

Long-term succession of oribatid mites after conversion of croplands to grasslands

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Abstract

The paper deals with the long-term development (55 years) of oribatid communities (Acari) during grassland succession following the conversion of arable fields. The study was carried out on a chronosequence of temperate grassland sites in the Lahn-Dill-Bergland (Central Hesse, Germany). The “space-for-time” substitution method was applied. Increasing abundance at early stages of the conversion process (until the age of 13–28 years) points to release from the stress exerted by arable management. Saturation of abundance and richness indicates strong limiting forces acting upon the oribatid community at intermediate and late stages of succession. The continuous increase in the dominance of surface-dwelling and non-specialized species suggests a considerable change in the nature of these limiting forces during the successional process. General Regression Model (GRM) analysis revealed an increasing impact of external factors on the oribatid community during grassland succession, and a shift in the major driving forces determining oribatid abundance from soil conditions to vegetation conditions and then to a combined effect of both soil and vegetation conditions.

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1. Introduction

Conversion of agricultural land into grassland is taking place in many regions of Europe (Stanners and Bourdeau, 1995). The gradual nature of this process creates landscape mosaics of grasslands at different stages of development. The change from arable land to grassland is known to significantly impact soils and soil related processes (Siepel, 1992). However, associated changes in the soil communities actually performing

these processes are poorly understood (Brown and Gange, 1992; Koehler, 1998, 2000; Skubała, 1999; De Deyn et al., 2003). A major aim of the study reported here was thus to fill this gap of knowledge by analyzing the response of oribatid mites to the conversion of arable land into grassland. Investigations were carried out by means of the ‘space-for-time substitution’ approach as a surrogate for a long-term study on mite succession (Pickett, 1989). This was possible through the simultaneous availability of grassland sites of different age that cover a time period of approximately 60 years (Waldhardt and Otte, 2003; Hietel et al., 2004).

We focussed on oribatid mites, since this taxon has proven to be a reliable indicator of agro-ecosystem processes (Behan-Pelletier, 1999). Though the sensitive response of oribatids to the conversion of grassland to

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arable land is well established (Lagerlöf and Andren, 1988; Krivolutsky, 1995), very little is known about the reverse process. A core question of our study, therefore, was how successional changes in aboveground biota affect the structure of the mite communities in soil. We expected dramatic changes in microhabitat conditions and food availability to cause major shifts in the functional structure of the mite community during early stages of the conversion process. Later stages of succession, in contrast, were expected to be mainly driven by ecomorph-specific responses to the increasing protection of the soil surface by vegetation cover. While, for example, soil-dwellers are much less exposed to microclimatic fluctuations than litter-dwellers, the former group is more sensitive to structural features of the soil than the latter (Krivolutsky, 1995).

2. Methods

2.1. Study region and sites

The study was carried out on 86 study sites located in the Lahn-Dill-Bergland (Hesse, Germany). Sites were situated within five administrative districts: Bottenhorn (BH, $n = 16$), Guenterod (GR, $n = 18$), Niedereisenhausen (NE, $n = 15$), Niederlemp (NL, $n = 20$) and Oberhoerlen (OH, $n = 17$). The altitude varies between 200 and 600 m a.s.l., with mean annual temperature ranging from 5 to 8 °C and mean annual precipitation ranging from 700 to 1200 mm. Dominating soil types are acidic regosols and moderately deep brown earths (cambisols) over Devonian claystone slates, gravelstone slates and greywackes on slopes of up to 20° or more.

The study region is characterized by the predominance of low-intensity farming systems that originate from disadvantageous natural site conditions and the historical, political and social evolution of the region (Nowak, 1988). A large part of the landscape is used by part-time farmers, who adhere to traditional agricultural

practices (Hietel et al., 2005), and most of the grassland is managed according to agro-environmental schemes focussing mainly on extensification (Wellstein et al., 2006). The implementation of the agro-environmental schemes ensures a late first mowing date not before mid of June, rare application of fertilizer (<30 kg NPK/ha year) or even no fertilizing, and extensive pasturing with not more than 1.5 standard livestock units (LU) per ha. All studied grasslands were managed without artificial fertilizer or pesticide input and did not involve fire. We could differentiate between two types of grassland management: (i) sheep grazed pastures with infrequent additional mowing and low stocking densities and (ii) mown grassland cut one or two times per year. These two types of grassland management were represented in every age class.

