



MALACOCENOSES OF FIVE BEECH FORESTS IN POLAND

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ABSTRACT: Eighty species of terrestrial gastropods were found in five beech forests in Poland: in two forests of W. Pomeranian Lakeland 36 species, in Wielkopolska 30 species, in Carpathian beech forests of the Pieniny Mts 49 species and in the Beskid Niski Mts 26 species. The mean density in the beech forests in the Pieniny, Beskid Niski, Wielkopolska, acid and rich beechwood of W. Pomeranian Lakeland was 185, 86, 36, 36 and 10 indiv. m⁻², respectively. Dominant species in the Pieniny and Beskid Niski were *Aegopinella pura* (Alder), *Carychium tridentatum* (Risso), and in the lowland forests *Discus rotundatus* (O.F. Müller) and *Aegopinella nitidula* (Draparnaud). European elements and forest species dominated in such habitats. Montane beech forests showed a higher species diversity compared to lowland forests. The Carpathian beech forest in the Pieniny Mts had the highest mean density, number of species and species diversity. *Aegopinella pura*, *Vitrea crystallina* (O.F. Müller), *Discus rotundatus* and *Cochlodina laminata* (Montagu) can be regarded as indicator species of beech forests.

KEY WORDS: terrestrial gastropods, beech forests, W. Pomeranian Lakeland, Wielkopolska, Pieniny, Beskid Niski, Poland

INTRODUCTION

The structure of malacocenoses of beech forests in various regions of Poland was studied in 1985–2002. They included the forests of W. Pomeranian Lakeland, Wielkopolska, Pieniny and Beskid Niski (SZY-

BIAK 2000, 2002, SZYBIAK et al. 2005a, b) (Fig. 1). The aim of this paper was to analyse the species diversity and compare the structure of malacocenoses of five beech forests in Poland.

MATERIAL AND METHODS

The beech forests were sampled quantitatively and qualitatively in 1985–1987 in the Drawa National Park in W. Pomeranian Lakeland (acid beech forest *Luzulo-Fagetum*, and rich beech forest [Pomeranian beech forest] – *Melico-Fagetum*), in 1987–1994 in the nature reserve Buki nad Jeziorem Lutomskim in Wielkopolska (*Quercus-Carpinetum stachyretosum*

silvaticae, variant with *Fagus silvatica*), in 1995–1998 in the Pieniny National Park (Carpathian beech forest *Dentario glandulosae-Fagetum*), and in 2001 and 2002 in the Magura National Park in the Beskid Niski Mts (rich Carpathian beech forest *Dentario glandulosae-Fagetum*). Each malacocenosis was sampled in a few sites; samples were taken with biocenometer. The

quantitative studies were supplemented with visual search. The methods used were the same in all sites, to make the results comparable. Detailed descriptions of habitats and methods have been presented in our earlier papers (SZYBIAK 2000, 2002, SZYBIAK et al. 2005a, b).

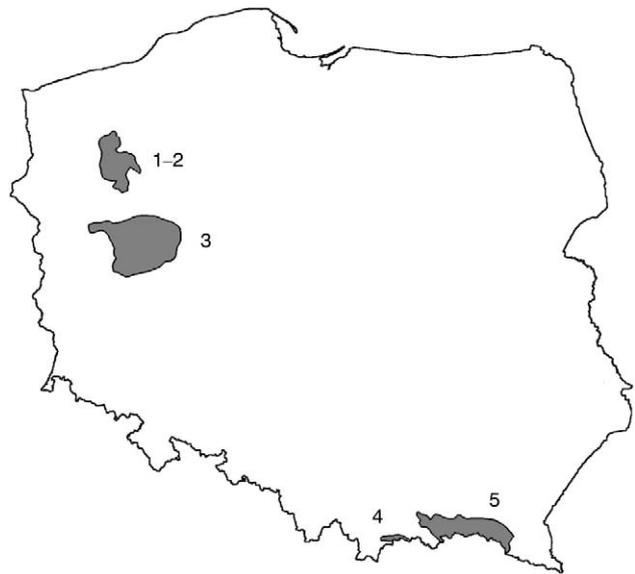


Fig. 1. Map showing the location of the studied beech forests: 1–2. Drawa Plain in W. Pomeranian Lakeland, with Drawa National Park, acid and rich beech forest; 3. Poznań Lakeland in Wielkopolska, with nature reserve Buki nad Jeziorem Lutomskim; 4. Pieniny Mts with Pieniny National Park; 5. Beskid Niski Mts with Magura National Park

RESULTS

Eighty terrestrial gastropod species were recorded from the studied beech forests, which is 46.5% species listed from Poland (RIEDEL 1988). The malacocenosis from the Carpathian beech forests was the richest in species (49 species). Thirty six species were found in the forests of W. Pomeranian Lakeland, 30 in Wielkopolska, 26 in the Beskid Niski (Table 1).

