

LONG-TERM CHANGES IN MALACOCOENOSSES OF OAK-HORNBEAM FOREST (*QUERCO-CARPINETUM MEDIOEUROPAEUM*): AN ATTEMPT TO APPLY THE CAROUSEL MODEL

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Abstract: The authors compare the species composition and dominance structure of a snail community in the oak-hornbeam forest (*Quercus-Carpinetum medioeuropaeum*) over the period of more than 20 years. The total number of species forming the community has not changed. The dominant species in the assemblage in both seasons of study were *Nesovitrea hammonis* and *Aegopinella nitidula*. Of the 23 species found, only 11 were recorded in both periods of study. The species which had dwindled from the community have been replaced by species with similar or slightly lower incidence of occurrence in western Poland, while hygrophilous species have been replaced with species living in brushwood or associated with grassland. The authors believe that malacocoenoses in specific types of forest communities have a dynamic character which corresponds to the carousel model.

Keywords: malacocoenoses, oak-hornbeam forest (*Quercus-Carpinetum medioeuropaeum*), the carousel model.

“ In Memory of Prof. dr hab. Elżbieta Koralewska-Batura, a relentless snail researcher...”

INTRODUCTION

The reality and stability of invertebrate assemblages in specific types of environment (especially forest environments) is very poorly studied. There is a lack of long-term studies concerning the same objects in relation to individual taxa. Like in other invertebrate assemblages, this also applies to malacocoenoses.

One of the first and few attempts to answer the question whether and to what extent snails in ash-elm forest (*Fraxino-Ulmetum*) are stable, was the paper of Koralewska-Batura and Błoszyk (2007). Those authors indicated that the species composition of a community has been very stable in two subsequent years of research, and that the resemblance was very high and amounted to 80%. Only four out of 20 species found (representing 10 families) were not constant in assemblage and appeared in only one year of study. The dominance structure

in the subsequent years of research was similar, in spite of a significantly lower frequency of snails in the samples collected in the first year.

This paper is an attempt to answer a similar question concerning assemblage that occurs in the oak-hornbeam forest (*Quercus-Capinetum medioeuropaeum*) with a high proportion of beech and in a much longer perspective of 24 years, as such was the period after which the studies on the species composition and structure of the terrestrial snail assemblage in the Jakubowo Reserve in the Wielkopolska Province (western Poland) were repeated. The starting point for the research were the results achieved by Koralewska-Batura (1989) in the same reserve in 1981–1984.

Previously in the same reserve similar observations concerning another group of invertebrates, mainly the mites of the suborder Uropodina (Acari: Mesostigmata), were conducted (Błoszyk 1999; Błoszyk, Olszanowski 1985; Błoszyk, Athias-Binche 1998; Błoszyk et al. 1984, 1994, 2002, 2003a, b; Napierała 2008; Napierała et al. 2009).

Pristine oak-hornbeam forests are among the richest flora and invertebrate fauna environments in Poland. The agricultural development of Wielkopolska has led to the replacement of forest area with farmland. Consequently, the oak-hornbeam forests became fragmented, resulting in the isolation of local populations. The Jakubowo Reserve is situated in a small (ca. 110 ha), isolated forest complex, which was separated from other forests a long time ago, probably in the 14th century.

Changes in the species composition of the malacocoenoses observed in the reserve over the period of 25 years concern the replacement of a substantial part of species, while their overall numbers remain the same, which suggests that the carousel model of species-richness proposed by van der Maarel and his colleagues (Van der Maarel; Sykes 1993) could be used in the case of terrestrial snail assemblage.

The carousel model has so far been tested solely in relation to plant communities and concerned the tendency of species to reoccupy previously abandoned places (eg. Palmer & Rusch 2001; Sykes et al. 1994; Van der Maarel 2006). The representatives of soil fauna, including terrestrial snails, form communities that change over time, and the selection of the components of these communities is conducted randomly, from the entire accessible pool of species. The authors are the first to address the question whether plant and animal communities may be formed in a similar way.

MATERIALS AND METHODS

The Jakubowo Reserve (4.22 ha) preserves one of the most beautiful fragments of an old oak-hornbeam forest (ca. 200 years old) in western Poland, with

its beech variant (*Galio-sylvatici-Carpinetum* var. with European beech, *Fagus sylvatica*) (UTM: WU 81).

In the years 1981–1984 snails were collected using two methods: biocenometre (25 x 25 cm) from the area of 1 m² and with 20 Barber traps at two-week intervals, from May to September.

In the years 2005–2006 only one method was used – samples were collected using the biocenometre method from the area of 0.5 m² from three previously selected areas, which overlapped with the areas studied by Koralewska-Batura in the 1980s.