The time-course of the conversion of crop fields into managed grasslands was analyzed using black-and-white aerial photographs (mainly at a scale of 1:12,000) complemented by field inventories in 1999 and 2000 (scale 1:5000; Hietel et al., 2004). Photographs were available for the years 1945, 1953, 1961, 1962, 1967, 1973, 1979, 1989 and 1999. Thus, five classes of grassland age (i.e. time since last cultivation) could be established at the time of sampling: 1–12 years (class 1), 13–28 years (class 2), 29–40 years (class 3), 41–48 years (class 4) and >49 years (class 5), respectively (Waldhardt and Otte, 2003; Dauber and Wolters, 2005). In addition, arable land was included as a surrogate for the initial conditions of the successional process (class 0; Pickett, 1989). Environmental characteristics for the age classes are summarized in Table 1. Each of the study districts provided sites of all age classes. Sampling and measurement of environmental variables is described in Waldhardt and Otte (2003).

2.2. Sampling and identification

A sampling campaign covering all 86 sites was performed in October 2001. Three replicate samples per

Table 1

Mean and standard deviation of soil (bioavailable P and K, C/N ratio, water content) and vegetation characteristics (richness and coverage of vascular plants) of arable land (age class 0) and five age classes of grassland (age classes 1–5, see text for explanations)

Age class	pH	P (mg per 100 g DM of soil)	K (mg per 100 g DM of soil)	C/N ratio	WC, %DM	Plants species richness	Vegetation coverage (%)
0	5.03 ± 0.69	12.3 ± 5.7	36.6 ± 14.9	9.4 ± 0.8	24.2 ± 3.3	–	–
1	4.80 ± 0.49	9.5 ± 2.1	24.5 ± 11.7	9.3 ± 0.9	34.9 ± 6.9	20.8 ± 5.8	80.8 ± 18.2
2	4.54 ± 0.27	5.8 ± 3.6	16.6 ± 10.6	9.7 ± 0.5	43.3 ± 14.2	22.7 ± 4.3	90.7 ± 6.3
3	4.34 ± 0.31	3.7 ± 2.3	10.8 ± 9.8	10.0 ± 0.7	49.6 ± 10.0	24.3 ± 2.0	89.6 ± 4.4
4	4.39 ± 0.27	3.8 ± 2.6	8.3 ± 6.8	9.8 ± 0.6	54.6 ± 9.1	25.6 ± 3.9	92.7 ± 5.8
5	4.34 ± 0.30	3.6 ± 1.6	12.0 ± 11.2	10.1 ± 0.5	55.6 ± 8.8	25.7 ± 4.5	90.3 ± 4.5

site were collected by means of soil corers (diameter: 5 cm). The samples included the organic layer and the top 5 cm of the mineral horizon. Microarthropods were extracted using a modified MacFadyen high-gradient canister method (MacFadyen, 1961). Emerging invertebrates were collected in ethylene glycol.

Oribatid mites (incl. nymphs and larvae) were transferred into 90% alcohol and counted. Individuals were then identified to species using the keys of Balogh and Balogh (1992a,b), Balogh and Mahunka (1983), Ghilarov (1975), Pérez-Íñigo (1993, 1997) and Willmann (1931). Species were allocated to genera and families according to the system of Balogh and Balogh (1992a,b) and Krivolutsky (1995). Whenever possible, oribatid nymphs and larvae were also identified to species and added to the respective adults. When this was not possible, they were separately counted as ‘unidentified nymphs and larvae’ (see Appendix A). Identification was performed under a light microscope. Species were assigned to ecomorphs (surface-, litter-, soil-dwelling, and non-specialized) following Krivolutsky (1995). Unidentified nymphs and larvae were categorized as ‘non-specialized ecomorph’. Species that were exclusively found in grassland sites and never occurred in samples from arable land are defined as ‘grassland species’.

