VARIATION IN SPATIAL STRUCTURE AND ABUNDANCE OF CLAUSILIIDS (MOLLUSCA: CLAUSILIIDAE) IN THE NATURE RESERVE DĘBNO NAD WARTĄ (W POLAND) DURING WINTERING

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Abstract *Studies on the distribution and abundance of* Cochlodina laminata, Ruthenica filograna *and* Clausilia bidentata *in wintering conditions were based on a network of four permanent monitoring plots. Of the three clausiliids present,* C. laminata *was the most widely distributed, while the occurrence of* R. filograna *was limited to one plot. The small distribution area of the snail was compensated for by its high abundance. The distribution of clausiliids was found to depend significantly on the soil humidity and temperature, these factors were, however, dependent on the litter composition which much better explains the observed variation. Canonical analysis (CCA) showed that* R. filograna *and* C. bidentata *preferred places with a sparse herb layer and a considerable proportion of litter of hornbeam* (Carpinus betulus*) and ash (*Fraxinus excelsior*).* C. laminata *was more tolerant with respect to the herb layer proportion, and the optimum of its occurrence was associated with alder litter (*Alnus glutinosa*). All three clausiliid species avoided litter of oak* (Quercus*), sycamore (*Acer pseudo-platanus) *and aspen* (Populus tremula).

Key words *Permanent monitoring plots, Clausiliidae, microhabitats, snail distribution, wintering*

INTRODUCTION

Clausiliids *Cochlodina laminata* (Montagu, 1803), *Ruthenica filigrana* (Rossmässler, 1836) and *Clausilia bidentata* (Ström, 1765) are forest-dwellers, only very rarely found in other habitat types (Urbański 1947, 1957; Ložek 1964, 1982; Kerney, Cameron, Jungbluth 1983; Aleksandrowicz 1987; Riedel 1988; Wiktor 2004). They prefer shaded, mesic habitats. Only *C. laminata* can, besides, occur rather abundantly in shrubs or, at a low abundance, in xerothermic habitats.

Clausiliid biology and ecology are still poorly known and only fragmentary data exist. This pertains especially to the distribution and abundance of local populations of these snails. In the lowlands of Poland they are much less frequent than in the mountains and adjacent areas. All three clausiliids mentioned above occur in the nature reserve Dębno nad Wartą; among them *Ruthenica filograna* is a relatively rare species (Dyrdowska 1928, Urbański 1933a, 1933b, Koralewska-Batura 1992, Szybiak 1996). According to Szybiak (1996) *R. filograna* occurs there only in a small area and is especially abundant in the buffer zone of the reserve.

Apart from publications dealing with the fauna of Israel (Heller & Dolev 1994), there is no literature information on the wintering of clausiliids. On the whole, publications dealing with the distribution of terrestrial snails in winter in the temperate climate are very few (Baur & Baur 1991; Kleewein 1999). Based on a new method of data collecting we attempted to estimate spatial distribution of clausiliids and their abundance in our study plots in winter conditions. We also analysed the effect of enviromental factors on the distribution and abundance of these snails.

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MATERIAL AND METHODS

The studies were carried out in December 2006 in the buffer zone of the nature reserve Dębno nad Wartą (UTM: XT67). It is an area of about 2 ha, covered by a riverine forest, in places passing into an oak-hornbeam forest. Because of the rather sparse tree and shrub layers the habitat is fairly open. The herb layer is diverse, and covers the sampling plots to a varied degree.

Four separate study plots were selected for detailed estimates of the distribution and population abundance of the snails. They were spaced every 50 m from the place where earlier the highest density of *R. filograna* had been observed (Fig. 1). Each plot was 15 m^2 in area. For practical reasons each plot was divided into 15 squares of 1 m sides, using a net covering the area of 15 m^2. From each such square a litter sample was taken randomly with Oekland frame (25 x 25 cm), resulting in a series of 15 unit samples from each plot. A total of 4 such series made a total of

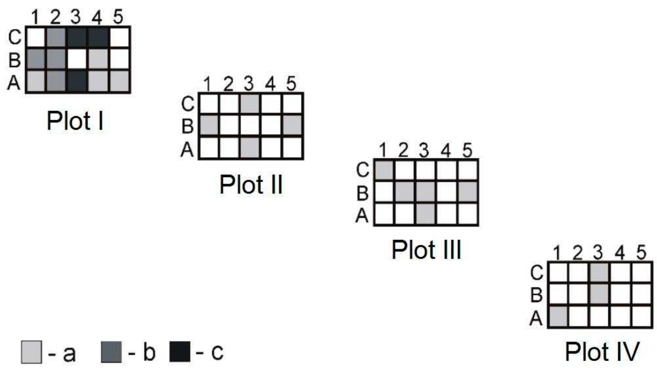

Figure 1 Spatial distribution and co-occurrence of clausiliids in the nature reserve Dębno in the sampling plots: a – one species, b – two species, c – three species

