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Woodland mollusc communities along environmental gradients in the East Carpathians

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Abstract: Mollusc communities were sampled quantitatively at eleven sites representing different environmental conditions in the Bieszczady National Park (East Carpathians Mts, Poland). Overall 61 species were recorded. Alder forest in the valleys (AF; *Alnetum incanae carpathicum*, *Caltho-Alnetum,* secondary alder forest) hosted the richest fauna, with up to 41 species occurring sympatrically on 100 m^2 of forest floor and average density ca. 750 specimens m^{-2}. Three important ecological controllers of species composition and community structure were found. The main predictor of mollusc assemblage composition was calcium content; the first DCA axis of molluscs most significantly and highly correlated with calcium content in the leaf litter and organic matter in the upper layer. The second axis significantly correlated with altitude and negatively with annual temperature, and thus can be explained as an elevational gradient. We observed slope aspect to constitute the third significant gradient. On the basis of forward selection in CCA analysis organic matter in the upper layer of soil was the best predictor of species composition, which explained 26% of total variance. It comes to prove that in mountain forest on non-calcareous bedrock molluscs obtain calcium mainly from leaf litter.

Key words: molluscs; community structure; woodland; calcium; leaf litter; elevation gradient

Introduction

Patterns of land snail distribution in various parts of the world have attracted much attention since the work of Solem (1984). Regional mollusc diversities are low in northern temperate regions, as their fauna derived from postglacial immigration, but some site diversities are high (Nekola & Smith 1999; Pokryszko & Cameron 2005). According to Waldén (1981) species with similar ecology tend to accumulate rather than replace each other in rich sites. Recently Barker & Mayhill (1999), Cowie et al. (1995), Tattersfield et al. (2001) and others have described the relationships between terrestrial gastropods and environment, but it was also found that the importance of the same ecological factors varied in different regions (Wäreborn 1969; Gosteli 1996). In comparison with the other parts of Central Europe, land snail distribution in the East Carpathians Mts is poorly known. The records were only qualitative (Kotula 1882; Ložek 1961–1962; Baidashnikov 1985, 1988) and allowed to distinguish species associated with different altitudinal zones in the region.

This study was aimed to explore relationships between diversity and structure of woodland malacocoenoses and environmental gradients in the Bieszczady Mts, a Polish part of the East Carpathians. The second goal was to find the main predictors of species composition and to explain ecological reasons for its variation.

Material and methods

Study area
The field work was carried out in 1997–2000 in the Bieszczady National Park situated in the Polish part of the East Carpathians bordering Slovakia and Ukraine. The bedrock of this area is formed by sandstones, siltstones and shales (flysch layers) with a locally significant content of calcium carbonate (up to 35%). Soils are predominantly Cambisols (mostly Dystric Cambisols; pH 4.0–5.0) (Skiba et al. 1998). Semi-hydrogenic soils and hydrogenic soils with higher soil reaction (pH 5.5–7.0) occupying scattered areas on slope bends and in valleys provide the most fertile forest habitats in the Bieszczady Mts.

In lower parts of the area the average annual temperature exceeds +6 °C, the growing season lasts 200–214 days and mean annual precipitation is ca. 900 mm (Nowosad 1996). On the highest ridges (1,300 m a.s.l.) the average annual temperature is lower than +3 °C, the growing season lasts 181–192 days and mean annual precipitation exceeds 1,200–1,300 mm.

The Bieszczady Mts are covered by deciduous forests, which ascend to upper timberline (ca. 1,000–1,200 m a.s.l.) (Michalik & Szary 1997). The fertile Carpathian beech forests (*Dentario glandulosae-Fagetum*) predominate (80% of forested area). More locally acidophilus mountain beech forests and sycamore forests (with *Acer pseudoplatanus*) occur. Stream banks up to 900 m a.s.l. are overgrown by alder forest (plant association *Alnetum incanae*). Alder swamps (*Caltho-Alnetum*) occur in isolated patches on low permeable soil. About 14% of the forested area is occupied by secondary forest communities, which spontaneously overgrew farmland deserted after 1944–1947. Humid places occurring between the timberline and alpine meadows are overgrown by shrubs of *Alnus viridis*.

Sampling sites

Eleven sampling sites were located along a transect crossing two main mountain ridges (Pasmo Graniczne and Pasmo Połonin). They represent the main forest communities of the area: beech forests (BF), sycamore forests (SF), alder forests (AF) and alder shrubs above the timberline (ASH).

1. Wielka Rawka Mts, typical fertile (eutrophic) Carpathian beech forest (*Dentario glandulosae-Fagetum typicum*).

2. Suche Rzeki, humid fertile Carpathian beech forest (*Dentario glandulosae-Fagetum lunarietosum*).

3. Połonina Caryńska Mts, humid fertile Carpathian beech forest with *Allium ursinum* (*Dentario glandulosae-Fagetum allietosum*).

