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On Abundance of West-European Millipedes

(Diplopoda)

by

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Abstract: The paper summarizes some of our knowledge of millipede populations in Western European habitats. Populations of millipede communities are considered, as well as those of individual species, and reference is made to their coexistence with other decomposers in the soil. Population densities are given for a large number of stations that were sampled quantitatively by means of taking soil samples and performing extractions with Berlese-Tullgren funnels, or by the use of pitfall traps. The sample sites were mainly located in Belgium. Ecological factors that govern the distribution and abundance of millipedes are discussed. There is mention of population fluctuations, and diversity. Possibly rare species are mentioned, together with reasons for their rarity. The question of conservation is raised — are there millipedes in need of protection?

1. Introduction:

We are beginning to have a good understanding of the abundance of many species of millipedes that live in Western Europe, knowing not only their geographical ranges, but also in which biotopes they may be found, and in some cases their likely population densities in various habitats. Their population densities are subject to periodic fluctuations due to both phenology and environmental circumstances (see, for instance BLOWER & GABBUTT 1964, BLOWER 1970, 1989, and GEOFFROY et al. 1981) and occasionally there are population explosions particularly commented upon in the genus *Ommatoiulus*, e.g. BAKER (1978).

2. Millipede Communities:

Millipedes are frequently a conspicuous component of the soil macrofauna, and small species — sometimes attributed to the mesofauna — often achieve high population densities. Hundreds of individuals per square metre of soil and litter have often been counted where there was no apparent aggregation; many species do aggregate, of course, such as blaniulids under the bark of dead trees or on decomposing objects in the soil, and large species e.g. *Ommatoiulus moreletii* (LUCAS) beneath grass tussocks (BAKER 1978). The species occurring in any one community may belong to a possibly large saprophagous guild; some species, especially smaller ones, tend to be microphytophagous (DAVID 1987 a). The saprophagous species may share resources especially with earthworms, isopods and insect larvae among the larger organisms, as well as with a large microfauna. The population densities of millipedes may sometimes depend on the numbers of other organisms therefore, as well as upon mesological parameters. The consumption of organic matter by a guild has not yet been worked out in any detail. DAVID (1987 b) made careful observations on the share of the litter consumed by *Allaiulus nitidus* (VERHOEFF) in France. He also demonstrated a numerical relationship between the size of the millipede populations and the quality of the humus, finding the highest populations in mulls (DAVID 1987 a). Results of quantitative sampling in Belgium entirely support this. The lowest recorded millipede densities often occur in areas with a large accumulation of litter; in some peat bogs and podsols no millipedes have been found, and in these acidic conditions it is not the quantity of organic matter that is limiting. LYFORD (1943) established that *Cylindroiulus caeruleocinctus* (WOOD)[1)] preferred leaves with a higher calcium content. We have found that this animal attains high population densities in calcareous grassland. BLOWER (1985) explains that preferred leaves such as ash and elm, rich in calcium, are also rich in nitrogen and contain little or no phenolic materials, and are subject to more rapid microbial decomposition. Tullgren extractions during the autumn from calcic mulls in Belgium have yielded an average of over 300 ind. m^{-2}. The highest yields in Belgium have come from mesotrophic mulls and a mull moder, all on basic soils, where over 700 ind. m^{-2} were recorded. Figures for a selection of Belgian stations are shown in Table 1. The highest population densities, as well as the greatest species