2.3. Statistics

The average abundance was estimated from the three replicates per site. Species richness was estimated as both actual and predicted richness per age class in a certain district. To eliminate differences in the sample size, predicted species richness was calculated from the individual samples per age class for every district using the Michaelis–Menten estimator provided by the software package EstimateS 7.0 (Colwell, 2004). This estimator has been found to deliver the most reliable results for datasets with small numbers of replicates and high data variability (Toti et al., 2000). The similarity between oribatid communities of the different age classes was analyzed with fuzzy-clustering analysis at $p < 0.05$ using NCSS 2001. This technique calculates the probability of a sample belonging to a cluster, as well as the optimal amount of clusters for the given dataset. It also determines the statistical significance of the clustering. The appropriate number of clusters in our case was chosen from 100 iterations.

A preliminary analysis of variance had shown that neither species richness nor abundance of oribatids was affected by the type of management. This corresponds to complementary studies on other taxa (e.g. Dahms

et al., 2005; Wellstein et al., 2006). Therefore, management was not included in the analysis. The impact of the factor ‘grassland age’ (classes 0–5) on oribatid species richness and abundance as well as on the species richness of ecomorphs was tested by means of ANCOVA with the factor ‘district’ (BH, GR, NE, NL, OH) as a covariate. If necessary the data were square root transformed prior to the analysis to achieve normality. Homogeneity of data was assessed with the Sen and Puri test. In cases where significant results were obtained, differences between means were tested with Tukey’s HSD test for unequal sample number per class at $p < 0.05$.

The impact of environmental variables on mite group abundances was separately analyzed for each class using General Regression Models (GRM; forward stepwise procedure). GRM implements stepwise and best-subset regression for Analysis of Covariance (ANCOVA) design with categorical and continuous predictor variables (StatSoft Inc., 2001). Soil parameters (pH, P-, K-content, C/N ratio, water content) and vegetation parameters (coverage and species richness per m²) were included in the models as continuous variables. The only categorical variable included was “District”. All analyses were performed using the STATISTICA 6.0 software package (STATISTICA software V 6.0, StatSoft Inc., Tulsa, USA, StatSoft, 2001).

3. Results

The abundance of oribatids markedly increased after the conversion from arable land to grassland and reached a level of saturation at age class 3 (29–40 years; Fig. 1). Surface-dwelling species were the only group that significantly responded to the factor ‘grassland age’ (Table 2), with the share of this group rapidly increasing at early stages of grassland succession (Fig. 2). Though this process slowed down at later stages, there was no indication found that the shift towards surface-dwelling oribatid mites had come to an end at the oldest grassland stage that was available for this study. The variance in oribatid abundance explained by the GRM analysis was comparatively low (age classes 0–2) or even zero (age class 3), but markedly increased at age class 4 and reached a very high value at age class 5 (R^2 in Table 3). The factors included in the models suggest a shift from soil driven processes at early stages (P-content for age classes 0 and 1) to vegetation driven processes at intermediate stages of grassland succession (vegetation coverage for age classes 2 and 4). Oribatid abundance at age class 5

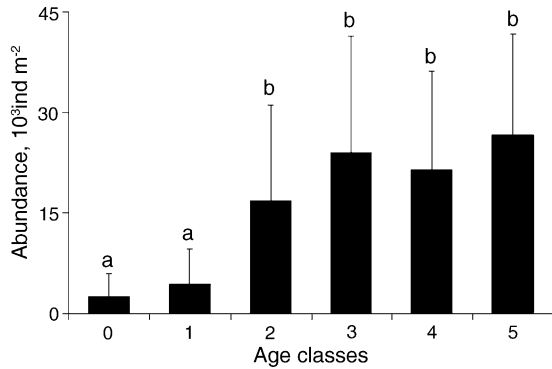


Fig. 1. Changes in oribatid abundance (average per age class \pm S.D.; age classes 0–5, see text for explanation). Columns with identical letters are not significantly different from each other (Tukey HSD test at $p < 0.05$).

was again strongly affected by a soil factor (K-content). However, the fact that this factor acted together with ‘vegetation richness’ suggests a differential response of oribatids to soil and vegetation at later stages of grassland succession.