The malacocenoses of the Carpathian beech forests of the Pieniny and the Magura National Park had the most species in common (20 species); the forest of the nature reserve Buki nad Jeziorem Lutomskim and the acid beech forest of the Drawa National Park shared 18 species (Table 1). The following species were components of all the studied malacocenoses: *Discus rotundatus*, *Vitrea crystallina*, *Aegopinella pura* and *Cochlodina laminata*. *Semilimax semilimax* and *Daudebardia brevipes* were found only in the Magura National Park, while *Acicula polita*, *A. parcelineata*, *Succinea oblonga*, *Vertigo substriata*, *Argna bielzi*, *Discus perspectivus*, *Eucobresia nivalis*, *Aegopinella epipedostoma*, *Vitrea subrimata*, *V. diaphana*, *Isognomostoma isognomostoma*, *Oxychilus orientalis* – only in the Pieniny National Park. Species exclusive to the beech forest of Wielkopolska were *Succinea putris*, *Arion intermedius*, *Vitrea contracta*, *Nesovitrea petronella*, *Limax maximus*, *Trichia hispida*, while *Cochlicopa nitens*, *Vertigo pusilla*, *Vallonia pulchella*, *Arion circumscriptus*, *Lehmania marginata*, *Deroceras reticulatum*, *Perforatella bidentata*, *P. rubiginosa*, *Helicigona lapicida* were found only in the acid beech forests of W. Pomeranian Lakeland. Species of the rich beech forest of W. Pomeranian Lakeland were found also in other beech forests (Table 1).

In the Carpathian beech forests of the Pieniny Mts the mean density of gastropods was 185 indiv. m⁻², in

the Beskid Niski – 86 indiv. m⁻². The lowland malacocenoses were characterised by a lower mean density: in Wielkopolska 36 indiv. m⁻², in acid and rich beech forests of W. Pomeranian Lakeland 36 and 10 indiv. m⁻², respectively.

Dominant species (super- and eudominants) – with relative abundance exceeding 10% – in both Carpathian beech forests were *Carychium tridentatum* and *Aegopinella pura*. Besides, in the Magura National Park another dominant was *Vitrea crystallina* and in the Pieniny National Park – *Vitrea diaphana*. *Discus rotundatus* and *Cochlodina laminata* were dominant in the nature reserve Buki nad Jeziorem Lutomskim, and in the acid beech forest of the Drawa National Park – *Discus rotundatus*. Besides, the malacocenosis of the acid beech forest was dominated by *Vitrea crystallina* and *Aegopinella nitidula*. Table 2 presents dominant species (superdominants, eudominants and dominants, exceeding 5% relative abundance) in the studied beech forests. The group includes 15 species; of these two, *Cochlicopa lubrica* and *Nesovitrea hammonis* are euryoecious, another two, *Carychium tridentatum* and *C. minimum* are higrophiles. The remaining species are forest-dwellers. No species was dominant in all the studied forests. Dominants in the three lowland forests were *Discus rotundatus* and *Aegopinella nitidula*. Malacocenoses of the Carpathian beech forests and the acid beech forest of W. Pomeranian Lakeland were characterised by the highest proportion of subprecedents (ca. 50%) (Table 3). In the communities of the beech forest of Wielkopolska and the rich beech forest of W. Pomeranian Lakeland the highest relative abundance was that of subdominants (41.2% and 41.7%, respectively).