4. Wielka Rawka Mts, dry fertile Carpathian beech forest (*Dentario glandulosae-Fagetum festucetosum*).

5. Wielka Rawka Mts, sycamore forest (*Aceri-Fagetum typicum*).

6. Czoło Mts, sycamore forest with *Allium ursinum* (*Aceri-Fagetum allietosum*).

7. Połonina Caryńska Mts, montane sycamore forest with *Lunaria rediviva* (*Lunario-Aceretum*).

8. Rzeczyca valley, Carpathian riverine alder forest (*Alnetum incanae carpathicum*).

9. Rzeczyca valley, montane alder swamp (*Caltho-Alnetum*).

10. Bereżki, secondary alder forest on formerly arable land abandoned after World War II.

11. Wielka Rawka Mts, subalpine shrubs with green alder (*Alnus viridis*).

Sampling procedure

At each plot (10 × 10 m) snails were collected from leaf litter twice: in spring (May – June) and in late summer (end of August, September) with Økland frame of 20 cm side. At each sampling occasion 25 sub-samples (together 1 m^2) were collected at a sampling plot. Samples were not collected randomly, but they reflected different microhabitats and vegetation within each plot. The same procedure was earlier applied by Dzięczkowski (1972). A total of 550 sub-samples were collected. The forest litter, superficial soil layer plus herbs were placed in plastic bags. Each sub-sample was hand-sorted twice: immediately after bringing to the laboratory and then after drying and sieving the material through sieves (mesh diameters: 5.0, 2.0, 1.0, 0.5 mm). Only living individuals were counted. The applied method is very efficient for sampling small, litter dwelling species, but the abundance of large snails, most slugs and tree dwellers can be underestimated (see Cameron & Pokryszko 2005). Thus, quantitative samples were supplemented with visual search.

Habitat description

The following features were noted for each site: altitude (m a.s.l.); slope angle; slope aspect; number of plant species; canopy cover; shrub cover; herb cover; organic matter content in superficial soil layer; carbon/nitrogen ratio in the leaf litter; calcium content in the leaf litter; soil acidity; soil porosity. The analyses of soil were conducted in the laboratory (Okregowa Stacja Chemiczno-Rolnicza) in Lodz. For slope aspect analysis the following values were used: +1 for S slopes, −1 for N, 0 for E and W, etc. Mean annual temperature was estimated separately for convex and concave forms of terrain on the basis of the site altitude using formulae from Nowosad (1996). At each site the occurrence and cover of plant species (6 grade scale) were recorded. Indices of light, humidity, trophy, acidity and organic matter content were counted on the basis of plant ecological prefer-

Table 1. Ecological description of sampled station.

Site number	1	2	3	4	5	6	7	8	9	10	11
Site	Wielka Rawka	Suche Rzeki	Połonina Caryńska	Wielka Rawka	Wielka Rawka	Czoło	Połonina Caryńska	Rzeczyca valley	Rzeczyca valley	Bereżki	Wielka Rawka
Altitude (m above sea level)	800	725	1060	730	1175	1120	930	665	670	650	1250
Slope aspect	SE	N	S	SSE	NE	N	ENE	SE	E	NE	NE
Slope angle	5°	5°	15°	10°	25°	10°	40°	1°	2°	10°	15°
Relief form	convex	concave	convex	convex	convex	convex	convex	concave	concave	convex	concave
Average annual temperature (°C)	5.3	4.7	4.0	5.6	3.2	3.4	4.3	5.1	5.1	5.6	2.8
Canopy cover	80%	90%	80%	95%	75%	80%	65%	70%	70%	85%	–
Shrub cover	40%	30%	15%	15%	5%	50%	20%	20%	25%	15%	40%
Herb cover	60%	60%	65%	80%	65%	90%	80%	100%	100%	95%	97%
Number of plant species	28	28	20	16	27	42	29	50	41	41	39
Organic matter content (%)	14.1	8.15	14.77	11.19	15.13	16.68	13.13	9.67	36.6	19.57	17.2
Soil pH H_2O	3.6	5.0	3.6	4.0	4.0	5.0	3.7	6.2	5.4	4.5	5.2
Soil porosity (%)	68.85	69.7	69.24	68.53	74.3	65.2	73.17	64.9	82.83	77.17	86.3
C/N in leaf litter	35.32	33.37	33.65	30.68	21.9	32.43	28.92	23.62	17.54	18.14	24.65
Calcium in leaf litter (mg dm^{-3})	295	500	235	285	310	400	400	690	935	605	550
Index of light – L	2.35	2.23	2.46	2.38	2.69	2.66	2.28	2.70	3.11	2.85	3.08
Index of humidity – W	3.44	3.53	3.48	3.52	3.55	3.70	3.22	3.58	3.86	3.62	3.64
Index of trophy – Tr	3.79	3.92	3.92	3.57	3.83	3.95	3.75	4.00	3.89	3.73	3.72
Index of acidity – R	3.85	3.98	3.94	3.76	3.90	4.09	3.92	4.08	3.98	3.98	3.70
Index of organic matter content – H	3.08	3.11	3.06	3.05	3.14	3.14	3.03	2.99	3.21	3.12	3.10

