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Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests

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Abstract Micro-samples of the surface organic horizons of 13 beech forests in Belgium were fixed immediately after collection in ethanol. Collembola (6255 animals) were sorted directly from micro-samples in the laboratory using a dissecting microscope, while the litter/soil matrix was analysed semi-quantitatively. The vertical distribution of Collembolan species was studied by correspondence analysis. Gut contents of animals were examined under a light microscope and their composition was compared with that of the matrix. A consistent association was found between the vertical distribution of gut contents and that of food resources in the immediate proximity of animals. Species differed in their feeding habits but most of them ingested a wide spectrum of food items. Plasticity in the food regime according to depth could be demonstrated in members of the Onychiuridae family.

Keywords Collembola · Food resources · Gut contents · Beech forests

Introduction

The vertical stratification of the topsoil is a main feature of forest heterogeneity (Hågvar 1983). Changes in species composition according to depth compare well with those due to other ecological factors such as litter quality, acidity, or water availability (Ponge 1980). Relationships have been demonstrated between the vertical distribution of Collembola and stages of litter decomposition (Takeda 1995), root systems of plants (Faber and Joosse 1993) and microbial distribution (Hassall et al. 1986). Nevertheless, the reasons why different animal species live in different soil and litter horizons remain largely unknown. Ecophysiological (Vannier 1983), nutritional (Ponge et al. 1993), behavioural (Didden 1987; Ernsting 1988), physical (Haarlov 1955) reasons, and species interactions (Lambert 1973; Faber and Joosse 1993), have been suggested to account for the observed patterns. Few studies, however, have directly addressed the common distribution of animals, food resources and habitats in soils, mostly because of technical difficulties. Recently the use of rhizotrons have enabled direct observations on soil animals feeding on roots, mycelial systems or soil aggregates (Gunn and Cherrett 1993), but generally viewing an animal feeding (or moulting or mating) on a given component of the soil matrix is accidental and such studies lack a quantitative basis. Micro-stratified sampling of micro-arthropods, roots and micro-flora displayed interesting relationships between them (Klironomos and Kendrick 1995), but unfortunately the need for soil fauna and micro-flora to be extracted by distinct methods makes impossible any inference with respect to the micro-sites where animals actually live. Sections in agar- or gelatin-embedded soil have been used successfully to correlate the distribution of soil micro-arthropods with components of their immediate environment (Anderson 1978), but these methods can be time-consuming when a large number of animals is needed.

The aim of this study was to analyse the relationships between the vertical distribution of Collembola and associated food resources. For this reason soil animals were collected at varying depths in 13 beech stands of the Belgian Ardennes (Ponge 1999).

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Materials and methods

Thirteen mature beech stands were selected in the Belgian Ardennes (western Europe), covering a wide range of acidic humus forms (Table 1). All these stands were located on low base-status substrates (schists, graywackes, quartzites) ranging from Cam-

Table 1 Main features of the 13 sites studied

Site	Altitude	Phytosociological type[a]	Soil type[b]	Humus form[c]
1	370 m	*Luzulo-Fagetum festucetosum*	Dystric cambisol	Dysmull
3	465 m	*Luzulo-Fagetum festucetosum*	Dystric cambisol	Eumoder
4	500 m	*Luzulo-Fagetum typicum*	Dystric cambisol	Dysmoder
5	505 m	*Luzulo-Fagetum vaccinietesosum*	Dystric cambisol	Eumoder to dysmoder
16	445 m	*Luzulo-Fagetum vaccinietesosum*	Dystric cambisol	Eumoder
17	430 m	*Luzulo-Fagetum typicum*	Dystric cambisol	Hemimoder to eumoder
22	400 m	*Luzulo-Fagetum typicum*	Gleyic cambisol	Eumoder to dysmoder
24	390 m	*Luzulo-Fagetum festucetosum*	Dystric cambisol	Dysmull to dysmoder
26	430 m	*Luzulo-Fagetum vaccinietesosum*	Leptic podzol	Dysmoder
28	375 m	*Luzulo-Fagetum festucetosum*	Dystric cambisol	Amphimull to eumoder
40	385 m	*Luzulo-Fagetum vaccinietesosum*	Ferric podzol	Dysmoder
100	350 m	*Melico-Fagetum festucetosum*	Dystric cambisol	Oligomull to dysmull
307	380 m	*Luzulo-Fagetum vaccinietesosum*	Leptic podzol	Amphimull

[a] Phytosociological types according to Thill et al. (1988)
[b] Soil types according to FAO-UNESCO classification (Driessen and Dudal 1991)
[c] Humus forms according to Brêthes et al. (1995)

brian to Devonian. Altitude and related regional factors (climate, mineral richness of parent rock) were found to be the main source of variation of soil animal communities over the studied range, with a decreasing diversity of soil animal groups from oligomull to dysmoder (Ponge et al. 1997). Chemical analyses of litter and soil were reported in Ponge et al. (1997), together with densities of macrofauna and mesofauna groups.

