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FOREST SNAIL FAUNAS IN THE KASZUBY UPLANDS (POMERANIA): A RICH NORTHERN REFUGE

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ABSTRACT: Forest snail faunas were sampled in three river gorges in the Kaszuby Uplands, Pomorze. 43 species were found, including 10 species of Clausiliidae. Taken with earlier records, these gorges hold 48 species. These faunas are markedly richer than most of those recorded in north and west Poland, especially for clausiliids, where up to eight species could be found in the same sample site. The fauna overall is very similar to that of the ancient Białowieża Forest much further east. The results suggest that many lowland forests in Poland have impoverished faunas, probably due to human activities, but there are a few refugia in which nearly all of the original forest fauna has survived. These give a better picture of natural patterns of distribution and change across the North European Plain.

KEY WORDS: forest snail faunas, Clausiliidae, Kaszuby

INTRODUCTION

Forest snail faunas in the North European Plain show rather slow turnover of species with distance, and, in comparable sites and localities, maintain rather similar levels of species richness (POKRYSZKO & CAMERON 2005). In some areas, however, faunas are poorer than expected. Samples from lowland Poland, with the notable exception of Białowieża Forest (CA-MERON & POKRYSZKO 2004) tended to be poor. In particular, although there were many clausiliids recorded in the region, there were few, often none, at any one site. This produced a very sharp contrast with the nearest montane faunas in the Sudetes, and POKRYSZ-KO & CAMERON (2005) suggested that these faunas might be adversely affected by human activity.

DROZDOWSKI (1981) reported on an exceptionally rich forest fauna from the Radunia gorge in the

STUDY AREA AND SAMPLE SITES

Figure 1 shows the positions of the sampled localities, and of the sample sites within each. Topographi-

Kaszuby Uplands west of Gdańsk. Both there, and in more heterogeneous habitats between Gdynia and Gdańsk (DROZDOWSKI 1979) there were more species of clausiliids, and of other regionally rare species than in other forests sampled in Pomerania and Wielkopolska. POKRYSZKO & CAMERON (2005) were unable to use these data in their study, because the sampling protocols used were not comparable. It appeared that there might be a refuge in which it would be possible to find a more complete forest fauna. We therefore resampled the Radunia gorge, together with two other smaller river gorges in August 2005 to obtain data comparable to others we had used. We discuss our results in relation to the forest faunas of north and west Poland, and in the broader context of the North European Plain.

cally, the area is one of low hills (up to c. 300 m a.s.l., but usually less than 200 m) formed by glacial and



Fig. 1. A map showing the study area, and the positions of sampling sites in each locality

periglacial deposits, interspersed with small river valleys and lakes. In general, soils are sandy, acid and low in plant nutrients. Most of the land is either in agricultural use or has a cover of heavily-managed coniferous forest, mainly Scots pine *Pinus sylvestris* or Norway spruce *Picea abies*.

The areas chosen for study are all river gorges, where the rivers have carved out relatively steep-sided valleys that have retained elements of natural, mixed forest vegetation. Of these, the Radunia gorge [Jar Raduni] near Żukowo is much the largest, with steep sides and mixed forest running along c. 5.2 km of the river. The gorge of the Reknica [Jar Reknicy] at Kolbudy is shorter (c. 2.5 km), and that of the Kłodawa [Dolina Kłodawy] just north of Trąbki Wielkie shorter still (c. 1.5 km). The forests in all three localities show signs of management, including some interplanting of conifers. The upper slopes of each are dominated by beech *Fagus sylvatica* or planted conifers; mixed deciduous forests are generally confined to the lower slopes and to the valley bottoms. In general terms, these forests fall into the *Ficario-Ulmetum* or *Tilio-Carpinetum* associations (DZIECZKOWSKI 1988).

Sample sites were therefore located close to the river, including the valley bottom and a part of the lowest slopes. They were chosen to include fallen and rotting timber. Apart from beech and scots pine, which were not abundant, trees present included linden Tilia cordata, elm Ulmus glabra, hornbeam Carpinus betulus, grey alder Alnus incana and in a few sites ash Fraxinus excelsior and oak Quercus robur. Understorey bushes were relatively uncommon, but there was hazel Corylus avellana or alder buckthorn Frangula alnus in a few sites. Planted conifers were more abundant at Trabki Wielkie than elsewhere. The commonest herbs were dog's mercury Mercurialis perennis and yellow archangel Galeobdolon luteum, but more acidophilous species such as wood sorrel Oxalis acetosella were present at some sites. Sampling was carried out in August 2005; it therefore missed some other typical plants such as wild garlic Allium ursinum recorded as dominant in Radunia by DROZDOWSKI (1981).