A total of 56 oribatid species was found (Appendix A). Grassland age affected both observed species richness and predicted species richness (Table 2). The time-course of changes in species numbers revealed by these two parameters showed some basic similarities, with richness being comparatively low at the first two stages (0 and 1) and higher at later stages (2–5) of the chronosequence (Fig. 3).

Table 2

Results of ANCOVA with ‘age class’ as an independent factor and ‘district’ as a covariate on various parameters of oribatid community structure

	<i>F</i> -values	Number of replicates
Abundance ^a	20.9	86
Species richness		
Observed	21.5	30
Predicted	4.58	30
Relative abundance of ecomorphs		
Soil-dwellers	0.41	30
Litter-dwellers	1.74	30
Surface-dwellers	3.61	30
Non-specialized	0.94	30
Species richness of ecomorphs		
Soil-dwellers	0.81	30
Litter-dwellers	1.47	30
Surface-dwellers	6.20	30
Non-specialized	7.08	30

Ecomorphs names are given according to Krivolutsky (1995). Bold figures designate significant *F*-values ($p < 0.05$).

^a Square-root transformed.

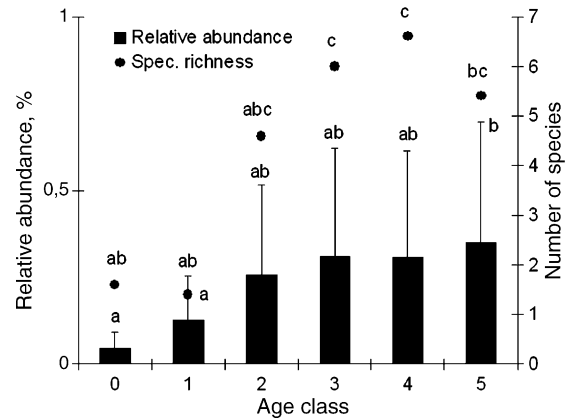


Fig. 2. Changes in relative abundance and species richness of surface-dwelling oribatids (average per age class \pm S.D.) along the chronosequence (age classes 0–5). Columns or dots with identical letters are not significantly different from each other (Tukey HSD test at $p < 0.05$).

However, while observed richness indicates a stepwise increase in the number of species, predicted richness suggests a decline shortly after the conversion process, constantly high values at intermediate stages and again a decline at the latest stage. Since predicted species richness strongly depends on between-site variability, this largely reflects a major change in intersite-specific differences along the chronosequence (Fig. 3). Among oribatid ecomorphs, the richness of both surface-dwelling and non-specialized species significantly changed along the chronosequence (Table 2). The species number of surface-dwellers was low in age classes 0 and 1, gradually increased until age class 4 and then slightly declined again in age class 5 (Fig. 2). In a very similar vein, the number of non-specialized species increased from 2.0 species in arable land to 7.4 in age class 4 and then declined to 6.0 species in age class 5. No impact of environmental factors on any parameter for species richness was revealed by the GRM analysis.

Appendix A reveals some aspects of the community change that were associated with the conversion process. The number of ‘grassland species’ (i.e. species that were not found on arable land) increased from age class 1 to age class 4, but slightly declined in age class 5. The number of species not occurring in any preceding stage was particularly high at age class 1 and then gradually declined along the chronosequence. There were only three species, which were exclusively found on arable land. Grasslands of age class 1 had no unique species, age classes 2, 3, 4 and 5 hosted 2, 4, 4 and 3 unique species, respectively. Notably, of the 12 samples in which not a single oribatid species was found, 11 belonged to arable land and 1 to age class 1 (data not