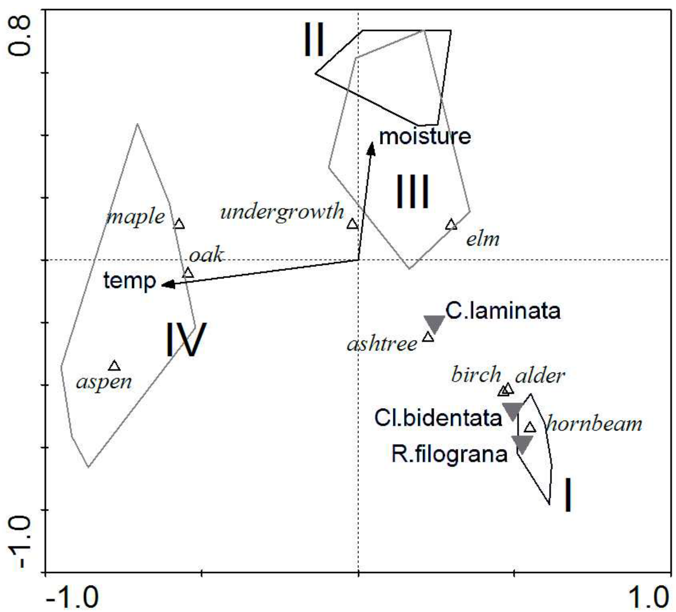

Figure 2 Correspondence Analysis triplot, showing composition of litter (hollow triangles) in the plots sampled (I-IV). The most outstanding samples from each area connected with solid lines. Snail species (solid inverted triangles) and soil temperature/moisture data (arrows) were included in the analysis as supplementary environment data (not influencing the ordination)

60 unit samples of litter (Fig. 1).

Each square was photographed and the percentage of microhabitats (litter, herb layer, moss, dead timber etc.) was estimatd based on the photo, using the programme LUPA 01. Besides, in each square the soil temperature was measured at the depth of 10 cm (accuracy 0.1^{o}C), the water content in the soil was estimated based on weight, and the proportion of leaves of particular tree species in the litter was assessed. The basic parameters of each square (1 x 1m) are presented in Table 1.

STATISTICA for Windows package (StatSoft Inc. 2005) was used for standard statistical calculations. We considered $p<0.05$ as a minimum level determining significance. All canonical analyses (CA, CCAs, CCA) were conducted using CANOCO for Windows 4.5. To determine the statistical significance of factors included in CCAs and CCA models, Monte Carlo permutation test set for 9999 permutations was applied (Jongman, Ter Braak, Van Tongeren 1995; Ter Braak 1996). To avoid autocorrelation, the permutations were restricted for split-plot design (ter Braak, Šmilauer 2002) with sampling areas as whole-plots arranged in a linear transect and individual samples as split-plots forming a spatial grid (5 rows x 3 columns). All the data were log-transformed prior to the analyses.

Results

Clausiliid community in the nature reserve Dębno nad Wartą

The clausiliid community in the permanent monitoring plots in the nature reserve Dębno nad Wartąincluded three species (Table 2), of which *Cochlodina laminata* was the most abundant. It constituted nearly half of all specimens collected. The differences between the mean abundance of the three species were statistically significant only for the pair *C. laminata* and *R. filograna* (ANOVA Kruskal-Wallis rank; $H = 8.52$; $p = 0.014$).

Only 23 out of he 60 litter samples contained clausiliids. Most of these positive samples (16) contained only one species. Most samples in which two clausiliid species were found contained *R. filograna* and *Cl. bidentata.* Abundance of snails in individual squares ranged from 16 to 320 indiv.m^{-2}, the highest abundance (144 indiv.m^{-2}) being reached by *R. filograna* (Table 3).