METHODS

Sampling, carried out in August 2005, basically followed the procedures used by CAMERON & POKRYSZ-KO (2004) in Białowieża Forest. Areas of c. 400 m² were searched by two people for one hour. About 15 l of litter was collected from patches at each site. This is more than was collected at Białowieża (10 l), and was done to increase numbers of shells retrieved. CAME-RON & POKRYSZKO (2004) found that the poorest samples might not reveal most of the fauna present (CA-MERON & POKRYSZKO 2005). The litter was sieved (10 × 10 mm mesh) in the field. Slugs and snails retained by this mesh were collected, and the residue discarded. Material passing through the sieve was

RESULTS

A total of 43 species of snail, and 8 species of slug were found in the samples. Table 1 shows the numbers of each snail species found at each site and at each lobagged, dried in the laboratory, and sorted down to 0.5 mm mesh. Large, easily identified species found were counted and left in the site. Slugs were identified, but not counted. They are omitted from our analyses and comparisons with other localities, as single visits are unreliable for making inventories (CAMERON et al. 2006).

All shells found or extracted were identified and counted, excluding very old or unidentified remains. Nomenclature follows KERNEY et al. (1983). Authorities are given in Table 1. Samples are held in the Museum of Natural History, Wrocław, or in the collection of RADC.

cality. Table 2 summarises data on snail species richness and sample size by locality, and shows the values of Whittaker's index ($I_w = S/\alpha$, where S = number of spe-

Table 1. Species composition of sites and localities in the Kaszuby Uplands

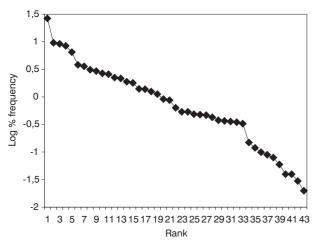
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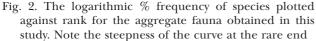
cies in the locality, and α = mean number of species per site), and of its modification, I_{max} , S divided by the number of species in the richest site. The richest sites held most of the fauna found in each locality, and the faunas have a degree of uniformity typical of N. European forests generally (POKRYSZKO & CAMERON 2005).

In terms of reliability, all samples yielded more than ten times as many individuals as species. The overall log % frequency on rank diagram (Fig. 2) shows a marked steepening at the rare end. Neither overall, nor in each locality considered separately, was any species represented by a single shell, and the Chao 1 estimator, based on numbers, of missed species overall is thus zero (SOUTHWOOD & HENDERSON 2000). Three species were found only at one site each, and five were found only in two; the Chao 2 estimator,

Table 2. Basic data for samples from the three localities from the Kaszuby Uplands. For $I_{\rm W}$ and $~I_{\rm MAX}$ see text

	Radunia	Kolbudy	Trąbki Wielkie	Total
Samples	6	5	3	14
Species	37	35	23	43
mean/sample	27.0	25.2	19.3	
range	22-31	21-30	17-21	
\mathbf{I}_{W}	1.37	1.39	1.19	
I _{MAX}	1.19	1.17	1.10	
Shells	3119	5343	1616	10078
mean/sample	521	1069	539	
range	403-846	667-1649	432-707	





based on occurrence, is thus 0.9 species. Within sites, numbers of singletons and doubletons are always low. Taking the average numbers of these per site in each locality, Chao 1 estimates of missed species per site are 0.95 for Radunia, 1.2 for Ręknica and 1.67 for Trąbki Wielkie. Sample sizes at Ręknica were more than double those at Radunia, but there was little difference in site species richness (Table 2). All the above suggest that inventories are nearly complete, at least for the particular range of habitats sampled (CAMERON & POKRYSZKO 2005).

Although Radunia and Reknica are very similar in richness both overall and at site level, their faunas are not identical (Table 3). Not only are some species missing from one or other of the sites, others also show substantial differences in mean abundance. There is no clear relationship between these differences and any recorded differences in habitats, except that sites in both Radunia and Trąbki Wielkie were on average slightly wetter than those in Kolbudy. Trąbki Wielkie sites were significantly poorer than those in the other two localities, and held no unique species. Ruthenica filograna and Perforatella bidentata, both typical of very wet places, were found there, and in Radunia, but not at Kolbudy. Some absences from Trąbki Wielkie involve species that were abundant in both the other localities, for example Cochlodina laminata, Clausilia bidentata, Macrogastra ventricosa, Laciniaria plicata and Aegopinella pura. Their absence is not simply a product of inadequate sampling.