Table 1. Species composition, dominance (D), frequency (F): 1–9 ecological groups: 1 – typical forest species, rarely penetrating into other habitats; 2 – species found mainly in forests but common also in parks, gardens and other fairly shady habitats; 3 – forest and shade-loving species typical of very humid or marshy habitats; 5 – open country species associated with habitats of varied humidity; 7 – euryoecious species; 8 – species of humid but not marshy habitats of various degree of shading; 9 – species of very wet, periodically flooded habitats; zoogeographical groups: Ba – Boreal-Alpine; Eb – Ponto-Caspian and Balkan; Ee – E. European; Em – S. European; Ep – European; Es – Euro-Siberian; Ew – W. European, Atlantic; Hl – Holarctic; Ma – montane, Alpine and Carpathian; Me – C. European, lowland-upland; Pl – Palaearctic. Species found in qualitative samples marked with +

Species	Magura National Park		Pieniny National Park		Buki nad Jeziorem Lutomskim		Drawa National Park acid		Drawa National Park rich	
	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%
<i>Carychium minimum</i> O.F. Müller, 1774 [9, Es]	5.2	3.1			9.5	11.3	1.4	10.4		
<i>C. tridentatum</i> (Risso, 1826) [8, Ep]	62.2	12.5	11.9	39.6	0.7	1.7				
<i>Cochlicopa lubrica</i> (O. F. Müller, 1774) [7, Hl]	0.6	3.1					8.0	32.6	0.8	2.8
<i>Columella edentula</i> (Draparnaud, 1805) [8, Hl]	0.6	3.1	1.3	6.3		+	0.2	12.8		
<i>Ena obscura</i> (O. F. Müller, 1774) [1, Ep]	0.6	3.1			4.1	7.9	2.6	21.2		
<i>E. montana</i> (Draparnaud, 1801) [1, Me]		+	0.7	6.3						
<i>Discus rotundatus</i> (O. F. Müller, 1774) [2, Me]	0.6	3.1	0.9	6.3	30.1	34.6	17.7	34.2	63.3	56.1
<i>Semilimax semilimax</i> (Férussac, 1802) [1, Me]	0.6	3.1								
<i>Vitrea crystallina</i> (O. F. Müller, 1774) [2, Ep]	5.8	12.5	2.3	18.9	1.1	2.1	13.1	24.2	2.5	30.0
<i>V. transsylvanica</i> (Clessin, 1877) [1, Ma]	3.5	12.5	5.6	41.7						
<i>Aegopinella pura</i> (Alder, 1830) [1, Ep]	11.6	21.9	11.3	50.0	5.8	10.0	4.3	17.9	2.5	12.8
<i>Nesovitrea hammonis</i> (Ström, 1765) [7, Pl]	3.5	18.8			0.6	1.3	4.5	24.0	6.7	38.4
<i>Daudebardia brevipes</i> (Draparnaud, 1805) [1, Em]	2.3	6.3								
<i>Euconulus fulvus</i> (O. F. Müller, 1774) [7, Hl]	0.6	3.1	0.7	8.3			1.2	8.6	2.5	8.4
<i>Cochlodina laminata</i> (Montagu, 1803) [1, Ep]		+		+	23.6	18.3	1.9	18.0	1.7	12.8
<i>C. orthostoma</i> (Menke, 1830) [1, Me]		+	0.2	2.1						
<i>Macrogastra plicatula</i> (Draparnaud, 1801) [1, Ep]		+	0.7	8.3						
<i>M. latestriata</i> (A. Schmidt, 1857) [1, Ma]		+	1.6	6.3						
<i>M. tumida</i> (Rossmässler, 1836) [3, Ma]		+	1.6	14.6						
<i>Clausilia pumila</i> C. Pfeiffer, 1828 [3, Me]		+	0.2	2.1						
<i>Balea biplicata</i> (Montagu, 1803) [2, Me]		+	6.5	20.1						
<i>B. stabilis</i> (Pfeiffer, 1847) [1, Ma]	0.6	3.1	0.5	2.1						
<i>Vestia gulo</i> (E. A. Bielz, 1859) [3, Ma]		+	5.4	27.1						
<i>Perforatella incarnata</i> (O. F. Müller, 1774) [1, Me]	1.2	6.3	0.4	4.2	1.9	1.7				
<i>P. vicina</i> (Rossmässler, 1842) [3, Ma]		+	0.4	4.2						
<i>Chilostoma faustinum</i> (Rossmässler, 1835) [1, Ma]	0.6	3.1	0.7	8.3						
<i>Acicula polita</i> (Hartmann, 1840) [1, Me]			4.0	27.1						
<i>A. parcelineata</i> (Clessin, 1911) [1, Ma]			0.2	2.1						
<i>Succinea oblonga</i> Draparnaud, 1801 [8, Es]			0.5	4.2						
<i>S. putris</i> (Linnaeus, 1758) [9, Es]						+				
<i>Vertigo substriata</i> (Jeffreys, 1833) [8, Ba]			0.2	2.1						
<i>Argna bielzi</i> (Rossmässler, 1859) [1, Ma]			0.9	4.2						
<i>Acanthinula aculeata</i> (O. F. Müller, 1774) [1, Eb]			1.8	14.6			0.4	4.3	0.8	2.8
<i>Discus perspectivus</i> (Mühlfeld, 1816) [1, Eb]			0.2	2.1						
<i>Punctum pygmaeum</i> (Draparnaud, 1801) [7, Pl]			0.7	4.2						+
<i>Arion subfuscus</i> (Draparnaud, 1805) [7, Ep]			0.2	2.1		+		+		+
<i>Eucobresia nivalis</i> (Dumont et Mortillet, 1852) [1, Ma]			0.9	4.2						

