails in the southern Appalachian mountains, U.S.A. *Malacological Review*, **27**: 61–74.

HOLM, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**: 65–70.

HORSÁK, M. 2000. The molluscs of the Oderský Floodplain Forest proposed National Nature Reserve in the Poodří Protected Landscape Area (Czech Republic). *Časopis Slezského Muzea Opava (A)*, **49**: 183–187. [In Czech]

HORSÁK, M. 2005. Molluscs. In: *Ecology and palaeoecology of spring fens in the western part of the Carpathians* (A. Poulíčková, M. Hájek & K. Rybníček, eds), 63–68. Palacký University, Olomouc.

HORSÁK, M. 2006. Mollusc community patterns and species response curves along a mineral richness gradient: a case study in fens. *Journal of Biogeography*, **33**: 98–107.

HORSÁK, M. & HÁJEK, M. 2003. Composition and species richness of mollusc communities in relation to vegetation and water chemistry in the Western Carpathian spring fens: the poor–rich gradient. *Journal of Molluscan Studies*, **69**: 349–357.

HORSÁK, M., HÁJEK, M., DÍTĚ, D. & TICHÝ, L. 2007a. Modern distribution patterns of snails and plants in the Western Carpathian spring fens: is it a result of historical development? *Journal of Molluscan Studies*, **73**: 53–60.

HORSÁK, M., HÁJEK, M., TICHÝ, L. & JUŘIČKOVÁ, L. 2007b. Plant indicator values as a tool for land mollusc autecology assessment. *Acta Oecologica*, **32**: 161–171.

HYLANDER, K., NILSSON, C., JONSSON, B.G. & GÖTHNER, T. 2005. Differenes in habitat quality explain nestedness in a land snail meta-community. *Oikos*, **108**: 351–361.

JACKSON, R.B., CARPENTER, S.R., DAHM, C.N., MCKNIGHT, D.M., NAIMAN, R.J., POSTEL, S.L. & RUNNING, S.W. 2001. Water in a changing world. *Ecological Applications*, **11**: 1027–1045.

JURKO, A. 1958. *Soil ecological conditions and woodland communities in the Pudunajská Nížina Lowland*. SAV, Bratislava. [in Slovak]

LISICKÝ, M.J. 1991. *Report on natural stage of the environment in the surrounding of the Gabčíkovo Hydraulic Structures from the viewpoint of biology and landscape ecology*. Final report, Institute of Zoology and Ecosozology, Bratislava. [Unpubl. ms., in Slovak]

LISICKÝ, M.J., ČARNOGURSKÝ, J., ČEJKA, T., KALÚZ, S., KRUMPÁLOVÁ, Z., PIŠÚT, P. & UHERČÍKOVÁ, E. 1997. Adaptive changes in the ecosystem related to the shift of the Danube river into the Gabčíkovo powerplant canal. *Ekológia*, **3**: 265–280.

LOŽEK, V. 1955. Report on the malacozoological survey in the ŽitnÝ Ostrov Lowland in 1953. *Práce II. sekcie SAV, séria biologická*, **6**: 5–31. [In Czech]

LOŽEK, V. 1992. Molluscs (Mollusca). In: *Red book of threatened and rare plant and animal species of the ČSFR. 3. Invertebrates* (L. Škapec, ed.), 24–25. Príroda, Bratislava. [In Czech]

MARTIN, K. & SOMMER, M. 2004. Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *Journal of Biogeography*, **31**: 531–545.

MILLAR, A.J. & WAITE, S. 1999. Molluscs in coppice woodland. *Journal of Conchology*, **36**: 25–48.

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

OGGIER, P., ZSCHOKKE, S., & BAUR, B. 1998. A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia*, **42**: 348–357.

OSWALT, S.N. & KING, S.L. 2005. Channelization and floodplain forests: impacts of accelerated sedimentation and valley plug formation on floodplain forests of the Middle Fork Forked Deer River, Tennessee, USA. *Forest Ecology and Management*, **215**: 69–83.

POLLOCK, M.M. 1998. Biodiversity. In: *River ecology and management: lessons from the Pacific Coastal Ecoregion* (R.J. Naiman, R.E. Bilby, eds), 430–452. Springer, New York.

POKRYSZKO, B.M. & CAMERON, R.A.D. 2005. Geographical variation in the composition and richness of forest snail faunas in northern Europe. In: *Pattern and process in land mollusc diversity* (R.A.D. Cameron, J.C. Nekola, B.M. Pokryszko & F.E. Wells, eds), 115–132. Records of the Western Australian Museum, Supplement No. 68, Perth, Western Australia.