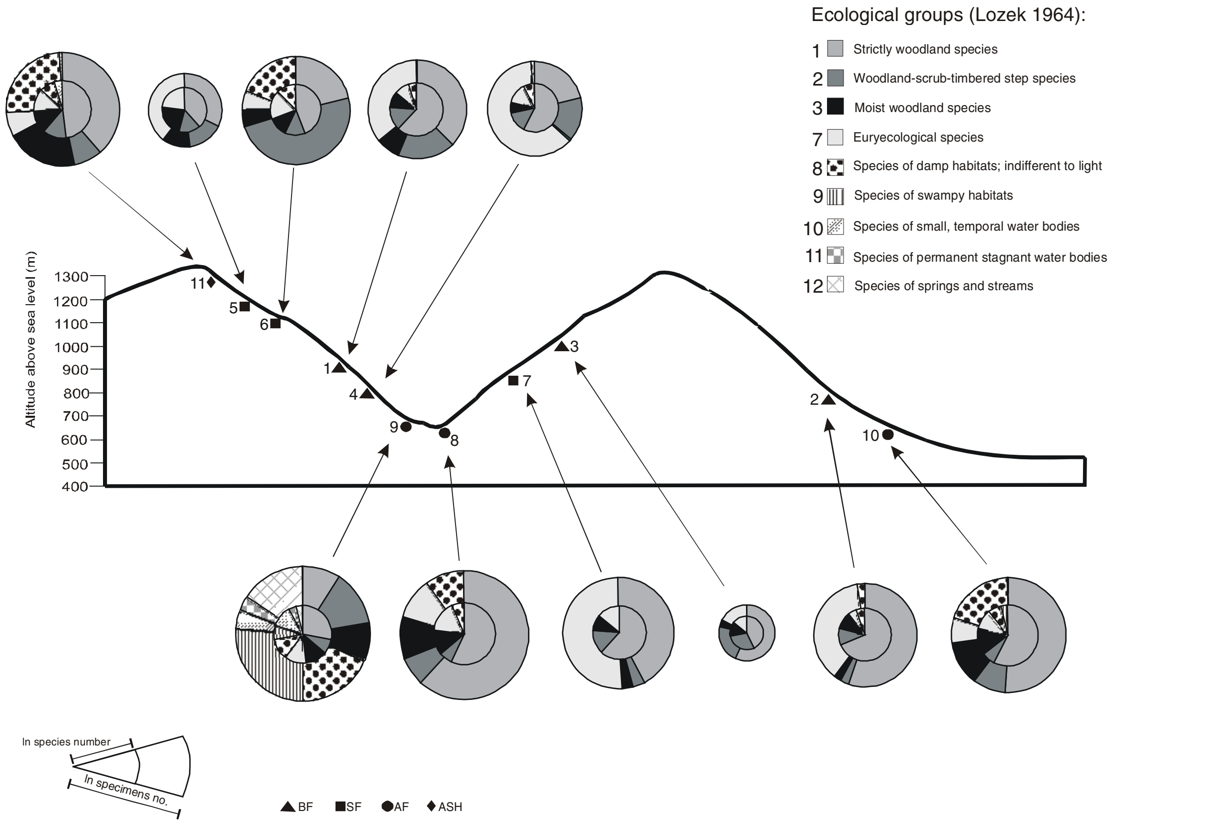

Fig. 1. Ecological characteristic of malacofauna at study sites in the Bieszczady National Park.

ences (Zarzycki 1984). Exact values of these parameters are given in Table 1.

Statistical analysis
The pattern of mollusc distribution was examined using species richness per site, the share of particular species in the malacocoenoses (dominance) and frequency (F) of their occurrence in sub-samples. The similarity of malacocoenoses was investigated using Jaccard index for present/absent data and Sørensen index, modified by Bray & Curtis, for quantitative data (Magguran 1988). For dendrogram construction Complete linkage and Ward's methods of agglomeration in *Statistica* package were employed.

The measured variables were log-transformed due to their un-normal distribution (assessment based on Kolmogorov-Smirnov test). The mollusc species-by-sample matrix was subjected to detrended correspondence analysis (DCA). Mollusc data were log transformed to reduce the influence of dominants. The vegetation composition was expressed as DCA ordination scores for each site (axes 1–4). To interpret ecological gradients related to the first two DCA axes of snail data, ordination scores (axes 1–4) of individual sites were correlated with explanatory variables using Pearson's correlation coefficient. In order to find the best predictor of snail species composition, forward selection in canonical correspondence analysis (CCA) was performed. The Monte Carlo test was applied for determining the significance of the canonical axes. Multivariate analyses were carried out with CANOCO 4.5 package (Ter Braak & Šmilauer 2002).