The sampling plots were compared with respect to abundance of leaves of different tree species using Correspondence Analysis (CA). Snail species, moisture and soil temperature were added as supplementary environment data. The analysis showed (Fig 2, Table 4) that plot I was the least varied with respect to litter diversity (close clustering of sample points in the diagram), with leaves of hornbeam, birch and alder. The proportion of vegetation-covered ground was the smallest, the soil temperature and moisture – the lowest. Plots II and III were rather similar, with

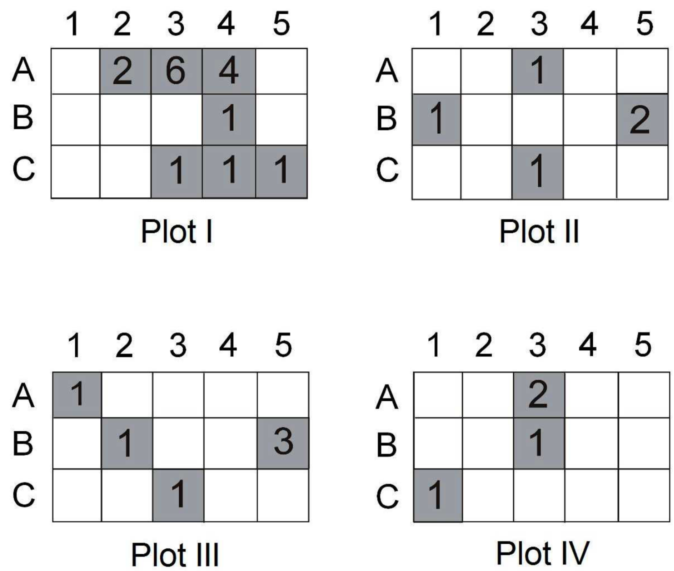

Figure 3 Spatial distribution and abundance of clausiliids in the sampling plots, 1 – 6 number of individuals: A - *Ruthenica filograna*, B - *Cl. bidentata*, C – *C.laminata*

elm litter prevailing, a considerable proportion of vegetation-covered ground and the highest soil moisture. Plot IV was much different from plot I, with aspen, maple and oak litter and the highest soil temperature. The analysis showed that plot I was optimal for *Cl. bidentata* and *R. filograna*. *C. laminata* was more tolerant, finding optimum conditions in plots I and III. Plot IV was the least suitable for the three snail species studied.

SPATIAL DIVERSITY OF CLAUSILIID OCCURRENCE

As could be expected, all three species and the highest clausiliid abundance were found in the first study plot (Plot I). With increasing distance from the plot, the number of clausiliid species and their abundance decreased. Clausiliids in the study plots tended to show an aggreated distribution (dispersal coefficient d=7.6). *C. laminata* was the most widespread, while *R. filograna* (Table 3, Fig.3) showed the most limited distribution.

It is interesting why the occurence of *R. filograna* is limited only to a small area in a seemingly rather uniform habitat. The answer should probably be sought in microhabitat and microclimatic conditions. *R. filograna* preferred places of a lower soil temperature (3.6–3.9°C) (Table 2). It occurred in places of 71.4-82.6% humidity. It chose soil surface with a large amount of litter (64-88%) and small proportion of herbs (12-36%). *C. laminata* was more catholic regarding these factors. It stayed in places with soil temperature of 3.2-4.4°C. It preferred moderately humid and humid places (73.1-97.3%). It occurred both in places with large amounts of litter (17-88%) and in those with a high proportion of herbs (12-82%). The third species, *Cl. bidentata* was intermediate between *R. filograna* and *C. laminata* in its tolerance to all the habitat factors considered.

Considering only the clausiliid-containing squares, statistically significant factors (Spearman's rho; $p<0.002$) affecting the spatial structure in the monitoring plots were: soil temperature and humidity, proportion of litter and herbs on the soil surface, and the occurrence of leaves of *Carpinus betulus, Alnus glutinosa* or *Populus tremula, Quercus robur, Acer pseudo-platanus* (Table 5, 6) in the litter. Negative correlations were found between the proportion of herbs and the abundance of clausiliids. For *R. filograna* a negative correlation was found with soil humidity, for *Cl. bidentata* – with soil temperature and humidity, for *C. laminata* – with soil temperature.

The distribution of all three clausiliids was positively correlated with the presence of litter and the low proportion of herbs. In the study plots the snails occurred wherever hornbeam and alder leaves were present in the litter (positive correlation), and avoided litter composed of aspen, oak and sycamore leaves (negative correlation). All three species showed the highest abundance in the first study plot (Plot I).

The effect of environmental factors on the distribution of the studied spcies was analysed with canonical community ordination methods. First, to determine the relative amount of variation in snail data explained by particular factors, the variation partitioning approach was used by performing two series of single-variable CCAs (separated Cannonical Correspondence Analysis) (Tab 7). In the first series all the environmental factors (percentage of vegetation cover and different litter composition; soil moisture and temperature) were analysed separately. The factors significantly explaining the variation observed were: percentage of hornbeam, elm, alder and ash leaves in the litter, vegetation cover and soil moisture.