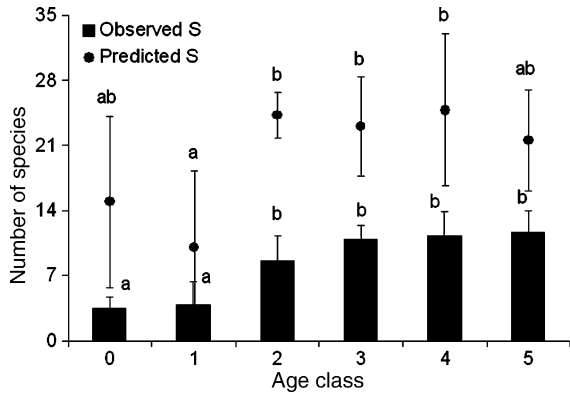


Fig. 3. Observed and predicted species richness (average per age class \pm S.D.) of oribatid mites along the chronosequence (age classes 0–5). Columns or dots with identical letters are not significantly different from each other (Tukey HSD test at $p < 0.05$).

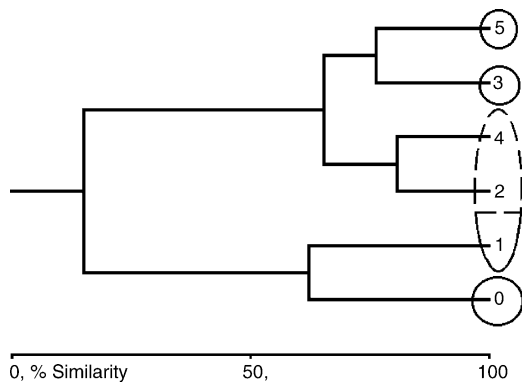


Fig. 4. Fuzzy clustering analysis of oribatid communities from the six age classes based on Euclidean distances. Age classes separated with rings belong to different clusters at $p < 0.05$. Communities from age classes within dashed rings are attached to the class with probability below the significance level.

shown). According to the results of the cluster analysis, communities of arable land and young grassland (age class 1) are significantly different from those inhabiting older grasslands ($p < 0.05$; Fig. 4). Moreover, significant differences were revealed for age classes 1, 3 and 5. Communities of age classes 2 and 4 occupy intermediate positions and do not belong to any of the distinguishable classes.

4. Discussion

This study presents the first investigation of the long-term development of oribatid communities during grassland succession. Some very consistent patterns have been found. First, the positive response of oribatids at early stages in the conversion process reflects the

release from the stress exerted by arable management. Then, saturation of abundance suggests strong limiting forces acting upon the oribatid community at intermediate and late stages of succession. There is no clear indication of species richness saturation at the oldest sites of our succession if we compare our results with those from Purvis (1982) who found 25 species in three samples from an old pasture site (against our 32 species in 33 samples). And finally, the increasing dominance of surface-dwelling and non-specialized species indicates a considerable change in the nature of these limiting forces. This contention is supported by the GRM analyses showing: (i) an increasing impact of external factors on the oribatid community and (ii) a shift in the major driving forces from soil conditions to vegetation conditions and then to a combined effect of both soil and vegetation conditions.

The basic successional pattern of oribatids revealed by our study corresponds to the observations made in other ecosystems (Horwood and Butt, 2000; Koehler, 2000; Frouz et al., 2001). Moreover, a similar time-course has been reported for other groups of the soil fauna, including enchytraeids, spiders, insects, collembolans and different mite groups (Purvis and Curry, 1980; Koehler, 2000). The fact that it was impossible to detect significant differences in oribatid species richness between early age classes simply reflects the extreme variability and patchiness of mite distribution during the early stages of secondary successions (Krivolutsky, 1995). According to the results of the GRM analyses, edaphic factors significantly affect oribatid abundance at the earlier stages of succession. This possibly indicates a narrowed set of driving forces at the earlier stages of grassland succession in the conditions of insufficient surface organic horizon development. This confirms the overriding role of soil conditions in driving early stages of secondary succession suggested for many ecosystems (Kaufmann, 2001).