Results

In quantitative samples of the leaf litter 56 species (including three freshwater snails and two bivalves) were recorded (Table 2). Frequency of every species at the study sites are also shown in Table 2. Additionally, *Cochlodina laminata*, *Clausilia cruciata*, *Macrogastra borealis* and *Helix pomatia* were found on tree trunks and logs and empty shells of *Succinea oblonga* in leaf-litter. At the sites studied 65% of species were subrecedent (overall dominance $< 1\%$). Zonitids, endodontids and ellobiids were most abundant, however, in terms of species richness clausiliids predominated. Number of species varied at study sites, the highest species richness being recorded in *Alnetum incanae carpathicum*, with a maximum richness of 18 taxa occurring in a single 0.04 m^2 sub-sample (mean for 50 sub-samples: 10.7 taxa).

Figure 1 shows the ecological characteristics of malacocoenoses described in terms of ecological groups (Ložek 1964). The highest number of woodland species (groups 1–3) was observed in communities in BF and SF, whereas the euryecological species (*Punctum pygmaeum*) often predominated in these habitats. Additionally, *Aegopinella pura*, *Ae. epipedostoma*, *Vitrea crystallina*, and *Acanthinula aculeata* were most abundant in BF (sites 1–4). They also predominated in other habitats, while *Semilimax semilimax, Vitrea transsylvanica, Oxychilus glaber, Balea stabilis, Eucobresia nivalis*, and *Bielzia coerulans* reached higher categories of dominance and frequency in BF compared with other types of forest. *Ena montana, Semilimax kotulae* and *Vitrea diaphana* were distinguishing species for SF (sites 5–7). The studied AF harboured numerous

Table 2. Abundance and frequency of the occurrence (%; in brackets) of particular mollusc species in quantitative samples (50 sub-samples at each site = 2 m^2); frequency > 50% in bold.

Species/Sites	1	2	3	4	5	6	7	8	9	10	11
Acicula parcelineata (Clessin, 1911)	1(2)	2(4)				6(8)		53(44)		14(16)	
Acicula polita (Hartmann, 1840)	1(2)							1(2)	3(4)	1(2)	
Carychium tridentatum (Risso, 1826)	1(2)	8(14)				366(42)		85(44)	126(**58**)	72(24)	66(20)
Carychium minimum O.F. Müller, 1774									428(**88**)	1(2)	
Succinea putris (L., 1758)									75(**54**)		
Cochlicopa lubrica (O.F. Müller, 1774)								29(40)	7(8)		
Columella edentula (Draparnaud, 1805)				2(2)		28(22)		41(**52**)	139(**68**)	35(38)	17(18)
Vertigo pusilla O.F. Müller, 1774								3(6)		1(2)	
Vertigo alpestris Alder, 1837							2(2)				
Vertigo substriata (Jeffreys, 1833)									75(50)		
Argna bielzi (Rossmässler, 1859)	7(4)						1(2)				
Acanthinula aculeata (O.F. Müller, 1774)	13(18)	16(26)	1(2)	18(26)		5(10)	57(**56**)	8(8)		29(34)	
Ena montana (Draparnaud, 1801)	3(4)				4(8)	11(20)	9(16)				
Punctum pygmeum (Draparnaud, 1801)	66(40)	123(**70**)	4(6)	111(**78**)	1(2)	29(34)	197(**76**)	29(26)	6(8)	29(34)	17(14)
Discus perspectivus (M. von Mühlfeld, 1818)	12(10)	1(2)						154(**80**)	45(36)	2(4)	1(2)
Arion subfuscus (Draparnaud, 1805)	5(10)	3(6)	7(14)	3(6)	1(2)	10(14)	7(12)	3(6)		4(8)	3(6)
Arion silvaticus Lohmander, 1937	9(14)	4(8)		9(14)	1(2)	5(6)	6(10)	5(8)		5(8)	2(4)
Vitrina pellucida (O.F. Müller, 1774)					14(22)	7(12)		70(46)		4(8)	4(6)
Eucobresia nivalis (Dumont et Mortillet, 1852)	2(4)	1(2)		4(8)			3(6)	46(26)		3(4)	2(4)
Semilimax semilimax (Férussac, 1802)	12(18)	9(14)		4(8)		3(6)	5(8)	14(18)		9(14)	
Semilimax kotulae (Westerlund, 1883)	3(6)		2(4)		8(14)	15(20)	4(4)				40(40)
Vitrea diaphana (Studer, 1820)		17(28)			1(2)	28(34)	1(2)	53(48)		29(30)	1(2)
Vitrea transsylvanica (Clessin, 1877)	4(4)	10(16)	1(2)	1(2)		42(34)	8(10)	82(**52**)		26(20)	19(30)
Vitrea crystallina (O.F. Müller, 1774)	40 (34)	5(10)	3(6)	27(38)	1(2)	23(20)	12(14)	80(**66**)	243(**80**)	36(36)	167(**68**)
Aegopinella pura (Alder, 1830)	14(16)	95(**72**)		2(4)	1(2)	47(34)	72(**68**)	62(44)	61 (50)	121(**64**)	60(48)
Aegopinella epipedostoma (Fagot, 1879)	11(14)	16(28)	11(16)	11(22)	11(20)	43(46)	28(40)	157(**86**)	18(20)	23(26)	
Oxychillus glaber (Rossmässler, 1835)	5(4)	3(6)		2(4)							
Oxychillus orientalis (Clessin, 1887)		1(2)								1(2)	
Nesovitrea hammonis (Ström, 1765)					9(8)						4(8)
Carpathica calophana (Westerlund, 1881)		10(20)		1(2)		1(2)	2(4)				
Deroceras rodnae Grossu et Lupu, 1965							1(2)				
Bielzia coerulans (M. Bielz, 1851)	2(4)	1(2)	2(4)	2(4)			3(6)			1(2)	1(2)
Lehmannia sp.juv.	2(4)	1(2)	2(4)				1(2)				
Euconulus fulvus (O.F. Müller, 1774)	27(28)			11(16)			40(34)	3(6)	4(8)	5(8)	
Cochlodina orthostoma (Menke, 1828)						14(8)	5(6)				
Ruthenica filograna (Rossmässler, 1836)								87(**64**)		2(4)	
Macrogastra tumida (Rossmässler, 1836)	7(12)	2(4)			1(2)	43(28)		83(**68**)	76(**66**)	10(16)	10(16)
Clausilia dubia Draparnaud, 1805						1(2)					
Balea stabilis (L. Pfeifer, 1847)	17(8)	1(2)		1(2)			5(8)	13(16)		3(6)	
Vestia gulo (E.A. Bielz, 1859)						6(10)		4(8)	98(**70**)	15(12)	
Vestia turgida (Rossmässler, 1836)		7(12)	1(2)		4(6)	60(42)	10(10)	31(38)	13(16)	15(20)	13(16)
Bulgarica cana (Held, 1836)	1(2)				2(4)						
Bradybaena fruticum (O.F. Müller, 1774)									2(4)		
Perforatella dibothrion (Klimakowicz, 1884)								15(26)		2(4)	
Perforatella vicina (Rossmässler, 1842)	14(10)			2(4)	2(4)		3(6)	19(28)		25(34)	
Trichia bakowskii (Poliński, 1924)						4(6)		27(32)	54(44)	6(12)	10(10)
Trichia lubomirskii (Ślósarskii, 1881)								2(4)			
Trichia bielzi (E.A. Bielz, 1860)								3(2)			
Chilostoma faustinum (Rossmässler, 1835)								2(4)	1(2)		
Isognomostoma isognomostoma (Schröter, 1784)		2(4)					1(2)				
Arianta arbustorum (L., 1758)						3(4)	1(1)	11(16)		15(16)	1(2)
Radix peregra (O.F. Müller, 1774)									4(6)		
Galba truncatula (O.F. Müller, 1774)						4(4)			67(**52**)		
Anisus leucostomus (Milett, 1813)									15(10)		
Pisidium personatum Malm, 1855									301(**66**)*		
Pisidium casertanum (Poli, 1791)									72		
No of species in quantitative samples	25	23	10	17	15	25	26	32	24	31	19