In the second series of CCAs we checked for interactions between groups of the above mentioned factors. Soil moisture and temperature (Group1) could depend on litter composition

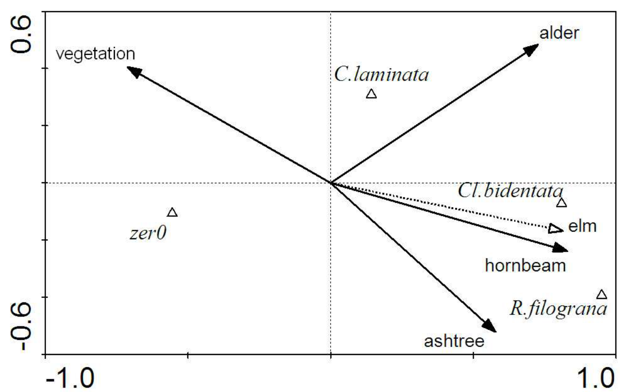

Figure 4 Ordination (CCA) diagram showing variation in the abundances of snail taxa (triangles) among different litter components (arrows);
zer0: samples with no Clausiliidae; dotted line: variable which was not significant according to Monte Carlo permutation test

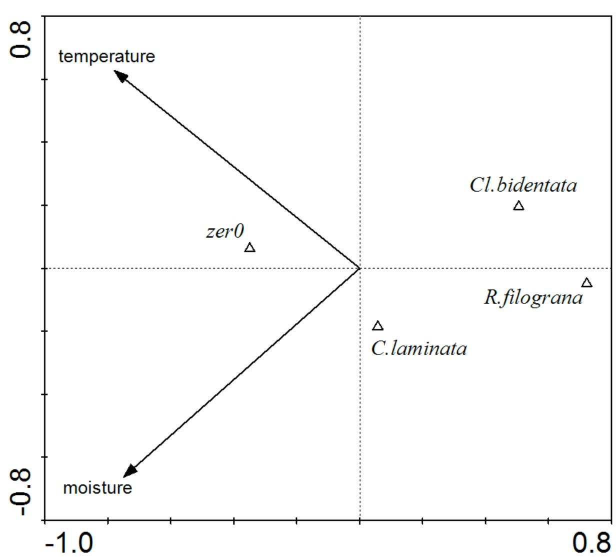

Figure 5 Ordination (CCA) diagram showing variation in the abundances of snail taxa (triangles) among different values of soil moisture and temperature (arrows);
zer0: samples with no Clausiliidae

(Group 2) and vice versa – different tree species could have specific optima especially regarding soil moisture, thus changing the litter composition. Therefore in all CCAs regarding the influence of factors from one of the groups, variables from the other group were used as covariables. Adding soil moisture and temperature to the analyses of litter composition influence did not change the results in any significant way and all the factors significantly explaining the observed variance in the previous series of CCAs retained their status. On the contrary, when data regarding the litter composition were used as covariables in the analyses of factors from the second group, soil moisture was no longer significant, showing that its influence was controlled by the litter composition and the proportion of vegetation cover.

To check how the factors which were significant in the previous analyses (litter composition) shaped the structure of clausiliid communities we used them all as explanatory variables in the next CCA (Fig 4). Samples with no Clausiliidae were included in the analysis as a separate species (zer0). The results explained 28.3% of the observed variance in the species data (Tab 8, 9). The first (horizontal) ordination axis could be interpreted as indicating abundance of leaves of all the tree species (to the right) against the percentage of vegetation cover. As indicated by the high eigenvalue (0.425), these are the major factors influencing the structure of clausiliid assemblages. The second axis (eigenvalue=0.062) explains the differences in litter composition. The third ordination axis has a negligible eigenvalue (0.002) and therefore is not discussed. *R. filograna* and *Cl. bidentata* preferred places with a low peoportion of herb layer and a high percentage of ash and hornbeam leaves. The latter species, however, had its optimum in the sampling plots with a higher percentage of aspen leaves. *C. laminata* was more tolerant to vegetation cover and preferred places covered by aspen leaves. Zero samples (with no Clausiliidae) came from places with a low proportion of litter and a high proportion of herb layer. Contrary to the CCAs results, the percentage of elm leaves did not significantly improve the model (F=0.048; p=0.941) because of the high correlation with the proportion of hornbeam leaves.