Table 3. Differences in the recorded faunas of Radunia and Kolbudy. The ×5 columns show species that are at least five times more abundant per sample in the named locality. Trabki Wielkie held no unique species

Radunia only	Radunia ×5	Kolbudy only	Kolbudy ×5
Carychium minimum	Cochlicopa lubricella	Vitrea crystallina	Cochlicopa lubrica
Succinea oblonga	Vertigo pusilla	Oxychilus alliarius	Macrogastra latestriata
Vertigo substriata	Vitrina pellucida	Clausilia pumila	Bradybaena fruticum
Vertigo alpestris	Arianta arbustorum	Balea biplicata	
Nesovitrea petronella		Helicigona lapicida	
Ruthenica filograna		Helix pomatia	
Perforatella bidentata			
Euomphalia strigella			

DISCUSSION

THE LOCAL FOREST FAUNA

Analysis of our data suggests that our inventories are very nearly complete. Within the area studied, the different localities show distinct differences in fauna, which we cannot completely explain. Trąbki Wielkie in particular is missing a number of widespread and abundant species. It is the smallest, and most disturbed of our localities, while Radunia is the largest and richest at both site and locality level. We can suppose that past disturbances (perhaps, in particular, felling and the removal of dead timber) have eliminated some species that could not survive there. A more sophisticated study of microenvironments would be needed to account for the differences between Kolbudy and Radunia.

When a comparison is made with the work of DROZDOWSKI (1981) in Radunia (Table 4), it can be seen that while our samples from Radunia yield more species than those produced by his strict Oekland frame samples, there are several recorded by him that we did not find. He does not give details of the vegetation associated with each frame, nor over what area they were distributed. Most of the species he records and we do not are often associated with wetter and more open habitats within forests. Most were rare in

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his samples. Clearly, our samples have missed some of the habitats available within the forest complex, while his have missed both some litter-dwelling species, perhaps with very patchy distributions, and larger species, especially clausiliids, more often found by visual search including specific microhabitats such as logs and tree trunks. Some of these species were abundant.

In making comparisons with other forest faunas, we have combined our data with those of DROZDOWSKI (1981), since it is often the case that comparable studies include a wide range of habitats associated with forest, including edges and very wet patches. Thus, overall, these three localities, very close to each other, have an aggregate fauna of 48 snail species, including ten clausiliids. RIEDEL (1988) lists 74 snail species definitely recorded from Pomerania. Of these, 20 are species not normally found in forests; thus of the remaining 54, only six are missing from these three gorges. Three of these, Clausilia dubia, Perforatella incarnata and P. umbrosa appear to be missing from the north of the region altogether (WIKTOR 2004), while of the others, Discus ruderatus, Balea perversa and Bulgarica cana, the first two are rare and possibly declining. Radunia and Kolbudy between them contain nearly all the northern Pomerania forest snail fauna.

DROZDOWSKI (1981) noted that although the number of specimens he retrieved from Radunia was smaller than for other sites he examined in Pomerania, it was much the richest in number of species. Earlier (DROZDOWSKI 1979) he had discovered rich faunas in the coastal zone between Gdynia and Gdańsk, very close to our localities. A wooded valley held 36 species, and the fauna overall included five clausiliids as well as *Acicula polita, Oxychilus cellarius* and *Helicigona lapicida,* all species present in our sam-

Table 4. Species found only by DROZDOWSKI (1981), or only in this study in the Radunia gorge. *Vitrea crystallina* was found at Kolbudy in this study. Bracketed numbers are the total number of individuals found

DROZDOWSKI only	This study only
Vallonia pulchella (1)	Carychium minimum (3)
Vallonia costata (44)	Cochlicopa lubricella (37)
Vitrea crystallina (38)	Vertigo pusilla (47)
Zonitoides nitidus (23)	Vertigo alpestris (47)
Perforatella rubiginosa (3)	Aegopinella nitidula (17)
Cepaea nemoralis (1)	Oxychilus cellarius (3)
	Cochlodina orthostoma (14)
	Macrogastra latestriata (7)
	Clausilia bidentata (100)
	Laciniaria plicata (76)
	Euomphalia strigella (8)
	Arianta arbustorum (37)

ples, but rare in north and west Poland as a whole. The area appears to be exceptionally rich.