* Frequency for *Pisidium personatum* & *P. casertanum*

snails of moist woodland and other damp habitats, but there were also some differences in species composition among them. In riverine forest (*Alnetum incanae*) *Ae. epipedostoma* and *Discus perspectivus* predominated and were found constantly in the sub-samples (F > 60%). Additionally, *Acicula parcelineata, Vitrea di-*

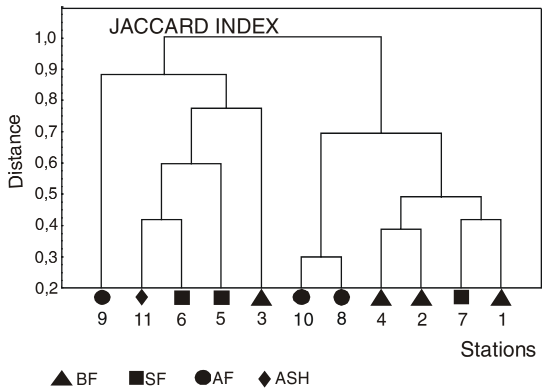

Fig. 2. Taxonomic similarity of mollusc communities at study sites in the Bieszczady National Park.

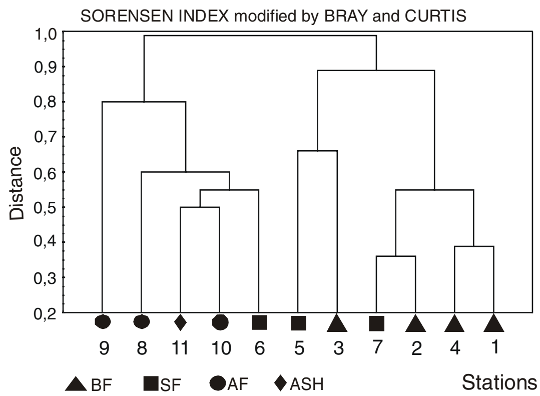

Fig. 3. Quantitative similarity of mollusc communities at study sites in the Bieszczady National Park.