A similar analysis was also performed, using soil moisture and temperature as explanatory variables. When both factors were included in the model, soil temperature (added as a second variable) gained more statistical significance (p=0.054; F=2.63; λ_A=4.1). The significance of moisture remained unchanged at p=0.45 (F=3.09; λ_A=5.1). The model explained 9.2% of variance (Tab 10). According to the results, all the species studied preferred places with small values of both factors analysed (Fig 5), although some differences were found. *R. filograna* preferred places with the smallest values of both factors analysed. *Cl. bidentata* had similar requirements regarding moisture, but the optimal soil tem-

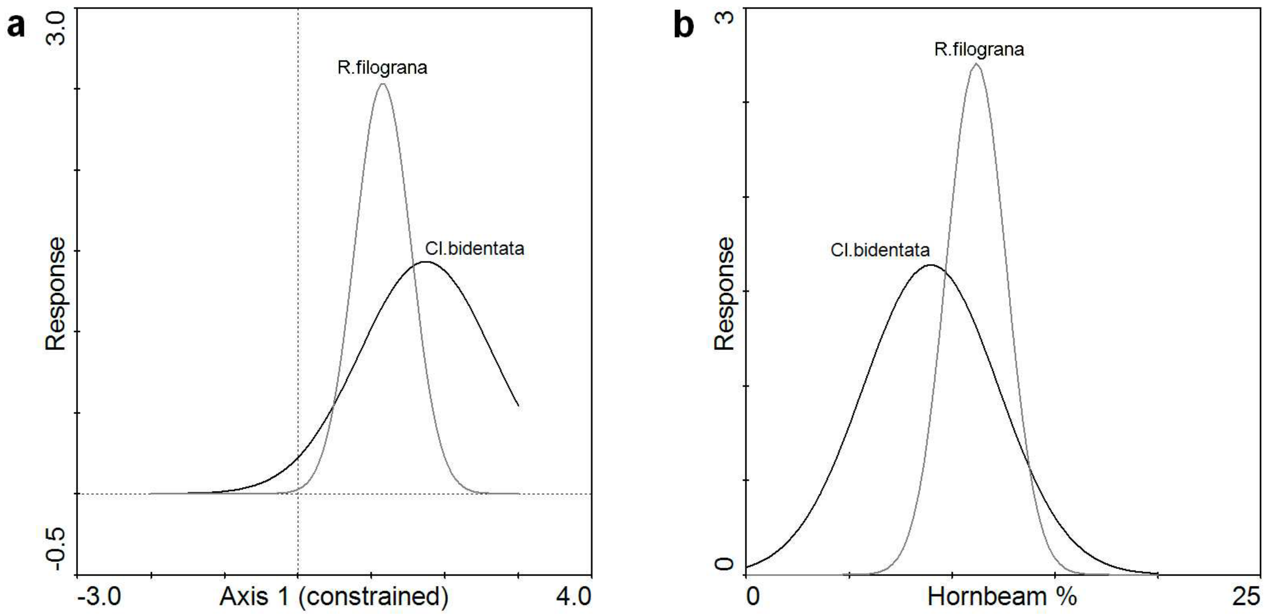

Figure 6 Response curves of *R. filograna* and *C. bidentata* describing relation between the species and: (a) the first ordination axis, interpreted as proportion of litter-covered against herb-covered area; and (b) the percentage of hornbeam leaves in the litter

perature was somewhat higher. *C. laminata* was the most tolerant to soil moisture (although still preferring its small values) and its requirements regarding temperature were comparable to those of *Cl. bidentata.* Zero samples were found most often in places with relatively high values of both factors. When the explanatory variables from the previous model (litter composition) were included in the analysis as covariables, none of the two factors was significant (moisture: p=0.540; F=0.60; λ_A=1.1; temperature: p=0.596; F=0.37; λ_A=0.3), confirming the earlier conclusions about the litter composition being the controlling factor.

The responses of the snail species to the environmental variables which were significant in all the earlier calculations were analysed using Generalized Linear Modelling (GLM: McCullagh, Nelder 1983), with stepwise selection based on the Akaike Information Criterion statistics (AIC: Hastie, Tibshirani 1990)(Tab 11). Only the models for responses of R. filograna and C. bidentata against the first (constrained) ordination axis (interpreted as overall proportion of litter vs vegetation cover: Fig 6a) and proportion of hornbeam leaves (Fig. 6b) explained more than 50% of variance in the data. Both models showed that responses of R. filograna and Cl. bidentata were unimodal, with optima of 1.16 against 1.74 (SD), respectively, in the model with the first ordination axis, and 11.18 against 8.97 (%) in the hornbeam model. R. filograna appeared to be a more stenotopic species, with tolerance of 0.382 against 0.903 in the first model and 1.46 against 3.28 in the second. Moreover, its response was always stronger, as indicated by the predicted response values for optimum estimate: 2.71 vs 1.64 in the first model; 2.53 vs 1.43 in the second.