RODWELL, J.S. (ed.) 1998. *British plant communities. Volume 1. Woodlands and scrub*. Cambridge University Press, Cambridge.

ROLLO, C.D. 1991. Endogenous and exogenous regulation of activity in *Deroceras reticulatum*, a weather-sensitive terrestrial slug. *Malacologia*, **33**: 199–220.

SCHNITZLER, A. 1994. European alluvial hardwood forests of large floodplains. *Journal of Biogeography*, **14**: 97–117.

SCHNITZLER, A., HALE, B.W. & ALSUM, E. 2005. Biodiversity of floodplain forests in Europe and eastern North America: a comparative study of the Rhine and Mississippi Valleys. *Biodiversity and Conservation*, **14**: 97–117.

SHANKMAN, D. 1996. Stream channelization and changing vegetation patterns in the U.S. Coastal Plain. *Geographical Review*, **86**: 216–232.

SIEBEL, H.N. & BLOM, C.W.P.M. 1998. Effects of irregular flooding on the establishment of treespecies. *Acta Botanica Neerlandica*, **47**: 231–240.

ŠTEFFEK, J. 1979. Malacological survey in the Podunajská Nížina Lowland focused on the area of Gabčíkovo Hydraulic Structures. *Acta ecologica*, **17**: 85–115. [In Slovak]

ŠTEFFEK, J. 1986. Importance of the Podunajská Nížina Lowland from the viewpoint of the mollusc gene pool conservation. *Správy Slevenskej Zoologickej Spoločnosti SAV*, **12**: 139–145. [In Slovak]

TEWARI, S., KULHAVÝ, J., ROCK, B.N. & HADAŠ, P. 2003. Remote monitoring of forest response to changed soil moisture regime due to river regulation. *Journal of Forest Science*, **49**: 429–438.

TER BRAAK, C.J.F. & ŠMILAUER, P. 2002. *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, New York.

TICHÝ, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science*, **13**: 451–453.

TRÈMOLIÉRES, M., SÁNCHEZ-PÉREZ, J.M., SCHNITZLER, A. & SCHMITT, D. 1998. Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. *Plant Ecology*, **135**: 59–78.

TURNER, H., KUIPER, J.G.J., THEW, N., BERNASCONI, R., RÜETSCHI, WÜTHRICH, M. & GOSTELI, M. 1998. *Atlas der Mollusken der Schweiz und Liechtensteins*. Fauna Helvetica 2, Neuchâtel.

VAŠÁTKO, J. 1972. On the mollusc component of the geobiocenoses of the alluvial forest near the community of Dolní Věstonice. *Zprávy Geografického ústavu ČSAV v Brně*, **9(2–3)**: 5–42.

WALDÉN, H.W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slope in SW Sweden. *Journal of Conchology*, **30**: 351–372.

WÄREBORN, I. 1969. Land molluscs and their environments in an oligotrophic area in southern Sweden. *Oikos*, **20**: 461–479.

WÄREBORN, I. 1970. Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. *Oikos*, **21**, 285–291.

APPENDIX

List of all recorded shelled land snail species

For each species a number of its records within each type of floodplain forests and mean relative abundances (calculated as a mean of relative abundances at all sites of a floodplain forest type) are given. Species are arranged according to their total frequency (the last column). Groups: A, initial stages of the softwood floodplain forest association *Salici-Populetum* (= S-P, I); B, softwood floodplain forest of the ass. *S.-P. phragmito-caricetosum*, *S.-P. myosotidetosum* and *S.-P. typicum* var. with *Rubus caesius* (S-P, II–IV); C, softwood floodplain forest of the ass. *S.-P. typicum* var. with *Urtica dioica* and *Swida sanguinea* (S-P, V & VI); D, transitional floodplain forests ass. *Fraxino-Populetum* (VII); E, hardwood floodplain forest of the ass. *Ulmo-Fraxinetum* and *Ulmo-Quercetum* (VIII–IX).