aphana, V. transsylvanica, and *Ruthenica filograna* occurred there with higher frequency than in other forests. Site 9 (alder swamp) differed by small number of woodland species (< 50% of species; < 30% of specimens) and abundance of freshwater and hygrophilous species. Among land snails, *Succinea putris, Vertigo substriata, Columella edentula, Vestia gulo*, and *Trichia bakowskii* were collected more frequently in alder swamp than in other forest communities. In other AF woodland species constituted more than 75% of the fauna, and predominated also in specimen composition. Study sites in AF harboured 48 terrestrial and 5 freshwater mollusc species. Mollusc fauna in ASH was composed mostly of woodland species with significant proportion of moist woodland and wetland species. Euryecological snails were not numerous here, and open-ground species were absent.

In comparison to BF and SF, in AF (sites 8–10) the abundance of various species was more equal: eudominants were missing and relative abundance of several species was higher than 5.1%. There were no constant species in assemblages 1, 3, 5 and 6, as snails were sparsely distributed or found only in particular microhabitats.

Mollusc assemblages at sites 8 and 10, which had more than 30 species in common showed the greatest taxonomic affinity (Fig. 2). Both sites overgrown by *Alnus incanae* and situated at similar elevation were well-moistened but not swampy. The communities in BF (sites 1, 2, 4) and SF (site 7) grouped together also in a quantitative clustering (Fig. 3). The third group consisted of malacocoenoses from SF (sites 5–6), BF (site 3) and ASH (site 11). Their close affinity was a result of the presence of hygrophilous species and the absence of species with limited altitudinal range. The most outlying site (site 9) differed from others due to the presence of four aquatic species (not found elsewhere) and the absence of Arionidae, Agriolimacidae, Limacidae and Vitrinidae.

The first DCA axis of molluscs accounted for 34.2%, the second for 13.5% and the third for 5.7% of the variance of the correlation matrix. On the basis of DCA, three ecological gradients governing mollusc species composition were observed. High loadings on the first axis, reflecting Pearson correlations with the sample scores, were obtained for calcium content in the leaf litter ($r = 0.82$, $P = 0.002$) and organic matter in the upper layer ($r = 0.77$, $P = 0.006$). The second axis expressed the elevational gradient; higher loading was obtained for altitude ($r = 0.70$, $P = 0.017$) and annual temperature ($r = -0.76$, $P = 0.007$). The third DCA axis significantly correlated with slope aspect ($r = 0.74$, $P = 0.009$). Soil reaction significantly contributed to the first ($r = 0.68$, $P = 0.022$) as well as to the third axis ($r = 0.62$, $P = 0.043$). The fourth axis accounted only for a minor part of the variability and it was not significantly correlated with any analysed variable. On the basis of forward selection in CCA analysis, organic matter in the upper layer of soil was the best predictor of snail species composition, which explained 25.9% of total variance. The second significant variable was soil acidity, which explained 16.0% of total variance.

The result of the DCA analysis was in good concordance with the results of cluster analyses (Figs 2–4). These concordances indicated that mollusc assemblages reflected the first main ecological gradients in different ways. The gradient of calcium content influenced mainly community structure. The first division of studied sites in cluster analysis (Fig. 3) with Bray & Curtis index (for quantitative data) can be similarly made along the first DCA axis (Fig. 4). On the contrary, the first division of sites based on Jaccard index (for presence/absence data) is possible along the second DCA axis. Thus, the elevational gradient had a major impact on species composition.

The vegetation showed similar behaviour only for the calcium gradient (Fig. 4). Plants reflected the gradient of calcium content in the same way, the sites scores on the first PCA axis of plants significantly correlated with those on the first DCA axis ($r = 0.74$, $P < 0.009$). Plant assemblages also expressed this gradient in species richness; high loading on the first DCA axis was obtained for number of plant species ($r = 0.65$, $P = 0.030$).

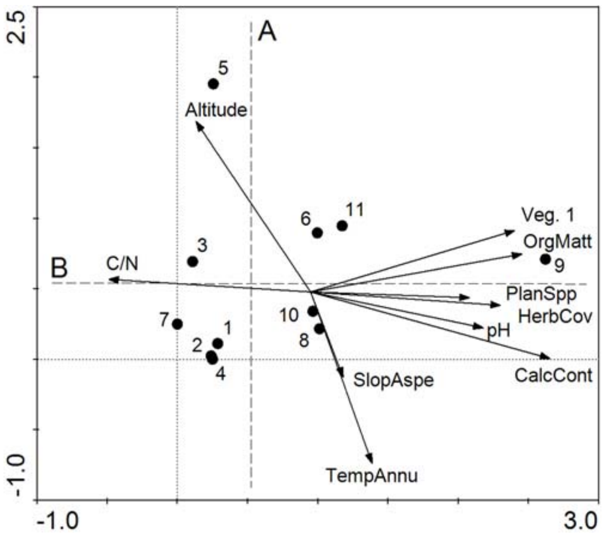

Fig. 4. DCA diagram of mollusc assemblages with a posteriori plotted explanatory variables: ordination plot of sites on the first two DCA axes. Only variables significantly correlated with sites' scores on first three DCA axes are shown. Eigenvalues: 1st axis 0.458, 2nd axis 0.180. Veg. 1 – sites' score on first DCA axis of vegetation, OrgaMatt – organic matter content in superficial soil layer, PlanSpp – number of plant species, HerbCov – herb cover, pH – soil reaction, CalcCont – calcium content in leaf litter, SlopAspe – slope aspect, TempAnnu – annual temperature. Dashed lines show first division of studied sites on the basis of cluster analysis using Bray and Curtis index (A) and Jaccard index (B).