DISCUSSION

The wintering clausiliid assemblage in the permanent study plots in the nature reserve Dębno nad Wartą is composed of three species; the most abundant of them, *Cochlodina laminata*, constitutes nearly half of all collected specimens. Clausiliids in the study plots show an aggregated distribution. The most widespread species is *C. laminata*, the least so - *R. filograna*. The latter species is regarded as a petrophilous calciphile while *Cl. bidentata* and *C. laminata* are classified as indifferent to the type and chemical poperties of the substratum (Aleksandrowicz 1987).

The anaysis of the effect of environmental factors on the distribution of the three clausiliid species shows that *R. filograna* has the narrowest range of ecological tolerance. It prefers habitats of the lowest soil temperature and humidity, and with a certain proportion of leaves of particular tree species in the litter. Such a close dependence between the occurrence of *R. filograna* and the habitat factors considered may be explained by the biology of this species. It never climbs tree trunks and is not found on rotting logs; it most often occurs in places devoid of herbs, with litter on the soil surface. Being a typical inhabitant of soil surface, it is directly affected by factors associated with the properties and structure of litter. These factors may become additionally more significant during hibernation which is a critical period for terestrial snails (Baur & Baur 1991). In the studied nature reserve *R. filograna* occupies only a small area which, however, is compensated for by its mean population density, higher than in the remaining two species. This is also confirmed by the strong response of the species to optimum conditions in the constructed GLM models. It is possible that the very pronounced agregated distribution of the species is an expression of its habitat selection during search for hibernation shelters. In will be possible to verify this hypothesis only when complete data on its distribution during the vegetation season are available.

Cl. bidentata and *C. laminata* show a wider ecological tolerance. They can occur in the same microhabitats as *R. filograna*, but are also found where the soil temperature and humidity are somewhat higher and the proportion of litter-covered soil surface - smaller. Besides, *C. laminata* tolerates a wider range of soil temperature and humidity. It occurs both in places with litter accumulation and in places with dense herbs, and among the three species it has the widest ecological tolerance. A similar picture emerges from the analysis of the results presented by Juřičková & Kučera (2005). The CCA diagrams presented by these authors indcate that *C. laminata* is distinctly less closely associated with litter of deciduous trees (in this case beech) than *R. filograna*, which clearly prefers this kind of litter. Such different requirements of the species with respect to the analysed factors result in a spatial diversity of clausiliids in a seemingly uniform habitat.

Leaves of particular tree species which compose the litter provide snails with food, shelter and places to hibernate. In our analysis the occurrence of the studied clausiliids was associated with the presence of leaves of *Carpinus betulus, Fraxinus excelsior* and *Alnus glutinosa* in the litter. At he same time they seem to avoid leaves of *Quercus robur, Acer pseudo-platanus* and *Populus tremula.* This may be associated with the different rate of litter decomposition, higher in the first group of trees. A similar dependence has been found for mites by Athias-Binche and Mignolet (1979).

The analyses of the data collected in winter show that the most important factor for the studied species is the proportion of litter-covered soil surface. Among the various components of the litter, the most important are hornbeam, alder and ash leaves. The effect of soil temperature and humidity is also significant but it should be remembered that these two factors depend most of all on the litter structure. Qualitative and quantitative diversity of trees is thus the main factor which controls the remaining variables.

The question which factors have a decisive effect on the spatial diversity of distribution of clausiliids in the nature reserve Dębno nad Wartą can be answered only after detailed studies during the remaining seasons. Since hibernation is a critical period for snails, it can be conjectured that the factors which are essential during that period may also affect clausiliid distribution in the vegetation season (Baur & Baur 1991).