The oribatid species richness saturation curves resemble those found for a spruce forest chronosequence on acid soil (Zaitsev et al., 2002). Various mechanisms may trigger community recovery. Though oribatids are very slow moving animals (Berthet, 1964), the significance of active dispersal in oribatid colonization processes has been demonstrated by proving the adverse effects of isolating tilled patches from the species source of adjacent grasslands on mite diversity (Gonzalez and Chaneton, 2002). Rapid passive dispersal by birds may also be important (Krivolutsky and Lebedeva, 2004). Moreover, some species may have already been present in arable soils and just increased to a 'detectable abundance' after the conversion to

Table 3
Results of the GRM analyses on the effect of soil and vegetation characteristics on oribatid abundance

Model parameters	Age classes					
	0	1	2	3	4	5
P-content	32.2 (–)	31.1 (–)	ns	ns	ns	ns
K-content	ns	ns	ns	ns	ns	54.9 (–)
Vegetation coverage	ns	ns	27.5 (+)	ns	45.0 (+)	ns
Richness of the vegetation	ns	ns	ns	ns	ns	20.3 (+)
Total R^2	32.2	31.1	27.5	0	45.0	75.2

Shown is the percentage of variance explained by those factors for which significant effects could be detected ($p < 0.05$). The direction of the effect is indicated by “+” and “–”; ns, not significant.

grassland. We hypothesize that oribatid succession relies on all these mechanism jointly acting together, with the relative importance changing with time in the order: recovery of existent species > passive dispersal > active colonization. Increasing dominance of surface-dwelling species can at least partly be explained by the fact that this group tends to have a higher dispersal potential (both active and passive) than soil-dwelling species (Berthet, 1964; Lebedeva and Krivolutsky, 2003).

We cannot exclude the possibility that our findings may be partly biased by a methodological shortcoming associated with the ‘space-for-time substitution’ approach. In particular, difference in the starting conditions between older and younger grasslands resulting from the change in the intensity of agricultural management during the last century may have affected community development (Krivolutsky, 1995; Mortimer et al., 2002). Also management type and intensity dynamics over the years of the grassland succession may affect resulting structure and diversity of oribatid communities as was shown by Gadzhiyev et al. (2002, pp. 201–221). However, the strong effect of vegetation cover at later stages of grassland development probably compensated for initial differences in starting conditions. The steady increase in surface-dwelling species, i.e. a group that has stronger ecological bonds with vegetation (Krivolutsky, 1995),

supports this contention. Unfortunately, the “tail” of the grassland succession could not be covered by our study, due to the absence of very old sites. However, based on earlier reports (e.g. Purvis, 1982) we assume the oribatid community develops further with grassland maturation over decades, due to minor disturbances (Walker and Chapin, 1987). Oribatid abundance remains stable with time as it is similar to that reported by Curry (1969) for a very old grassland of low management intensity. Overall species richness however may still increase (Purvis, 1982). This could indicate that stabilization of oribatid community characteristics takes longer than 55 years during the grassland succession.

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Appendix A

See Table A.1.

Table A.1
Species list and abundance of oribatid species in grasslands from different age classes, 10^3 ind. $m^{-2} \pm$ S.D.