Discussion

Land snail fauna of the Polish East Carpathians Mts comprises 80 species (Stworzewicz & Pawłowski 2000; Sulikowska-Drozd 2002), 70% of which were found at the study sites. Species richness recorded here is similar to other Carpathian sites, but is outstanding in comparison to lowland forests in northern Europe (Pokryszko & Cameron 2005). Over 50% of the regional fauna occurred within 100 m^2 on a single site, which corresponds to North American richness pattern documented by Nekola & Smith (1999). The species diversity in microscale was only slightly lower than the diversity recorded by Dyduch-Falniowska & Tobis (1989) in beech forests in the calcareous Tatra Mts.

Hitherto, malacocoenoses of Carpathian beech forests were considered most rich, with 70 species recorded in Poland (Dzięczkowski 1972). Even more taxa (108) were recorded in beech forest in Ukraine, where sycamore forests were inhabited by 96 and alder forests by only 72 species (Baidashnikov & Emelianov 1996). The presented paper looks at the differences between the assemblages from another point of view. If studied in small spatial scale (100 m^2), alder forests were most valuable in terms of mollusc syntopic richness, density and presence of rare species. Even small patches of floodplain forests in the East Carpathians seem to be important in terms of nature conservation. In contrast to other regions, those alder forests have not shrunk recently to give place for agriculture or been trampled by grazing cattle. On the other hand, the lower species richness in small special scale in beech and sycamore forest (here more oligotrophic) was clearly a result of even poorer frequency distribution of species, consequently requiring much bigger sampling effort (Cameron & Pokryszko 2005). Heterogeneity of fauna in these habitats was also suggested by low species frequency in sub-samples.

The assemblage composition in swampy alder forest is worth special attention. Pill-clams, which are able to survive periods of drying up (Piechocki & Dyduch-Falniowska 1993) were found here very frequently (> 60% of sub-samples). On the other hand, this habitat was avoided by semi-slugs and slugs, even by small species usually found in quantitative samples (Cameron & Pokryszko 2005). According to Wiktor (1989) slugs are missing on periodically submerged areas, where hiding places in the soil are lacking.

Regional differences between malacocoenoses of Carpathian beech forests were observed in the family Zonitidae. In the Bieszczady Mts, *V. crystallina* was more abundant than *V. diaphana*, which in turn predominated in malacocoenoses of the West Carpathians (Dzięczkowski 1972). In the study area the latter species was more frequently found in sycamore and alder forests than in beech forests. Three species of the genus *Aegopinella* could be dominants or subdominants in the malacocoenoses of the Carpathian beech forests, but replaced each other in different geographical regions. *Ae. epipedostoma* was characteristic of the Bieszczady Mts, and was absent or very rare in other regions. *Ae. nitens* was common in the Tatra Mts and the Babia Góra Mts (Dzięczkowski 1972) and *Ae. minor*, which avoided cold montane climate, occurred only in warmer or calcareous regions (uplands of the southern Poland, the Pieniny Mts) (Riedel 1988). The differences in the relative abundance of snails of the genus *Vitrea* and dominance of *P. pygmeum* in the beech forests in the Bieszczady Mts supported Dzięczkowski's (1988) view that these malacocoenoses resembled more the faunas of lowland beech forests than those of the West Carpathians.

The studied malacocoenoses of sycamore forests had taxonomic composition and dominance structure similar to that of beech forests (the same phytosociological alliances), which is in accordance with Dzięczkowski's (1988) conclusions about the level of the differentiation of malacocoenoses. The author found 38 species of Gastropoda in sycamore forests in the Bieszczady Mts, while malacocoenosis in *Lunario-Aceretum* situated at 1,000 m a.s.l. in the Alps was found very rich with 40 species and over 1,000 individuals collected from m^{-2} (Tröstl 2001).

The secondary forests in the Bieszczady Mts have grown between *Alnetum incanae* along the riverbeds and *Dentario glandulosae – Fagetum* at higher elevations. Native woodland fauna from these reservoirs could have gradually colonized previously agricultural land. Natural succession in this zone led to beech forests (Michalik & Szary 1997), but temporary presence of alder is probably advantageous for snails, as it results in the increase of the porosity, carbon and nitrogen contents and the decomposition rate in the soil (Kulig et al. 1974). Presently, mollusc assemblage from secondary forest had transitional character in respect of relative abundances and species composition. Taxonomically, it had a greater affinity to malacocoenoses of *Alnetum incane*. However, the lower frequency categories indicated less even distribution of specimens. The alder shrubs malacocoenosis also had a transitional character with many less demanding species reaching high abundance; the same was recorded for other invertebrates in subalpine zone (Pawłowski et al. 2000).