COMPARISONS ACROSS NORTH AND WEST POLAND

CAMERON & POKRYSZKO (2004) used data from 31 forest site surveys (including Radunia) in Pomerania, Wielkopolska and Nizina Mazowiecka to examine broad geographical trends across the North European Plain. For comparisons here, we have used the same data (less Radunia), for which references are given in CAMERON & POKRYSZKO (2004), with the addition of data from forest sites at Płutowo (DROZDOWSKI 1961) and at Drawa (SZYBIAK et al. 2005) to give a total of 34. Several of these studies appear to have included some open or very wet areas, and in making comparisons we have left out records of the following species that were recorded from some sites: Truncatellina costulata, Vertigo antivertigo, V. pygmaea, V. angustior, Pupilla muscorum, Vallonia excentrica, Chondrula tridens, Oxyloma elegans and O. sarsi. Of these, only V. pygmaea was at all frequent (c. 30% of sites).

Table 5 shows some comparisons between this data set and that obtained in this study. Overall, the numbers of species recorded (less those excluded above) in all these studies are no greater than those recorded for Kaszuby, despite the much larger area covered. The mean number of species per site is lower than that recorded in Radunia and Kolbudy, and only marginally greater than that for Trąbki Wielkie (see Table 2 for locality data). Some individual sites, however, are comparable to the richest in Radunia and Kolbudy. Only the nature reserve Buki nad Jeziorem Lutomskim, NW of Poznań (SZYBIAK 2002) has a mean site richness (27.5 species) comparable to that of Radunia. In general, species are more frequent among Kaszuby samples than among those from elsewhere.

The clearest evidence of a difference between the sites in Kaszuby and those elsewhere can be seen in the case of the Clausiliidae (Tables 5 and 6). Although

Table 5. Basic data on sites from north and west Poland compared with those from Kaszuby. Note that DROZDOWSKI's data are treated as coming from a single extra site in Kaszuby

	N. & W. Poland	Kaszuby
Sites	34	15
Species	48	48
mean/sample	20.6	25.2
range	11–32	17-32
Clausiliidae species	9	10
mean/sample	1.8	5.6
range	0-5	3–8

Table 6. Proportion of sites (%) occupied by Clausiliidae species in north and west Poland, in Kaszuby, and in Białowieża Forest. Note that *Macrogastra latestriata* was not recognised by CAMERON & POKRYSZKO (2004) in samples from Białowieża, and was segregated from *M. plicatula* later

	N. & W. Poland	Kaszuby	Białowieża
Cochlodina laminata	59	80	100
Cochlodina orthostoma	3	33	47
Ruthenica filograna	0	53	6
Macrogastra ventricosa	11	80	53
Macrogastra plicatula	3	100	100
Macrogastra latestriata	0	27	18
Macrogastra tumida	0	0	12
Clausilia pumila	6	13	24
Clausilia bidentata	62	67	6
Clausilia dubia	6	0	12
Laciniaria plicata	21	93	71
Balea biplicata	0	13	0
Bulgarica cana	12	0	53
Number of sites	34	15	17

other sites overall have only one less species than Kaszuby, the mean number of species per site is far lower, and only two species, *Cochlodina laminata* and *Clausilia bidentata* are present in more than 50% of sites. Even the rich nature reserve Buki nad Jeziorem Lutomskim has only three species, both overall and in each site. Within Kaszuby, Trąbki Wielkie sites are strange, in that although they hold only three species, they lack both these common and widespread species. The dominant clausiliid there, *Macrogastra plicatula*, is extremely uncommon in the north and west Polish sites away from Kaszuby. Amongst other species, *Acicula polita* occurred in 80% of Kaszuby sites, but only in 10% of the others.

Omitting the excluded species listed above, the whole array, including Kaszuby, contains 54 species, of which 42 are in common between Kaszuby and the rest, giving a Nei index of similarity of 87.5%. This takes no account of differences in frequency, and compares very different sized areas. When the sites in north and west Poland are split into three geographical groups, within which similarities are greatest, the similarities with Kaszuby decline slightly, and show a geographical pattern (Fig. 3): it is the cluster nearest to Kaszuby which shows the greatest similarity. Despite the larger geographical areas, none of the clusters is as rich in species as Kaszuby. Table 7 shows the species unique to one or the other series. Apart from geographical effects, noted above, there is evidence that Discus ruderatus, found only in three sites, has declined and retreated in the region in the last 100 years (DZIECZKOWSKI 1988), along with some other species such as Helicigona lapicida (DROZDOWSKI 1964).