Table 1: Numbers of millipdes found in some Belgian sites (ind. m^{-2}. From soil and litter samples. The symbol + indicates presence on the site, but not obtained in the samples.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
				b	b	b				b									chalk and limestone								
Glomeris hexasticha intermedia	-	+	-	3	-	-	8	-	-	-	-	+	8	3	20	-	20	-	4	48	-	21	12	72	-	-	4
G. marginata	-	+	-	-	-	-	20	-	-	-	3	-	-	-	-	-	-	-	-	-	+	-	-	-	-	3	18
Stygioglomeris crinita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	90	-
Ceratosphys amoena confusa	-	-	-	-	-	-	+	19	-	-	9	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Chordeuma silvestre	-	+	-	-	4	+	16	-	18	35	-	28	-	-	-	-	5	6	20	-	7	7	12	+	-	+	+
Craspedosoma spp.	-	22	+	+	+	+	45	4	7	-	69	12	3	12	-	-	-	-	-	-	3	-	12	+	-	+	+
Melogona gallicum	-	15	20	230	40	104	110	11	107	385	43	85	8	3	152	4	75	170	16	8	38	7	6	87	110	50	13
Orthochordeumella pallida	-	-	18	-	12	16	12	196	18	35	46	57	5	3	-	8	-	-	111	-	-	-	-	+	-	-	-
Brachydesmus superus	-	15	20	3	-	+	+	15	18	92	6	80	-	-	425	29	65	20	139	-	+	-	-	-	+	25	-
Macrosternodesmus palicola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	8	175	45	111	-	-	4	-	40	570	-	4
Ophiodesmus albonanus	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polydesmus angustus	-	+	+	+	4	+	+	-	+	-	3	10	3	52	-	-	-	-	16	-	+	-	-	-	-	-	+
P. denticulatus	-	-	+	+	-	+	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. inconstans	-	-	-	-	-	-	-	-	-	7	-	-	-	-	25	-	-	-	-	-	-	-	-	-	-	-	-
Archiboreoiulus pallidus	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
Blaniulus guttulatus	-	-	-	-	+	-	-	-	-	7	-	-	-	-	50	-	-	45	12	-	-	-	-	105	30	18	-
Nemasoma varicorne	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Proteroiulus fuscus	-	-	-	-	-	+	-	-	-	+	-	-	-	-	10	-	-	-	+	-	-	-	-	-	-	-	-
Allajulus nitidus	-	-	-	-	-	+	-	-	3	-	-	-	3	-	-	4	95	-	71	40	118	73	19	40	-	70	+
Cylindroiulus caeruleocinctus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. parisiorum	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. punctatus	-	+	+	+	4	+	-	15	-	41	-	-	-	-	15	-	-	12	+	+	-	-	-	-	-	+	-
Julus scandinavius	3	+	+	+	-	+	-	-	-	74	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptoiulus belgicus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-
L. kervillei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	66	5	-	8	-	-	-	-	-	-	5	-
Ommatoiulus sabulosus	6	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tachypodoiulus niger	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	10	+	+	+	3	-	-	22	-	3	4
TOTAL	9	61	53	242	66	146	214	260	174	733	181	273	38	73	747	127	450	299	512	98	172	112	61	379	712	267	47

1 Riymenam 5 m, VI.78, Alnetum; **2** Houthulst 15 m, II.82, Oak/hazel; **3** Meerdaelbos 60 m, XI.78, Oak/hazel; **4** Angre 90 m, V.80, Oak/ash; **5** Arquennes 105 m, XI.78, Oak/ash; **6** Villers la Ville 100 m, IV.78, Oak/hazel; **7** Angleur 170 m, IV.78, Oak/beech; **8** Gesves 190 m, III.79, Oak; **9** Ham sur Heure 175 m, XII.80, Oak/beech; **10** Haltinne 190 m, V.78, Oak/beech; **11** Bourseigne Neuve 250 m, V.79, Oak/hornbeam; **12** Bohan 315 m, X.80, Oak/beech; **13** Bellefontaine 330 m, XI.84, Oak/hornbeam; **14** Croix Rouge 330 m, XII.84, Oak/beech; **15** Onoz 100 m, XII.85, Sycamore; **16** Marche les Dames 120 m, III.79, Beech; **17** St. Martin 120 m, XII.85, Oak/hazel; **18** Fouron le comte 120 m, X.78, Oak/hornbeam; **19** Arbre 150 m, X.78, Oak/hornbeam; **20** Dion 160 m, X.85, Oak/hornbeam; **21** Thynes 160 m, XI/77, Oak/hornbeam; **22** Dourbes 160 m, X.77, Oak/hornbeam; **23** Han sur Lesse 190 m, IV.78, Oak/hornbeam; **24** Crupet 195 m, X.77, Oak/hornbeam; **25** Fouron St. Martin 210 m, II.82, Beech; **26** Remersdael 215 m, X.78, Beech; **27** Ruette 300 m, V.78, Beech. b basic. Additional montane sites (ind m^{-2}): **28** Schoenberg 540 m, VI.80, Beech: *Mycogona germanicum* (8), *Tachypodoiulus niger* (1); **29** Brachtopf 540 m, XI.77, Oak/birch: *Mycogona germanicum* (9).