Age class	Ecomorph ^a	0 (arable land)	1 (1–12 years old)	2 (13–28 years old)	3 (29–40 years old)	4 (41–48 years old)	5 (>49 years old)
Number of samples per class (<i>n</i>)		45	39	48	36	57	33
Number of 'grassland species' (i.e. not found on arable land)		–	11	16	20	22	17
Number of species not occurring in an earlier age class		–	11	9	7	4	3
<i>Achipteria coleoptrata</i> (Linnaeus, 1758)	sf	11 ± 76	–	361 ± 1480	425 ± 1781	922 ± 2578	1020 ± 3438
<i>Berniniella bicarinata</i> (Paoli, 1908)	s	204 ± 886	209 ± 558	361 ± 880	1318 ± 5264	331 ± 854	726 ± 3318
<i>Berniniella serratiostris</i> Golosova, 1970	s	34 ± 168	13 ± 82	117 ± 810	57 ± 266	63 ± 306	23 ± 98
<i>Brachychthonius berlesei</i> Willmann, 1928	ns	–	–	21 ± 147	99 ± 362	9 ± 68	77 ± 444
<i>B. bimaculatus</i> Willmann, 1936	ns	–	–	–	–	–	108 ± 621
<i>B. hirtus</i> Moritz, 1976	ns	11 ± 76	–	542 ± 2695	43 ± 255	54 ± 209	–
<i>B. immaculatus</i> Forsslund, 1942	ns	–	157 ± 769	404 ± 861	213 ± 429	358 ± 987	263 ± 626
<i>B. impressus</i> Moritz, 1976	ns	23 ± 152	–	–	–	63 ± 473	–
<i>Carabodes</i> sp.	sf	11 ± 76	–	–	–	–	–
<i>Ceratozetes mediocris</i> Berlese, 1908	sf	11 ± 76	–	74 ± 515	213 ± 1044	376 ± 1588	15 ± 89
<i>Eniochthonius minutissimus</i> (Berlese, 1903)	ns	–	13 ± 82	–	170 ± 657	134 ± 1013	31 ± 124
<i>Eupelops acromios</i> (Hermann, 1804)	sf	–	–	255 ± 801	893 ± 1814	1074 ± 1707	1144 ± 2256
<i>Galumna alata</i> (Hermann, 1804)	sf	–	–	–	–	9 ± 68	–
<i>G. lanceata</i> Oudemans, 1900	sf	–	–	–	–	9 ± 68	–
<i>G. obvia</i> (Berlese, 1914)	sf	–	65 ± 335	329 ± 1698	184 ± 680	698 ± 2567	124 ± 460
<i>Hypochothonius rufulus</i> C.L.Koch, 1835	ns	–	–	21 ± 147	14 ± 85	9 ± 68	–
<i>Latilamellobates incisellus</i> (Kramer, 1897)	sf	11 ± 76	13 ± 82	43 ± 177	71 ± 216	45 ± 175	46 ± 196
<i>Liacarus coracinus</i> (C.L.Koch, 1840)	sf	–	–	–	43 ± 188	–	–
<i>Hemileius initialis</i> (Berlese, 1908)	ns	–	26 ± 114	691 ± 1898	907 ± 2258	617 ± 1230	1167 ± 1678
<i>Liochthonius dilutus</i> Moritz, 1976	ns	–	–	–	–	–	31 ± 178
<i>L. propinquus</i> Niedbala, 1972	ns	–	–	–	71 ± 302	–	62 ± 355
<i>L. sellnicki</i> (Thor, 1930)	ns	–	–	21 ± 103	28 ± 170	89 ± 555	232 ± 866
<i>L. simplex</i> (Forsslund, 1942)	ns	–	–	–	14 ± 85	18 ± 135	–
<i>Mediopppia subpectinata</i> (Oudemans, 1901)	s	11 ± 76	26 ± 114	–	–	54 ± 343	–
<i>M. media</i> Michelcic, 1956	s	23 ± 106	65 ± 266	74 ± 278	128 ± 411	9 ± 68	1020 ± 5591
<i>Metabelba papillipes</i> (Nicolet, 1855)	sf	–	65 ± 408	–	–	9 ± 68	–
<i>M. pulverulenta</i> (C.L.Koch, 1839)	sf	–	–	–	28 ± 170	–	–
<i>Minunthozetes semirufus</i> (C.L.Koch, 1841)	s	102 ± 319	105 ± 314	2221 ± 5263	5313 ± 9945	3024 ± 5990	2813 ± 5603
<i>Nothrus silvestris</i> Nicolet, 1855	l	–	13 ± 82	21 ± 147	–	–	–
<i>Oppia falcata</i> (Paoli, 1908)	s	–	13 ± 82	–	–	9 ± 68	–
<i>O. minus</i> (Paoli, 1908)	s	57 ± 162	92 ± 495	1658 ± 5886	1233 ± 2491	1423 ± 2447	1994 ± 4528
<i>Oppiella nova</i> (Oudemans, 1902)	s	23 ± 106	353 ± 1716	542 ± 1349	227 ± 1114	358 ± 1307	294 ± 1420
<i>Oribatula tibialis</i> (Nicolet, 1855)	ns	–	–	11 ± 74	–	–	31 ± 178