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Table 1 Variation in habitat conditions in the squares of the sampling plots in the nature reserve Dębno (21 December 2006): T (°C) – soil temperature at the depth of 10 cm; Ww (%) – % soil humidity (based on wight); Herbs – proportion of herb-covered area; Litter – proportion of litter-covered area

Plot/Square	T (°C)	Ww (%)	Herbs	Litter
A-I A1	3.9	82.6	35%	65%
A-I A2	3.6	76.7	32%	68%
A-I A3	3.9	73.1	12%	88%
A-I A4	3.9	75.8	24%	76%
A-I A5	3.4	71.4	21%	79%
A-I B1	3.8	80.6	26%	74%
A-I B2	3.8	71.4	31%	69%
A-I B3	3.4	76.0	30%	70%
A-I B4	3.8	81.8	22%	78%
A-I B5	3.9	81.5	14%	86%
A-I C1	3.8	82.9	38%	62%
A-I C2	3.8	80.6	36%	64%
A-I C3	3.9	82.6	27%	73%
A-I C4	3.6	76.7	36%	64%
A-I C5	3.9	73.1	15%	85%
A-II A1	3.8	83.3	82%	18%
A-II A2	3.8	84.4	82%	18%
A-II A3	3.2	89.3	82%	18%
A-II A4	3.8	88.9	80%	20%
A-II A5	3.6	92.5	73%	27%
A-II B1	3.6	88.0	47%	53%
A-II B2	3.6	82.8	69%	31%
A-II B3	3.4	84.6	81%	19%
A-II B4	3.4	59.5	70%	30%
A-II B5	3.2	82.9	76%	24%
A-II C1	3.8	85.0	86%	14%
A-II C2	3.8	76.5	79%	21%
A-II C3	3.6	83.3	81%	19%
A-II C4	3.8	81.8	58%	42%
A-II C5	3.6	89.7	52%	48%
A-III A1	3.9	85.3	66%	34%
A-III A2	4.2	88.4	61%	39%
S-III A3	4.1	88.9	78%	22%
A-III A4	4.4	85.7	75%	25%
A-III A5	4.2	86.1	86%	14%
A-III B1	3.8	85.7	58%	42%
A-III B2	3.9	87.8	57%	43%
A-III B3	4.1	86.5	74%	26%
A-III B4	4.1	85.7	71%	29%
A-III B5	3.8	86.2	76%	24%
A-III C1	3.8	86.2	75%	25%
A-III C2	3.9	80.0	50%	50%
A-III C3	4.2	77.8	76%	24%
A-III C4	4.2	77.4	80%	20%
A-III C5	4.1	97.3	83%	17%
A-IV A1	4.4	81.1	80%	20%
A-IV A2	4.4	79.5	76%	24%
A-IV A3	4.2	73.0	63%	37%
A-IV A4	4.1	76.7	64%	36%
A-IV A5	4.2	81.1	66%	34%
A-IV B1	4.8	80.5	63%	37%
A-IV B2	4.2	82.2	50%	50%
A-IV B3	4.4	75.7	46%	54%
A-IV B4	4.2	79.1	44%	56%
A-IV B5	4.1	83.3	41%	59%
A-IV C1	4.4	85.4	68%	32%
A-IV C2	4.7	84.4	91%	9%
A-IV C3	4.4	81.1	83%	17%
A-IV C4	4.4	79.5	53%	47%
A-IV C5	4.2	73.0	40%	60%

Table 2 Clausiliid assemblage in the sampling plots in the nature reserve Dębno nad Wartą: N – number of squares, X – mean number of individuals, SD - ±standard deviation; MED – median, X rank – X rank statistic

Species	Number of individuals	Dominance (%)	N	X	SD	MED	X rank
Clausilia bidentata	17	25	24	0.79	2.06	0	29.25
Cochlodina laminata	32	47	24	0.71	1.20	0	33.94
Ruthenica filograna	19	28	24	1.33	1.40	1	46.31
Total	68	100					

Table 3 Occurrence and co-occurrence of clausiliids in the sampling plots in the nature reserve Dębno nad Wartą

Occurrence and co-occurrence	No. of squares	%	Density (indiv./m^2)
Three species	3	5	48-320
Two species	4	7	32-64
One species	16	27	16-48
No clausiliids	37	62	0
R. filograna	6	10	16-144
Cl. bidentata	10	17	16-80
C. laminata	18	30	16-96
R. filograna & *Cl. bidentata*	6		
R. filograna & *C. laminata*	3		
Cl. bidentata & *C. laminata*	4		

Table 4 Summary of Correspondence Analysis of litter composition

Axes	1	2	3	4	Total variance
Eigenvalues:	0.542	0.174	0.133	0.129	1.000
Cumulative percentage variance of species data:	54.2	71.6	84.9	97.8	
Sum of all eigenvalues					1.000