Species	Magura National Park		Pieniny National Park		Buki nad Jeziorem Lutomskim		Drawa National Park acid		Drawa National Park rich	
	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%
<i>Aegopinella epipedostoma</i> (Fagot, 1879) [1, Me]			0.5	6.3						
<i>Vitrea subrimata</i> (Reinhardt, 1871) [1, Em]			4.0	25.0						
<i>V. diaphana</i> (Studer, 1820) [1, Em]			17.3	66.7						
<i>Cochlicopa lubricella</i> (Porro, 1838) [7, HI]					0.7	1.7	2.8	22.7	0.8	2.8
<i>C. nitens</i> (Gallenstein, 1848) [9, Ep]							0.4	6.6		
<i>Vertigo pusilla</i> O. F. Müller, 1774 [1, Ep]							0.2	2.4		
<i>Vallonia costata</i> (O. F. Müller, 1774) [5, HI]					+		0.2	3.2		
<i>V. pulchella</i> O. F. Müller, 1774 [5, HI]							0.2	2.2		
<i>Discus ruderatus</i> (Férussac, 1821) [1, PI]							0.5	8.2	5.0	28.4
<i>Arion rufus</i> (Linnaeus, 1758) [2, Ew]					+		+			
<i>A. circumscriptus</i> Johnston, 1828 [1, Ep]							+			
<i>Vitrina pellucida</i> (O. F. Müller, 1774) [7, PI]					4.3	6.7	0.4	5.3		
<i>Aegopinella nitidula</i> (Draparnaud, 1805) [1, Ew]					4.1	7.5	31.9	69.9	9.2	25.6
<i>Zonitoides nitidus</i> (O. F. Müller, 1774) [9, HI]					+		1.3	6.3		
<i>Limax cinereoniger</i> Wolf, 1803 [1, Ep]			0.2	2.1	+		+			
<i>Malacolimax tenellus</i> O. F. Müller, 1774 [1, Ep]							+		+	
<i>Lehmania marginata</i> (O. F. Müller, 1774) [1, Ep]							+			
<i>Deroceras reticulatum</i> (O. F. Müller, 1774) [7, Ep]							+			
<i>Macrogastra ventricosa</i> (Draparnaud, 1801) [3, Ep]			2.0	6.3			0.8	8.9		
<i>Clausilia bidentata</i> (Ström, 1765) [1, Ew]					3.9	7.5	2.3	16.9	4.2	8.4
<i>Bulgarica cana</i> (Held, 1836) [1, Me]			0.7	4.2			0.1	1.1		
<i>Perforatella bidentata</i> (Gmelin, 1788) [3, Ee]							3.2	21.3		
<i>P. rubiginosa</i> (A. Schmidt, 1853) [9, Es]							+			
<i>Helicigona lapicida</i> (Linnaeus, 1758) [7, Ew]							0.1	1.1		
<i>Cepaea hortensis</i> (O. F. Müller, 1774) [2, Ew]						+	0.1	1.1		
<i>Helix pomatia</i> Linnaeus, 1758 [2, Em]				+		+	0.1	1.1		
<i>Arion intermedius</i> Normand, 1858 [1, Ew]						+				
<i>Vitrea contracta</i> (Westerlund, 1871) [7, Ep]					3.2	6.3				
<i>Nesovitrea petronella</i> (L. Pfeiffer, 1853) [8, Ba]						+				
<i>Limax maximus</i> Linnaeus, 1758 [1, Em]						+				
<i>Laciniaria plicata</i> (Draparnaud, 1801) [7, Ep]			3.8	4.2	2.6	3.3				
<i>Trichia hispida</i> (Linnaeus, 1758) [7 Ep]					2.6	5.0				
<i>Isognomostoma isognomostoma</i> (Schröter, 1784) [1, Me]			2.3	16.7						
<i>Oxychilus orientalis</i> (Clessin, 1887) [1, Ma]			0.7	6.3						
<i>Daudebardia rufa</i> (Draparnaud, 1805) [1, Em]			1.1	10.4						
<i>Ruthenica filograna</i> (Rossmässler, 1836) [1, Me]			3.6	22.9						
<i>Clausilia dubia</i> Draparnaud, 1805 [7, Me]				+						
<i>Vestia turgida</i> (Rossmässler, 1836) [3, Ma]			0.9	6.3						
<i>Bradybaena fruticum</i> (O. F. Müller, 1774) [2, Ep]				+						
<i>Trichia unidentata</i> (Draparnaud, 1805) [1, Ma]			0.7	4.2						
<i>T. villosula</i> (Rossmässler, 1838) [8, Ma]				+						
<i>Arianta arbustorum</i> (Linnaeus, 1758) [2, Me]				+		+				
<i>Bielzia coerulans</i> (M. Bielz, 1851) [1, Ma]				+						
Total species			26	49	29	35	35	15		