The difference in the sampling methods and the inability to acquire the initial samples from the first period of studies, preclude the testing of statistical differences. For this reason all the results are based solely on the constancy (*C*) and dominance (*D*) indices.

The long-term research conducted in various types of forest ecosystems near the Jakubowo Reserve enabled the researchers to isolate the set of species that forms communities in the deciduous forests of Wielkopolska.

RESEARCH RESULTS

A hypothetical malacocoenoses of the deciduous forests of Wielkopolska

In the deciduous forests of Wielkopolska near the Jakubowo Reserve, where the research was conducted – including oak-hornbeam and riparian forests – 31 terrestrial snail species were found (Tab. 1) (Koralewska-Batura 1989; Koralewska-Batura 1993; Koralewska-Batura, Błoszyk 2007; Koralewska-Batura et al. 2006). 17 most frequently represented species (55%) are usually comprised in the malacocoenoses, which are formed at individual sites. The remaining species appear randomly in various communities, usually as single specimens (subrecedents).

Differences in the species composition and dominance structure of malacocoenoses over time.

The comparison of the species composition and dominance structure of snail assemblages over the period of more than 20 years revealed significant differences, although the total number of species forming the community remained at the same level. In both cases there were 17 snail species (Tab. 2). Species similarity (*S*) in both compared communities was lower than it could be expected in that situation and amounted to 48%.

Out of the 23 species found in the Jakubowo Reserve, 11 were found in both study periods. 6 species which dwindled from assemblage over the period of 24 years have been replaced by the same number of species which were not previo-

Table 1. List of snail species found in the investigated areas in Wielkopolska

Species	Total	D [%]
<i>Nesovitrea hammonis</i> (Ström)	2750	25.85
<i>Columella edentatula</i> Draparnaud	1547	14.54
<i>Vallonia costata</i> O.F. Müll	994	9.34
<i>Cochlicopa lubricella</i> (Porro)	854	8.03
<i>Punctum pygmaeum</i> Draparnaud.	850	7.99
<i>Vitrea crystallina</i> (O.F. Müll.)	603	5.67
<i>Carichium minimum</i> O.F. Müll.	461	4.33
<i>Vertigo pusilla</i> O.F. Müll.	399	3.75
<i>Aegopinella pura</i> (Adler)	385	3.62
<i>Cepea hortensis</i> (O.F. Müll.)	335	3.15
<i>Aegopinella nitidula</i> (Drap.)	313	2.94
<i>Vertigo substriata</i> (Jeffreys)	291	2.74
<i>Monachoides incarnates</i> (O.F. Müll.)	293	2.75
<i>Acanthinula aculeate</i> (O.F. Müll.)	226	2.12
<i>Euomphalia strigella</i> Draparnaud	105	0.99
<i>Euconulus fulvus</i> (O.F. Müll.)	93	0.87
<i>Cochlicopa lubrica</i> (O.F. Müll.)	77	0.72
<i>Perforatella bidentata</i> (Gmelin)	17	0.16
<i>Fruticicola fruticum</i> (O. F. Müll.)	15	0.14
<i>Succinea oblonga</i> Draparnaud	8	0.08
<i>Vallonia pulchella</i> (O.F. Müll.)	6	0.06
<i>Arion subfuscus</i> (Draparnaud)	4	0.04
<i>Pupilla muscorum</i> (L.)	2	0.02
<i>Vitrina pellucida</i> (O.F. Müll.)	2	0.02
<i>Succinea putris</i> (L.)	2	0.02
<i>Zonitoides nitidus</i> (O.F. Müll.)	2	0.02
<i>Cochlicopa nitens</i> Kobelt	1	0.01
<i>Merdigera obscura</i> (O.F. Müll.)	1	0.01
<i>Trichia hispida</i> (L.)	1	0.01
Number of specimens	10 637	100.00
Number of species	29	

usly recorded. The dominant species in both study periods, which constituted more than 25% of the community, were *Nesovitrea hammonis* and *Aegopinella nitidula*. However, their participation in the assemblage was generally much lower than 24 years ago. *Nesovitrea hammonis* is a snail with a high ecological tolerance. It lives in forests or open biotopes, both dry and moist. *Aegopinella nitidula* resides in moist beech or alder forests. At the same time four species increased their participation in the community, almost threefold compared to the previous study period. These were: *Vitrea crystallina*, *Acanthinula aculeata*, *Carychium minimum* and *Vallonia pulchella*. These species are common, and live in the brushwood or occur in the litter. A distinct decrease was observed