1) I have followed READ (1990) in reinstating the genus *Cylindroiulus*.

diversity, are found on basic soils. Mesotrophic mulls and mull moders may have more millipedes than calcic mulls because the litter is very thin in calcic mulls, and is fully decomposed, or at least fully buried by worms before the end of twelve months; the litter cover is less effective and the soil surface eventually becomes exposed. There are several burrowing species in calcic mulls. Interesting exceptions to the "more millipedes in mulls" theory are some communities dominated by *Polyzonium germanicum* BRANDT: DAVID & COURET (1985) found an estimated population of 820 ± 190 ind. m^{-2} of this species alone in the Forest of Orléans in strongly acid moder. Similar populations have been found in acidic woodland in Normandy, where *P. germanicum* is associated with *Chordeuma proximum* RIBAUT, and the site normally contained bracken (*Pteridium aquilinum* (L.) KUHN) and often bilberry (*Vaccinium myrtillus* L.). *P. germanicum* is a specialized liquid-feeding species. Summarizing, densities from litter and soil samples vary from nothing in very wet, acid or cold situations to well over 800 per m^2.

Table 2: Numbers of millipedes caught in pitfall traps. All figures are comparable quantitatively, except for Elsenborn and Mt. Rigi, which are roughly comparable perhaps, but sampled at a different time. *Calamagrostis* grass ("calaminaire") = grassland suffering from metal pollution. *Filipendula* = meadows with *Filipendula*. 15 Visé: Crosses for population in units, tens, hundreds and thousands.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Glomeris hexasticha intermedia	-	-	-	-	-	-	1	-	-	1	-	-	5	31	+	-	5	2	14	11	3	-	-	-
G. marginata	-	-	-	-	-	-	-	-	-	-	-	-	9	15	++	25	24	-	29	25	6	-	1	-
Chordeuma silvestre	-	-	-	-	-	27	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	8	-
Craspedosoma spp.	6	-	-	-	-	1	-	2	-	3	-	2	-	-	-	-	-	-	-	-	-	5	1	5
Melogona gallicum	-	-	-	-	-	-	-	-	-	-	-	-	1	1	++	-	1	-	-	-	1	-	-	-
Mycogona germanicum	8	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orthochordeuma pallida	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Orthochordeumella pallida	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
Brachydesmus superus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Ophiodesmus albonanus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Polydesmus angustus	-	-	-	-	-	-	1	-	-	-	-	-	-	3	-	-	-	-	3	-	1	1	1	-
P. denticulatus	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. inconstans	-	-	-	-	-	-	-	-	-	-	-	1	-	-	++	5	-	-	-	-	-	-	-	-
P. testaceus	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	2	-	-	-	-	-	-
Choneiulus palmatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Proteroiulus fuscus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Allajulus nitidus	-	-	-	-	-	-	-	-	-	-	-	-	47	9	-	2	4	1	-	-	-	-	-	-
Brachyiulus pusillus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	++	2	-	-	-	-	-	-	-	-
Cylindroiulus caeruleocinctus	-	-	-	-	-	-	-	-	-	-	-	-	36	4	++++	145	108	53	5	238	7	-	-	-
C. punctatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	1	-	-	-	-
Julus scandinavius	-	-	-	1	-	1	1	1	-	3	20	-	9	9	+	-	-	-	-	-	-	-	20	6
Leptoiulus belgicus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	-	-	-	-	-	-	-	-
L. kervillei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	++	10	-	-	-	1	-	-	-	-
L. simplex glacialis	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ommatoiulus rutilans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+++	103	-	-	40	-	-	-	-	-
O. sabulosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	5	-	-	29	-	-	-
Tachypodoiulus niger	-	-	-	-	-	-	-	-	-	-	-	-	8	9	++	1	4	2	-	1	-	-	-	-
TOTAL	14	3	0	1	0	9	4	3	0	6	20	4	116	88	++++	301	157	65	93	277	47	8	31	11

1 Mt. Rigi 680 m, moor; **2** Elsenborn 550 m, grass moor; **3** Tailles 610 m, *Sphagnetum;* **4** Rocherath 585 m, river bank; **5** Bihain 560 m, *Sphagnetum;* **6** St. Hubert 553 m, raised bog; **7** Recogne 450 m, edge of pond; **8** Anlier 434 m, river bank; **9** Heinsch 348 m, *Carex* marsh; **10** Sampont 343 m, *Filipendula;* **11** Etalle 333 m, *Filipendula;* **12** Trooz 200 m, *Calamagrostis* grass; **13** Velosnes 300 m, *Mesobrometum;* **14** Belvaux 245 m, *Mesobrometum;* **15** Vise 115 m, *Mesobrometum;* **16** Wonck 105 m, Chalk meadow; **17** Dourbes 220 m, *Xerobrometum;* **18, 19** Han sur Lesse a, b, *Xerobrometum;* **20** Sosoye 180 m, *Xerobrometum;* **21** Dinant 170 m, *Xerobrometum;* **22** Maasmechelen 90 m, *Callunetum;* **23** Stambruges 66 m, *Callunetum;* **24** Lanaken 50 m, *Callunetum.*