<i>Parachipteria punctata</i> (Nicolet, 1855)	sf	–	–	–	28 ± 170	–	–
<i>Peloptulus phaenotus</i> (C.L.Koch, 1844)	sf	34 ± 168	157 ± 470	457 ± 1187	907 ± 1412	1253 ± 1775	2009 ± 2722
<i>Pilagalumna allifera</i> (Oudemans, 1919)	sf	–	–	–	184 ± 773	–	–
<i>P. tenuiclava</i> (Berlese, 1908)	sf	–	–	202 ± 742	354 ± 935	483 ± 1796	201 ± 674
<i>Platynothrus peltifer</i> (C.L.Koch, 1839)	l	–	13 ± 82	712 ± 2947	510 ± 1542	510 ± 1493	2689 ± 6733
<i>Poecilochthonius spiciger</i> (Berlese, 1910)	ns	34 ± 228	39 ± 245	64 ± 271	241 ± 684	358 ± 1099	232 ± 827
<i>Punctoribates punctum</i> (C.L.Koch, 1839)	s	623 ± 1012	785 ± 2039	1711 ± 3314	1162 ± 1987	1825 ± 3347	1553 ± 2922
<i>Scheloribates laevigatus</i> (C.L.Koch, 1835)	sf	34 ± 129	942 ± 2114	1902 ± 2859	3188 ± 4986	2308 ± 2076	3864 ± 4590
<i>Sellnickochthonius cricoides</i> Weis-Fogh, 1948	ns	–	–	74 ± 379	99 ± 595	125 ± 627	15 ± 89
<i>S. hungaricus</i> (Balogh, 1943)	ns	–	–	–	–	–	15 ± 89
<i>S. suecicus</i> (Forsslund, 1942)	ns	–	–	–	–	242 ± 1756	–
<i>Suctobelbella acutidens</i> (Forsslund, 1941)	s	11 ± 76	26 ± 163	53 ± 368	14 ± 85	45 ± 242	–
<i>S. alloanasuta</i> Moritz, 1971	s	–	–	–	–	18 ± 95	–
<i>S. palustris</i> (Forsslund, 1953)	s	–	–	21 ± 147	–	–	–
<i>S. perforata</i> (Strenzke, 1950)	s	–	–	–	99 ± 595	9 ± 68	–
<i>S. sarekensis</i> (Forsslund, 1941)	s	45 ± 239	–	–	113 ± 388	81 ± 251	124 ± 460
<i>S. similis</i> (Forsslund, 1941)	s	11 ± 76	–	–	–	–	–
<i>S. singularis</i> (Strenzke, 1950)	s	–	39 ± 245	–	–	18 ± 135	–
<i>S. sp. 1</i>	s	11 ± 76	–	–	–	–	–
<i>S. sp. 2</i>	s	–	–	32 ± 221	–	–	–
<i>S. subcornigera</i> (Forsslund, 1941)	s	–	39 ± 245	64 ± 326	213 ± 602	63 ± 256	93 ± 450
<i>Tectocephus alatus</i> Berlese, 1913	ns	1116 ± 2122	876 ± 1254	3134 ± 3864	4647 ± 4519	3624 ± 4751	3933 ± 4998
<i>Trichoribates oxypterus</i> Berlese, 1910	sf	–	65 ± 335	191 ± 466	184 ± 475	170 ± 424	294 ± 687
Nymphs and larvae (not yet identified)		57 ± 271	183 ± 567	414 ± 543	354 ± 515	528 ± 746	479 ± 597

^a Ecomorphs: sf, surface dwelling; l, litter dwelling; s, soil dwelling; ns, non-specialized.

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