Table 2. List of species and dominance structure of snail community in the Jakubowo Reserve in both periods of study: Jakubowo A – years 1981-1984. Jakubowo B – years 2005-2006. D % - domination. F% - frequency

Species	Jakubowo A		Jakubowo B	
	D %	F %	D %	F %
<i>Nesovitrea hammonis</i>			29.71	46.3
<i>Aegopinella nitidula</i>			27.41	42.6
<i>Cochlicopa lubricella</i>	44.36	64.0	0.46	1.4
<i>Cochlicopa lubrica</i>	31.13	50.0	2.91	6.5
<i>Vitrea crystallina</i>		12.0	10.41	19.0
<i>Monachoides incarnatus</i>	5.55	12.0	2.60	6.51
<i>Aegopinella pura</i>	4.65	9.0	3.52	8.3
<i>Acathinula aculeata</i>	3.04	10.0	4.75	10.7
<i>Euconulus fulvus</i>	2.50	6.0	1.53	3.7
<i>Carychium minimum</i>	2.15	8.0	3.68	7.4
<i>Fruticicola fruticum</i>	1.43	6.0		
<i>Vitrina pellucida</i>	1.25	3.0	0.61	1.9
<i>Zonitoides nitidus</i>	1.07	4.0		
<i>Vallonia pulchella</i>	0.72	4.0	1.07	1.9
<i>Pupilla muscorum</i>	0.72	2.0		
<i>Cochlicopa nitens</i>	0.54	2.0		
<i>Trichia hispida</i>	0.36	1.0		
<i>Punctum pygmaeum</i>	0.18	1.0	8.73	21.8
<i>Columella edentula</i>	0.18	1.0	1.84	3.7
<i>Vertigo pusilla</i>	0.18		0.31	0.9
<i>Euomphalia strigella</i>			0.31	0.9
<i>Vallonia costata</i>			0.15	0.5
Number of species	17		17	
Average density/m ²	89		48	
Number of specimens	559		653	
Number of unit samples	100		216	

in the presence of common species associated with the community, such as *Cochlicopa lubricella* and *Cochlicopa lubrica*. The hygrophilous species (*Zonitoides nitidus*, *Cochlicopa nitens*, *Trichia hispida*) in the community were replaced by species that live in brushwood or species associated with grasslands (*Punctum pygmaeum*, *Columella edentula*, *Euomphalia strigella*, *Vallonia costata*).

Another alarming issue is an almost twofold decrease in the number of snails in the reserve at the last quarter of the previous century. In the previous study an average snail density was 90 specimens per 1 m² (Koralewska-Batura 1989). Since then it has declined to under 50 specimens (Wąchnicka 2007).

The analysis of the graph (Fig. 1) shows that the main change in the dominance structure of snail assemblages in the subsequent years of study was mainly the

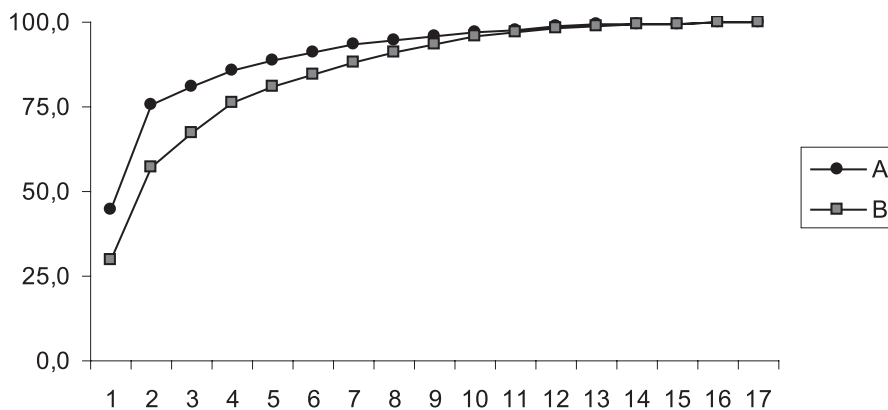


Fig. 1. Cumulative value of snail community dominance in the Jakubowo Reserve in subsequent years of study : A – in the years 1981-1984. B – in the years 2005-2006.

evening out of the participation of the most abundant species. In the first period of research (1981–1984), 2/3 of the entire community consisted of two dominant species in the reserve, in the second period of research (2005–2006) there were already four species.

DISCUSSION

The Jakubowo Reserve is undoubtedly one of the few places in the world, in which comparative studies on species composition and community structure of different groups of invertebrates have been conducted, using the same methods and in the same places, for more than 20 years (Błoszyk 1999; Błoszyk et al. 2003; Napierała 2008; Napierała et al. 2009).