Table 2 show numbers of millipedes obtained by pitfall trapping in Belgium and one station (Velosnes) just in France. Whereas almost all soil sampling was carried out in forests, the pitfalls were set almost entirely in open situations. The results give some indication of abundance, but more obviously indicate the vagility of surface-active species. For some of these species only adults were captured, in a few species mainly males, indicating a connection with sexual activity, but we have not yet fully analysed the results. It is again noticeable that the largest captures were made in habitats on basic rocks, essentially calcareous grassland. Comparing our results with those of DUNGER & STEINMETZGER (1981) we find a close fit with respect to those species that occur in both regions, and a similar dominance of iteroparous species in open drier sites. As in Germany, in Belgium the semelparous species are more in evidence in the more "oceanic" forests. The wettest sites yielded no millipedes, though there were some in a raised bog at St. Hubert, including the alpine *Leptoiulus simplex glacialis* (VERHOEFF), which also occurs in the Black Forest, the Vosges and the Eifel. PEDROLI-CHRISTEN (1977) found eight species in a peat bog in the Swiss Jura, particularly around the edge in association with *Betula pubescens* EHRH. and *Calluna vulgaris* (L.) HULL, and in progressively smaller numbers towards the spagnetum centre. Thus, our results are similar. Studies again show a decline in numbers with increasing altitude. So, extreme wetness, coupled with acidity and cold temperatures seem to be negative factors. There are, however, species, for instance *Craspedosoma alemannicum* VERHOEFF, which prefer relatively cold conditions (see HAACKER 1968, PEDROLI-CHRISTEN 1977, 1981).

3. Millipede Species:

There are several hundred species of diplopods in West Europe, some of which are extremely abundant while others are believed to be rare. But how can one confidently describe a millipede as rare, when only a minute portion of the ground has been sampled? As our knowledge of relevant ecological parameters advances, and we are increasingly able to predict where we are likely to find a particular species, so we are regularly beginning to find species that were not often encountered in the past. For example, 25 years ago there were very few records of the small *Macrosternodesmus palicola* BROLEMANN: now we know that it is a widespread species in calcareous localities. Many infrequently recorded species may in the end turn out to be quite common. But some will not, because they are confined to small areas. These include species isolated in caves, endemics on islands, some on ecological islands – a mountain massif, or a remnant of native vegetation – maybe extreme specialists, and those species that are intrinsically rare for whatever reason. These species have problems of dispersal, a subject that has not received much attention, indeed is difficult to study, and their geographical range is often very small, even one site. The list of known local endemics is a long one. At the moment, however, it is difficult to draw up a list of rare species with a wider geographical range. There are quite a lot of species that are common in a fairly restricted area, such as *Chordeuma muticum* RIBAUT and *Chordeuma utriculosum* RIBAUT in the Pyrenees, or *Cylindroiulus fulviceps* (ATTEMS) in the Central Alps. A species with a wider range and few records is *Leptoiulus bertkaui* (VERHOEFF) reported from woods near rivers in the Rhine basin. But this has been found several times recently in Switzerland by PEDROLI (this congress). South of the Pyrenees there are large areas that have not been worked, and a species with about the same known range and number of records as *L. bertkaui*, let us say *Cylindroiulus perforatus* (VERHOEFF) might prove to be common over a large area of Iberia.

4. Discussion:

The abundance of millipedes can obviously be related to environmental factors. In Belgium we have now taken soil samples from more that 50 woodland stations, most of which are in semi-natural forest. Some early results were published (KIME & WAUTHY 1984) and indicated which factors most strongly influenced the species composition and the abundance of the millipede communities. Soil texture and temperature were clearly very important. DAVID (1988) carried out a more precise study in a limited area of the Forêt d'Orléans in France where temperature differences were small, and also established the importance of soil texture, and pH and hydrology as well, especially the depth of the water table. He made significant observations about the humus, already referred to, and found some correlation for open as opposed to closed woodland canopy. Now Table 2 shows a number of species caught in open sites that have rarely turned up in closed woodland — *Cylindroiulus caeruleocinctus, Ommatoiulus rutilans* (C.L. KOCH), and *Polydesmus testaceus* C.L. KOCH in particular, in Belgium.