Table 5 Values of significant correlations between clausiliid distribution and habitat factors: T (°C) – soil temperature at the depth of 10 cm; Ww (%) – % soil himidity (based on weight); Herbs – proportion of herb-covered area; Litter – proportion of litter-covered area; N.S. - not significant

Species	Correlation for all samples			
	T (°C)	Ww (%)	Herbs	Litter
Ruthenica filograna	N.S.	-0.379434	-0.443547	+0.443547
Clausilia bidentata	-0.313595	-0.300123	-0.461751	+0.461751
Cochlodina laminata	-0.474470	N.S.	-0.333638	+0.333638
Total	-0.552482	-0.258137	-0.540123	+0.540123

Table 6 Values of significant correlations between the distribution of clausiliids and the proportion of leaves of various tree species in the litter; N.S. - not significant

Species	Correlation for all samples					
	Carpinus betulus L.	*Fraxinus excelsior* L.	*Populus tremula* L.	*Quercus robur* L.	*Acer pseudoplatanus* L.	*Alnus glutinosa* Gaertn.
Ruthenica filograna	+0.507243	+0.372115	N.S.	-0.333411	N.S.	+0.457177
Clausilia bidentata	+0.428455	+0.318792	-0.307390	-0.352618	-0.296166	+0.509601
Cochlodina laminata	+0.460375	N.S.	N.S.	-0.317956	N.S.	N.S.
Total	+0.661856	N.S.	-0.387804	-483047	-0.353501	+0.388908

Table 7 Percentage variance of data explained by each variable in separated CCAs. Series 1: analyses without covariables, Series 2: data from the other group used as covariables. Significance of the Monte Carlo test of the first or all canonical axes: *P<0.1; **P<0.05; ***P<0.005; NS, not significant

		Series 1	Series 2
Group I	Hornbeam	17.2^{***}	10.4^{***}
	Elm	16.4^{***}	10.5^{***}
	Alder	13.8^{***}	9.1^{**}
	Vegetation cover	13.1^{***}	6.8^{***}
	Ashtree	9.2^{**}	8.7^{**}
	Birch	NS*	NS
	Aspen	NS	NS
	Maple	NS	NS
	Oak	NS	NS
Group II	Moisture	5.1^{**}	NS
	Temperature	NS	NS

Table 8 Summary of Canonical Correspondence Analysis of Clausiliidae with regard to litter composition

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.425	0.062	0.002	0.712	1.724
Species-environment correlations :	0.685	0.325	0.080	0.000	
Cumulative percentage variance					
of species data :	24.6	28.2	28.3	69.6	
of species-environment relation:	87.0	99.7	100.0	0.0	
Sum of all eigenvalues					1.724
Sum of all canonical eigenvalues					0.488

Table 9 Effect of of litter composition on species distribution (Forward Selection results)

	p	F	λ_A
ashtree	0.017	5.88	9.2
herbs	<0.001	5.60	8.1
alder	0.011	5.09	6.6
hornbeam	0.019	3.05	4.3
oak	0.227	1.52	2.0
aspen	0.371	0.88	0.3
birch	0.541	0.38	0.3
maple	0.848	0.11	0.2
elm	0.941	0.05	0.1

Table 10 Summary of Canonical Correspondence Analysis of Clausiliidae with regard to soil moisture and temperature

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.141	0.019	0.876	0.571	1.724
Species-environment correlations :	0.402	0.172	0.000	0.000	
Cumulative percentage variance					
of species data :	8.2	9.2	60.0	93.2	
of species-environment relation:	88.4	100.0	0.0	0.0	
Sum of all eigenvalues					1.724
Sum of all canonical eigenvalues					0.159

Table 11 Summaries of fitted General Linear Models describing relations between the species and the first (constrained) ordnination axis and the precentage of hornbeam leaves in the litter

	C.bidentata	*C.laminata*	*R.filograna*	Zer0
First ordination axis				
p	<0.001	0.016	<0.001	<0.001
AIC	43.54	86.92	47.63	30.49
variability	51.2	11.6	58.0	20.4
Optimum	1.74	N.A.	1.16	-0.83
Tolerance	0.90	N.A.	0.38	1.15
Peak max value	1.43	-	2.53	1
Hornbeam				
p	<0.001	0.026	<0.001	0.001
AIC	37.99	87.64	39.94	32.05
variability	54.5	13.9	64.8	17.0
Optimum	8.97	8.38	11.18	N.A.
Tolerance	3.28	4.83	1.46	N.A.
Peak max value	1.64	1.54	2.71	-