The results obtained in the course of research, confirm earlier observations conducted by Błoszyk and his colleagues in relation to soil mites of the suborder Uropodina (Napierała 2008). The changes in the vegetation of the reserve which occurred over the period of 24 years as a result of the natural succession of undergrowth and ground cover vegetation undoubtedly had an impact on the species composition of the terrestrial snail communities of the reserve. The hygrophilous species were replaced by species living in brushwood or associated with grasslands. The basis of the dominance structure did not change, because in both periods of study the dominant species were *Nesovitrea hammonis* and *Aegopinella nitidula* from the Zonitidae family. The only difference was relative decrease of the number of those species in relation to the rest of the

species which form the community (75 to 57%). *N. hammonis* is one of the most common species in the Wielkopolska (407 sites – Koralewska-Batura et al – data in the study). This was also confirmed by the observations of the authors in other forest complexes (Koralewska-Batura et al. 2006; Koralewska-Batura, Błoszyk 2007). *A. nitidula* occurs in western Poland and is an infrequent species in the region of Wielkopolska, (Wiktor 2004). However, in the oak-hornbeam forests it is one of the most abundant and most frequently occurring species. It is interesting that species which dwindled from the community over the period 24 years, were replaced by species with similar or slightly lower incidence of occurrence in Wielkopolska. It has been so in the case of: *Fruticicola fruticum* (98), *Monachoides incarnatus* (156), *Zonitoides nitidus* (510), *Pupilla muscorum* (301), *Cochlicopa nitens* (80), *Trichia hispida* (236) replaced by *Punctum pygmaeum* (156), *Columella edentula* (91), *Vertigo pusilla* (109), *Euomphalia strigella* (129), *Vallonia costata* (391). Data in brackets indicate the numbers of known sites in Wielkopolska (Koralewska-Batura et al. 2010). These observations indicate that malacocoenoses in specific types of forest complexes have a dynamic character. Nearly half of the species have been replaced over the quarter of the century, while the species richness remained at the level of 17 taxa forming community. These are often common species (*Fruticicola fruticum*, *Monachoides incarnatus*, *Zonitoides nitidus*, *Pupilla muscorum*, *Trichia hispida*), which for unknown reasons are removed from the assemblage and replaced by another species, equally frequent in the given region (*Punctum pygmaeum*, *Columella edentula*, *Vertigo pusilla*, *Vallonia costata* – widespread species in Poland) (Wiktor 2004). Therefore, it can be assumed, that from the pool of all species, which can potentially form a community in a particular type of forest, only part of them occur simultaneously in a given site and time. They may also substitute for each other in the long run. Such changes in species composition have a fluctuating character, but so far there are no premises to maintain that they are directed in any particular way. This corresponds to the assumption of the carousel model proposed by van der Maarel and his colleagues (van der Maarel and Sykes 1993) as an outcome of the research on the species-richness of limestone grasslands on the Swedish island of Oland. It can be assumed that if the research presented above is repeated in 30 years, the results will be similar. The total number of species will remain at 17, and more species will fall out from the community and will be replaced by other species from the pool of 31 occurring in the deciduous forests in this area.

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WIELOLETNIE ZMIANY W ZGRUPOWANIU ŚLIMAKÓW LĄDOWYCH GRĄDU (*QUERCO-CARPINETUM MEDIOEUROPAEUM*) (REZERWAT JAKUBOWO, ZACHODNIA POLSKA): PRÓBA ZASTOSOWANIA MODELU KARUZELI

Streszczenie

Autorzy porównują skład gatunkowy i strukturę dominacji zgrupowań ślimaków w lesie grądowym (*Quercus-Carpinetum medioeuropaeum*) na przestrzeni ponad 20 lat. Ogólna liczba gatunków tworzących zgrupowania nie uległa w tym czasie zmianie. Gatunkami dominującymi w zgrupowaniu w obydwu okresach badań były *Nesovitrea hammonis* i *Aegopinella nitidula*. Spośród stwierdzonych 23 gatunków tylko 11 (48%) z nich odnotowano w obydwu okresach badań. Gatunki, które ubyły ze zgrupowania, zostały zastąpione gatunkami o zbliżonej lub nieco niższej częstości występowania w zachodniej Polsce. Ponadto gatunki hygrofilne zostały zastąpione gatunkami żyjącymi w zaroślach bądź związanymi z terenami trawiastymi. Autorzy uważają, że malakocenozy w poszczególnych typach zbiorowisk leśnych mają dynamiczny charakter, co może odpowiadać modelowi karuzeli Van der Maarela (2006).