The aforementioned ecological factors relate to each other and also to phytosociological associations, a point already referred to by PEDROLI-CHRISTEN (1981). In our most recent analysis of Belgian results (KIME et al., in press) we find all of these factors emerging again, and a highly significant difference between populations on basic and non-basic soils. This is no surprise, the existence of calcicolous millipedes has been known for a long time. *Allaiulus nitidus,* in Belgium, shows a very strong preference for basic soils and a preference for moderate winter temperatures, though not very mild. DAVID found a strong correlation between this species and mulls: in Belgium it is usually in mulls but uses the habitat more largely than on the edge of its range in France. This highlights a point made in the Bulletin of the British Ecological Society (1989), that scant attention is paid to the location of a study site in relation to a species' range, that there may be differences in demographic parameters in different parts of the range. *A. nitidus* has been found in small numbers in a moder in Switzerland, and in a dysmoder in Belgium, but it is usually in mulls, especially calcic mulls.

We have pitfall records for over 70 sites. These were set by DUFRÊNE to capture carabids, however all captured animals were retained. A glance at Table 2 suggests that very significant results will emerge from a full analysis. Some species may not fall into pitfall traps; in the study of PEDROLI-CHRISTEN (1981) near Neuchatel *Stygioglomeris crinata* BROLEMANN did not, and a number of mobile species not found in the soil samples did. Bearing this in mind, an interesting comparison of Table 1 and Table 2 may be made. There are striking differences between the faunas of open and closed and basic and non-basic sites.

The effect of altitude is worth some comment, and is based on more observations than appear in the tables. *Glomeris marginata* (VILLERS) is widespread in Belgium below 300 m, but is much less common in woodland than in Britain. It is an atlantic species, absent from most of Scotland, but does occur up to over 2000 m in the Alps. *G. hexasticha intermedia* LATZEL reaches the northern limit of its distribution in Belgium and is commoner in the hilly southern areas. It shows a strong preference for basic soils and is much more common than *G. marginata* in woods on this type of ground. It has not been found on the highest ground in Belgium which is, however, generally acidic, and it must be said that much of the lowland North of the Country is sandy or silty with an acid to neutral reaction. The two species overlap considerably and occur together frequently. *Chordeuma silvestre* C.L. KOCH has approximately the same northern limit as *G. hexasticha intermedia,* but in this case is absent from the sort of soil on which it often occurs. The same is true of *Orthochordeumella pallida* (ROTHENBÜHLER) which shows a strong preference for silt, and dies out in the North. Though they may have different soil preferenda, there is a whole cluster of species that die out in the North of Belgium; they could be termed as Central European species. Some of these have only been found on high ground above 500 m in the montane zone defined by ELLENBERG (1963), these include *Mycogona germanicum* (VERHOEFF) and *Leptoiulus simplex glacialis* (VERHOEFF). The atlantic *L. belgicus* (LATZEL), *L. kervillei* (BROLEMANN) and *Polydesmus coriaceus* PORAT (= *gallicus* LATZEL) on the other hand only occur in the low-lying areas, almost entirely in the North. Directly or indirectly there is an altitudinal effect. There is a strong correlation between the two species of *Craspedosoma* and cold winter temperatures, *C. alemannicum* VERHOEFF occurs in the montane zone and the submontane zone. *C. rawlinsi* LEACH occurs on the plain and in the submontane zone. These two species have not been separated in the table because of the inability to distinguish between the immature animals. Even adult males had very variable gonopods. Perhaps mainly because of temperature, altitude affects the size of the populations, and the species found, but there may be other factors involved.

Returning to the rare species, some may need to be protected if they are to survive. They are hardly under threat from collectors, but their habitats may have to be safeguarded in some cases, especially if they are confined to one cave or a small surviving patch of native vegetation. The question of protection is currently under review at the European level. Some species are also at risk from the greenhouse effect. MAURIES (pers. com.) has referred to a recent deficiency in snowfall in the Pyrenees and the very small ranges of the nival species of *Pyreneosoma* (see MAURIES 1974).

5. Conclusions:

Millipedes occur on or in most of the ground in Western Europe, but their abundance varies very much from possible total absence to about 1000 ind. m^{-2}. Each species has ecological preferenda which limit it to particular habitats. Even so-called ubiquists do not occur everywhere, and are most abundant in certain places. Soil texture, temperature, soil water content, mineral content, humidity and humus type are worthy of consideration, at least. These also determine vegetation, so phytosociological factors are indicative, and certain types of vegetation may be preferred as food. Interaction with other detritivores/herbivores may be significant.

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