WIDER COMPARISONS

POKRYSZKO & CAMERON (2005), in an analysis of forest snail faunas across northern Europe, found that the "Baltic" region, including one cluster of samples from each of Wielkopolska, Pomerania and Mazurian

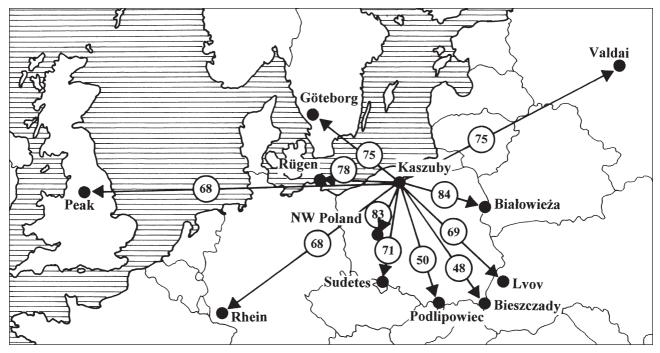


Fig. 3. A map showing the faunal similarities (Nei index, %) of the Kaszuby forest fauna to other forest faunas in northern Europe. Data for other localities from POKRYSZKO & CAMERON (2005)

Lakeland, was poorer in species than areas to the NW (Rügen and S. Sweden) and to the east (Białowieża and the Valdai Hills in W. Russia), as well as to the mountains to the south (Sudetes and Carpathians). The scarcity of clausiliids in this Baltic region contributed significantly to this effect, and differentiated its fauna from those of the mountains to the south, to the extent that faunas resembled those of England, where clausiliids are few in number, to a greater extent than those of the much closer Sudetes. While it was possible that different sampling techniques contributed to this effect, our own sampling round Lake Hańcza, near Suwałki, revealed forest faunas with no clausiliids at all (POKRYSZKO & CAMERON 2006).

In this context, these forest faunas from Kaszuby enable us to reassess faunal change across N. Europe. Overall, the richness of the fauna is very similar to that of Białowieża, both overall and at site level; the clausiliid fauna of Kaszuby is much more like that of Białowieża than that of most areas of north and west Poland so far studied (Table 6). Overall, at a Nei similarity index of 85%, the forest snail faunas of Białowieża and Kaszuby are just as similar as the latter is to the fauna recorded for all other sites in the north and west. By a small margin (71 to 68%) the Kaszuby fauna is more similar to that of the Sudetes (POKRYSZ-KO & CAMERON unpublished) than it is to that of C. England, and, apart from the clausiliids, especially *R*. filograna and M. latestriata, the presence of such species as V. alpestris and H. lapicida strengthen the southern and eastern connections. The connection with Białowieża is stronger than with Rügen (78%) or with S. Sweden (75%) although both are closer (data from POKRYSZKO & CAMERON 2005).

Table 7. Species unique to forest faunas in north and west Poland and to Kaszuby in comparing the two. The % columns indicate the proportion of sites in which the species was found

N. & W. Poland	%	Kaszuby	%
Cochlicopa nitens	21	Vertigo alpestris	13
Discus ruderatus	9	Oxychilus cellarius	20
Clausilia dubia	6	Ruthenica filograna	53
Bulgarica cana	12	Macrogastra latestriata	27
Perforatella incarnata	41	Balea biplicata	13
Perforatella umbrosa	3	Cepaea nemoralis	7

The occurrence of such rich faunas in Kaszuby suggests that particular features of the landscape have provided relatively stable refugia for the original forest fauna. There may be other rich sites in the north to be discovered. Recently, MARZEC (2005) reported on the discovery of populations of Chilostoma faustinum in the Romincka Forest north of Suwałki. This otherwise southern and montane species was accompanied by clausiliids, and local faunas are very rich (MARZEC in preparation). The contrast with the poor faunas round Lake Hańcza nearby is stark. The disjunction between such rich northern faunas and their equivalents in the south, and the absence or very scattered distribution of many species in between (WIK-TOR 2004) suggests that many other areas in the lowland north have suffered from human activities, possibly including atmospheric pollution, to the extent that no single locality retains all the original fauna.

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