In individual beech forests the same species occupied the main positions, both with respect to dominance structure and frequency. The most frequent were forest dwellers: *Aegopinella pura*, *A. nitidula* and *Discus rotundatus*. They were constant, accessory or accidental species, depending on the malacocenosis.

The malacocenoses of of the nature reserve Buki nad Jeziorem Lutomskim and of the rich beech forest of the Drawa National Park (Table 4) were the most similar in their dominance structure. The Morisita index (HORN 1966) for them was 0.687. Other pairs of high similarity in their dominance structure were the

Table 2. Dominant species of the studied beech forests

Dominant species (D >5.0)	Magura National Park	Pieniny National Park	Buki nad Jeziorem Lutomskim	Drawa National Park acid	Drawa National Park rich
<i>Aegopinella nitidula</i>			+	+	+
<i>Vitrea crystallina</i>	+		+	+	
<i>Discus rotundatus</i>			+	+	+
<i>Cochlicopa lubrica</i>			+	+	
<i>Carychium tridentatum</i>	+	+			
<i>C. minimum</i>	+		+		
<i>Aegopinella pura</i>	+	+			
<i>Vitrea diaphana</i>		+			
<i>V. transsylvanica</i>		+			
<i>Discus ruderatus</i>					+
<i>Cochlodina laminata</i>			+		
<i>Vestia gulo</i>		+			
<i>Balea biplicata</i>		+			
<i>Acicula polita</i>		+			
<i>Nesovitrea hammonis</i>					+

Table 3. Percentage and number of of species in dominance categories in the studied malacocenoses

Malacocenosis	Eudominants & dominants combined >5.1%	Subdominants 2.1-5.1 %	Recedents 1.1-2.0 %	Subrecedents <1.1 %
Magura National Park	25%	18.8%	6.3%	45.0%
16 species	4 species	3 species	1 species	8 species
Pieniny National Park	14.3%	14.3%	14.3%	57.1%
42 species	6 species	6 species	6 species	24 species
Buki nad Jeziorem Lutomskim	23.5%	41.2%	11.8%	23.5%
16 species	4 species	7 species	2 species	3 species
Drawa National Park acid	14.8%	22.2%	14.8%	48.1%
27 species	4 species	6 species	4 species	13 species
Drawa National Park rich	25.0%	41.7%	8.3%	25.0%
12 species	3 species	5 species	1 species	3 species

Table 4. Morisita similarity index as modified by HORN (1966) for dominance structure of the studied beech forests

Beech forest	Magura National Park	Pieniny National Park	Buki nad Jeziorem Lutomskim	Drawa National Park acid	Drawa National Park rich
Magura National Park	–	0.373	0.066	0.058	0.026
Pieniny National Park	0.373	–	0.093	0.081	0.038
Buki nad Jeziorem Lutomskim	0.066	0.093	–	0.479	0.687
Drawa National Park acid	0.058	0.081	0.479	–	0.518
Drawa National Park rich	0.026	0.038	0.687	0.518	–

rich and acid beech forests of W. Pomeranian Lakeland ($M=0.518$), and the beech forest of Wielkopolska and acid beech forest of W. Pomeranian Lakeland ($M=0.479$).