Impact of ecological factors on species richness and community structure

The highest species richness and mollusc abundance were recorded at the sites with the highest calcium content and the highest pH in the upper layer of soil. The close relationship between land molluscs and calcium content is well-known and it was observed by many authors in different geographical regions (Horsák 2006).

The relation between bedrock, soil properties and forest communities in the Bieszczady Mts is rather complex (Skiba et al. 1998). Most of the soil cover is not rich in alkalies. As a result of weathering processes the soil is decalcified even on flysch rocks abounding in $CaCO_3$. Higher value of soil reaction (pH 5.5–7.0) is characteristic of soils which are enriched in calcium cations by groundwater discharge. It is true for our data where the highest calcium content was measured in concave sites, close to sapping springs or brooks. Carpathian beech forests contribute significantly to the cycle of nutrients as they allow illuviated elements to get to the surface through deep reaching root system. This was also the case in oligothrophic areas in Sweden, where calcium content in leaf litter is more important for snail distribution than in underlying mineral soil (Wäreborn 1969). As snails utilize calcium mainly from their food and they are predominantly detritivorous animals, feeding on decaying litter (Dallinger et al. 2003), the composition of vegetation and leaf litter could be crucial for them, especially in areas with oligotrophic bedrock (i.e. very often higher mountains). Wäreborn (1970, 1979) showed that not every chemical form of calcium produces the same effect: oxalate salts, which prevail in beech leaf litter, were difficult to dissolve and did not increase immediately soil pH. Conversely, in leaves of lime, maple and elm calcium salts [Ca citrate] more easily dissolved, increased pH of soil and exerted positive influence on molluscs abundance and reproduction. Differences in palatability of different kinds of litter are also related to C/N ratio in fallen leaves (Ghilarov 1971). Beech leaves have higher C/N ratio and are decomposed at slower rate than alder leaves (Zimka & Stachurski 1976). At least in these two aspects the tree species composition played crucial role for snails.

The relationship between species richness and elevation were usually described by one of two patterns: a humped-shaped relationship, with peak in richness at intermediate elevations (Rahbeck 1995) or a monotonous decrease in species richness with increasing elevation (Stevens 1992). The latter corresponds well with results of malacological investigations in medium high mountains, where mountain summits are inhabited by lowland impoverished fauna (Bishop 1977; Cameron & Greenwood 1991). Similarly, in the Ukrainian East Carpathians the number of species was highest at the foothills (450–550 m a.s.l.) and in lower montane zone (1,200–1,300 m a.s.l.) and then it declined in the highest parts, where only few high-montane taxa occurred (Baidashnikov 1985; Baidashnikov & Emelianov 1996). On the contrary, some investigations (e.g., Pfleger 1982) showed that elevation had minor influence on the composition of malacocoenoses and species abundance. The effect of elevation can be detectable only within wide vertical range of studied sites and habitats, which did not differ in soil chemistry or general structure (e.g., only forests). In the Bieszczady Mts, only *Semilimax kotulae* which occurred usually above 700 m a.s.l. (Umiński 1980), could be regarded as high-montane species. *Nesovitrea hammonis*, was collected only above 1,100 m a.s.l. in the region. Its occurrence at lower altitudes was probably reduced by abundant carnivorous snails of the genus *Aegopinella* (see Mordan 1977). The same distribution pattern of *N. hammonis* was known from the Ukrainian Carpathians (Baidashnikov 1985, 1989). Distribution of the species recorded only in lower parts of the studied transect, such as *Carychium minimum, Ruthenica filograna, Bradybaena fruticum, Perforatella dibothrion, Trichia lubomirskii*, was limited by the mean annual temperature, the length of growing season, differences in productivity or, as suggested by Bishop (1977) and Getz & Uetz (1994), by the presence of suitable habitats.

In the Bieszczady Mts, slope aspect also influenced mollusc distribution. Southern slopes are warmer while northern and western slopes get the highest rainfall. These climatic differences caused by common dry winds from the south (36.5% days/year) are clearly visible in plant communities (Winnicki & Zemanek 1998). On the southern slopes dry fertile beech forests occur, while fertile plant communities with sycamore prefer northern, more shadowed and humid slopes (Michalik & Szary 1997). The same factors probably limit distribution of some hygrophilous snails dwelling in shadow places.

This study allowed us to identify three significant environmental gradients governing mountain forest mollusc assemblages. The gradient of calcium content is the main ecological gradient. Our findings proved organic matter to be the best predictor of species composition, providing also evidence that in the studied area snails obtain calcium mainly from leaf litter. We can conclude that this environmental gradient significantly outdid the others as the majority of measured factors corresponded to the gradient.

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