Individual group of sites	A	B	C	D	E	No. of sites
Species/Number of sites	3	9	11	8	11	42
Monachoides incarnatus (O.F. Müller, 1774)	0	4/0.4	11/6.4	8/6.6	11/6.9	34
Aegopinella nitens (Michaud, 1831)	0	1/0.4	11/25.4	8/39.7	11/49.5	31
Arianta arbustorum (Linné, 1758)	1/4.8	9/9.3	10/4.6	5/2.2	2/2.9	28
Cochlicopa lubrica (O.F. Müller, 1774)	0	0	10/3.5	8/4.1	9/2.6	27
Cochlodina laminata (Montagu, 1803)	1/1.2	9/6.1	10/8.4	3/2.1	4/0.9	27
Helix pomatia Linné, 1758	0	0	8/0.6	8/1.2	10/1.5	25
Urticicola umbrosus (C. Pfeiffer, 1828)	1/1.2	2/0.2	7/1.8	8/2.2	8/4.1	25
Clausilia pumila C. Pfeiffer, 1828	0	2/0.1	7/3.9	7/2.9	7/3.1	23
Fruticicola fruticum (O.F. Müller, 1774)	1/4.2	5/0.7	11/3.7	4/1.1	2/1.8	23
Cepaea hortensis (O.F. Müller, 1774)	0	8/2.5	9/0.7	2/0.2	3/1.5	22
Petasina unidentata (Draparnaud, 1805)	0	0	6/3.6	7/12.1	10/4.3	22
Alinda biplicata (Montagu, 1803)	0	0	10/4.2	6/4.6	3/1.3	19
Succinea putris Linné, 1758	3/38.8	9/13.8	5/0.3	2/0.7	0	19
Zonitoides nitidus (O.F. Müller, 1774)	2/14.8	9/18.7	6/1.7	2/0.3	0	19
Carychium minimum O.F. Müller, 1774	1/14.3	9/28.3	5/4.1	2/0.7	1/0.2	18
Punctum pygmaeum (Draparnaud, 1801)	0	2/0.2	6/6.8	4/2.9	6/11.8	18

Continued

APPENDIX *Continued*

Individual group of sites Species/Number of sites	A 3	B 9	C 11	D 8	E 11	No. of sites 42
Vitrea crystallina (O.F. Müller, 1774)	0	6/2.3	7/7.0	2/2.5	3/0.3	18
Semilimax semilimax (Férussac, 1802)	0	0	7/3.2	4/0.8	4/0.9	15
Trichia striolata danubialis (Clessin, 1874)	0	6/3.8	7/2.8	2/1.7	0	15
Pseudotrichia rubiginosa (A. Schmidt, 1853)	1/6.1	8/4.7	2/0.4	1/0.3	0	12
Trichia hispida (Linné, 1758)	2/10.4	2/0.3	6/3.5	2/0.5	0	12
Euconulus fulvus (O.F. Müller, 1774)	1/1.9	5/0.7	3/0.1	2/0.4	0	11
Vitrina pellucida (O.F. Müller, 1774)	0	1/0.1	1/0.1	4/1.3	4/0.6	10
Vallonia costata (O.F. Müller, 1774)	0	0	5/0.7	2/0.7	2/0.1	9
Oxyloma elegans (Risso, 1826)	1/2.4	6/1.8	0	0	0	7
Succinella oblonga (Draparnaud, 1801)	0	4/4.8	1/0.2	2/0.4	0	7
Columella edentula (Draparnaud, 1805)	0	0	0	0	6/1.4	6
Discus rotundatus (O.F. Müller, 1774)	0	0	2/1.4	2/7.1	2/3.4	6
Vallonia pulchella (O.F. Müller, 1774)	0	0	3/0.1	2/0.2	0	6
Cepaea vindobonensis (Férussac, 1821)	0	0	1/0.1	1/0.1	3/0.4	5
Carychium tridentatum (Risso, 1826)	0	1/0.1	1/0.4	2/0.3	0	4
Euconulus praticola (Reinhardt, 1883)	0	3/0.8	0	0	0	3
Monacha cartusiana (O.F. Müller, 1774)	0	0	2/0.1	0	0	2
Truncatellina cylindrica (Férussac, 1807)	0	0	0	0	2/0.1	2
* *Acanthinula aculeata* (O.F. Müller, 1774)	0	0	0	0	1/0.4	1
* *Aegopinella minor* (Stabile, 1864)	0	0	0	0	1/0.1	1
* *Cochlicopa nitens* (Gallenstein, 1848)	0	1/0.1	0	0	0	1
* *Euomphalia strigella* (Draparnaud, 1801)	0	0	0	1/0.1	0	1
* *Perpolita hammonis* (Ström, 1756)	0	0	1/0.1	0	0	1
* *Pupilla muscorum* (Linné, 1758)	0	0	1/0.2	0	0	1
* *Vitrea contracta* (Westerlund, 1871)	0	0	0	0	1/0.1	1
Species total	11	23	32	30	25	41

*Species excluded from the DCA analysis.