The malacocenoses of the beech forest of Wielkopolska and the acid beech forest of W. Pomeranian Lakeland, besides their dominance structure, were the most similar in their species composition (Table 5). Their similarity index (MARCZEWSKI & STEINHAUS

1958) was $s=0.422$. Also the rich and acid beech forests of W. Pomeranian Lakeland were similar in their species composition ($s=0.389$); the same is true of the forests of the Pieniny Mts and Beskid Niski ($s=0.364$). The similarity indices consider species found in both quantitative and qualitative samples.

Species diversity H' (TROJAN 1992) of the studied forests ranged from 2.065 to 4.65 (Table 6), the diversity index TDI (ALEXANDROWICZ 1987) was

Table 5. Marczewski & Steinhaus similarity index for species composition of the studied beech forests

Beech forest	Magura National Park	Pieniny National Park	Buki nad Jeziorem Lutomskim	Drawa National Park acid	Drawa National Park rich
Magura National Park	–	0.364	0.217	0.200	0.200
Pieniny National Park	0.364	–	0.145	0.169	0.146
Buki nad Jeziorem Lutomskim	0.217	0.145	–	0.422	0.314
Drawa National Park acid	0.200	0.169	0.422	–	0.389
Drawa National Park rich	0.200	0.146	0.314	0.389	–

Table 6. Species diversity indices H' and TDI for the studied beech forests

Beech forest/index	Magura National Park	Pieniny National Park	Buki nad Jeziorem Lutomskim	Drawa National Park acid	Drawa National Park rich
H'	2.222	4.650	3.220	3.218	2.065
TDI	0.593	0.930	0.664	0.836	0.584

Table 7. Ecological classification (%) of component species of the studied malacocenoses

Ecological group Beech forest	Forest species	Euryoecious species	Species of humid and marshy habitats	Open country species of dry, warm habitats
Magura National Park	77.0	11.5	11.5	–
Pieniny National Park	79.6	10.2	10.2	–
Buki nad Jeziorem Lutomskim	46.7	26.7	20.0	6.7
Drawa National Park acid	55.8	20.6	11.8	11.8
Drawa National Park rich	56.3	37.5	6.3	–

Table 8. Zoogeographical composition (%) of the studied malacocenoses. Symbols as in Table 1

Beech forest Zoogeographic group	Magura National Park	Pieniny National Park	Buki nad Jeziorem Lutomskim	Drawa National Park acid	Drawa National Park rich
Ep (19 species)	23.1	20.4	34.5	37.1	33.3
Ma (15)	26.9	30.6			
Me (14)	26.9	26.5	10.3	5.7	6.7
Hl (7)	11.5	4.1	13.8	20.0	20.0
Em (6)	3.8	8.2	6.9	2.9	
Ew (6)			17.2	14.3	13.3
Pl (6)	3.8	4.0	6.9	11.4	26.7
Es (4)	3.8	2.0	6.9	5.7	
Ba (2)		2.0	3.4		
Eb (1)		2.0			
Ee (1)				2.9	

0.584-0.930. The highest diversity ($H' = 4.65$ and $TDI = 0.93$) was that of the malacocenoses from the Carpathian beech forest in the Pieniny Mts; among the lowland forests the nature reserve Buki nad Jeziorem Lutomskim was the most diverse ($H' = 3.222$, $TDI = 0.664$).

In all the studied beech forests forest-dwelling species formed a majority (Table 7); the forests of the Pieniny Mts (79.6%) and Beskid Niski (77.0%) holding the highest proportion of such species. All the mala-

cocenoses included species of humid and marshy habitats. Open-country and xerothermophilous species were found only in the nature reserve Buki nad Jeziorem Lutomskim and in the acid beech forest of the Drawa National Park. Malacocenoses of Carpathian beech forests were mainly composed of montane species Ma (Tables 1 and 8), C. European lowland-upland species Me and European species Ep. European and Holarctic Hl species predominated in the lowland malacocenoses.

DISCUSSION

The diversity in the structure of malacocenosis is affected not only by the geographical position of the site but also by numerous environmental factors (DZIĘCZKOWSKI 1988). Likewise, they exert a considerable influence on the species diversity. Each malacocenosis, though dwelling in a similar habitat, is characterised by a specific dominance structure. The structure changes also seasonally (SZYBLAK 2002). Additionally, the methods applied affect the number of recorded species and their density. The quantitative studies on malacocenoses of the five beech forests were conducted at different times during 18 years. The longest time (eight years) was devoted to the beech forests of Wielkopolska; the studies in the acid and rich forests of W. Pomeranian Lakeland lasted three years, in the Carpathian forests – four, in the Beskid Niski – two. The quantitative studies in different forests included different areas: in Wielkopolska we sampled a total area of 15 m², in W. Pomeranian Lakeland 47 m², in the Pieniny Mts and Beskid Niski 3 and 2 m², respectively. Everywhere, the quantitative sampling was supplemented with visual search which gives a more complete picture of species composition (CAMERON & POKRYSZKO 2005). Quantitative samples, except for the beech forests of Wielkopolska, were taken in different months which could affect the dominance structure of individual malacocenoses. The number and size of the samples, as well as the time of sampling, also affect the estimates of mean density in malacocenoses (CAMERON & POKRYSZKO 2005). The most reliable results were those obtained in the beech forest of Wielkopolska, which was sampled monthly during 15 months. The mean density there was 36 indiv. m⁻² at the range of 5–104 indiv. m⁻², depending on the month.

Among the 80 species recorded from the studied beech forests, 55 occur in the Carpathian forests (Pieniny and Beskid Niski). The lowland beech forests, with their 39 species, are poorer in species. Only four species are common to montane and lowland beech forests. They are typical forest-dwellers. *Aegopinella pura*, which inhabits nearly entire Europe, lives mainly in deciduous and mixed forests, and is a dominant species in Polish Carpathian beech forests

(RIEDEL 1988). In the studied malacocenoses of the Pieniny Mts and the Beskid Niski, as well as in Wielkopolska, it is a dominant; it is a subdominant in the beech forests of W. Pomeranian Lakeland. *Vitrea crystallina* is widespread in Europe. It lives in various kinds of forests, is common in the whole country but becomes increasingly less frequent eastward and southward. In the studied forests it is a eudominant in the acid beech forest of W. Pomeranian Lakeland, a dominant in the Beskid Niski, a subdominant in the Pieniny Mts and in the rich beech forest of W. Pomeranian Lakeland, and a recedent in Wielkopolska. *Discus rotundatus* is widespread in Poland, common in the west and less so eastward. It is a superdominant in Wielkopolska and the rich beech forest of W. Pomeranian Lakeland, eudominant in the acid beech forest of that lakeland, and a subrecedent in the Carpathian beech forests. *Cochlodina laminata* inhabits nearly the whole of Europe; it lives in deciduous and mixed forests; in Poland it is common in the entire area. It is a eudominant in Wielkopolska, a recedent in the beech forests of W. Pomeranian Lakeland, while in the Carpathian beech forests it was found only in visual search.

Dominant species in the Carpathian beech forests are *Aegopinella pura* and *Carychium tridentatum*, in the lowland beech forests *Discus rotundatus* and *Aegopinella nitidula*. Typical forest species occurring in the malacocenoses of all the studied forests, both montane and lowland, and not necessarily being members of the dominant group, are the earlier mentioned four species. These species (*Aegopinella pura*, *Vitrea crystallina*, *Discus rotundatus*, *Cochlodina laminata*) can be regarded as indicator species of beech forests.

Malacocenoses of the montane and lowland beech forests do not show a high similarity of their dominance structure and species composition which is obvious in view of their geographic position (for distributions of their component species see maps in WIKTOR 2004).

In the beech forests European species form the most numerous group (19 species), but in the Carpathian forests a majority is formed by montane species



whereas in the lowland forests a high proportion, besides European species, is constituted by Holarctic species. Compared to the Carpathian forests, in the lowland beech forests the percentage of euryoecious species is higher.

The malacofauna of the Carpathian beech forests is much richer than that of the lowland forests. Among the five compared beech forests the Pieniny Mts is the one with the highest mean density, species number and species diversity.

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