In each site two humus profiles were sampled for micro-morphological descriptions of horizons (Ponge 1999). These profiles were chosen to represent the range of observed within-site variation of humus forms. Sampling was completed in June 1989. Preparation of the samples (two 5×5-cm section monoliths in each stand) was carried out according to the method described by Bernier and Ponge (1994), except that only the 0- to 1-cm layer of the A horizon (still rich in organic matter) was sampled. Preliminary observations indicated that below this layer the density of soil arthropods was negligible. Micro-layers (sub-samples) were separated directly in the field on the basis of visible variation, then immediately fixed in 98% ethyl alcohol, care being taken that animals could not escape the samples before being transferred to alcohol. Micro-layers were classified into OL (entire leaves), OF (fragmented leaves), OH (holorganic faeces) and A (hemorganic) according to the classification of forest humus horizons by Brêthes et al. (1995), and they were numbered according to their order from the top to the bottom of a given horizon, i.e. OL1, OL2, OL3, OF1, OF2, etc.. All 172 sub-samples were immediately immersed in ethyl alcohol then transported to the laboratory. The composition of each sub-sample was analysed by observing the soil matrix in alcohol under a dissecting microscope. No attempt was made to quantify the volume or mass of each component. A visual score was given to each component: 0 absent; 1 present but scarce; 2 present and common; 3 present and dominant. A total of 185 components were thus recognized (Appendix 1). Most of them were plant organs, at varying degrees of decomposition or comminution by fauna. Animal faeces were classified according to the animal group, their degree of further tunnelling by fauna, and their physical links to uneaten plant components (free, tightly appressed or included in composite assemblages).

Animals were recovered in each sub-sample either directly or after thorough dissection of decaying plant organs into which fauna might tunnel (twigs, bark pieces, petioles). Collembola were mounted in chloral-lacto-phenol (50 g/25 ml/25 ml) then examined by phase contrast microscopy at $\times 400$ magnification for identification at the species level and examination of gut contents (Ponge 1991). Eight categories of gut contents were identified: empty guts; hemorganic humus; holorganic humus; mycorrhizae; fungal material (spores, hyphae); higher plant material; pollen; micro-algae. The identification of components of the food bolus by transparency was greatly facilitated by the fact that springtails often eat continuously on the same food source until they have completely filled their intestine; then digestion occurs before rapid voiding of the intestine and the start of a new cycle of ingestion/digestion/defecation (personal observations). Thus gut contents are rarely of a composite nature and most intestines are either full or empty. When full, gut contents generally fall into one of the above-mentioned categories, more rarely into two of them. When banding of two different foods was apparent in a gut, then fuzzy coding was used in order that the sum of scores for the whole gut was always 1. Higher plant material included decaying leaf as well as root tissues, and it was hard to distinguish between these two types of plant material when crushed by mouth parts. Mycorrhizae were recognized by the intimate mixing of fungal and root material. Mantle and Hartig net fragments were easy to recognize by phase contrast microscopy, according to anatomical features (Agerer 1996). Spores and hyphae of fungi, although easy to discern, were not separated, because they were often present together in the same intestine. This category comprised also the extra-matrical material and the mantle of mycorrhizae when just the fungal part of ectomycorrhizal roots had been browsed by the animals. Humus was characterized by dark-coloured components, the absence (or scarcity) of recognizable plant and fungal tissues and the abundance of fine particles < 1 μm. Probably it includes bacteria and clay particles (personal observations). Hemorganic humus was distinguished from holorganic humus by the presence of fine silt and gross clay particles (1–5 μm, rarely larger).

Statistical methods involved both multivariate and correlation analyses. The vertical distribution of Collembola over the whole range of studied profiles was analysed by the help of correspondence analysis, a multivariate method using the χ^2 distance (Greenacre 1984). This method indicates underlying global trends in a multidimensional data matrix (here comprising 172 sub-samples and 45 springtail species) by defining a set of a few orthogonal axes (factorial axes or principal components, determined by eigen vectors of a distance matrix) which maximize components of the total variance. Projection of rows (sub-samples) and columns (species), as clouds of points, on factorial axes, allows one to visualize the structure of the data, more especially gradients and clusters occurring at the community level (Ponge 1993). Data at the intercept of a row and a column were numbers of animals of a given species found in a given sub-sample (micro-layer). All springtail species, rare or not, were considered as active (main) variables. Other variables were included in the analysis, but only as passive (additional) items. They were projected on factorial axes together with main variables.

Two types of passive items were included in this analysis, as additional columns. Components of the immediate environment of animals were categories found during sorting of the material,

coded as above for each micro-layer. Gut content categories were coded by totalling the scores achieved by the different animals which had this category in their gut in a given sub-sample.

Such an integrated analysis does not allow species-specific trends to be addressed. These were analysed additionally for each of the ten most abundant species by totalling the scores achieved by the different gut content categories over all individuals of a given species present at a given depth. Significant shifts in the composition of gut contents according to depth were detected using run tests (Sokal and Rohlf 1995; Rohlf and Sokal 1995). For that purpose we used the following procedure: the distribution of the scores of a given gut content category over the different depth classes was compared with a theoretical distribution based on the independence of categories and depth classes, as for the measurement of a χ^2. The presence of a given category at some depths more frequently than expected was considered significant when it was shifting rather than erratic. In this case, the succession of plus and minus signs along depth classes forms a chain, whose significance can be tested with methods currently used in run experiments.

Results

Table 2 shows the composition of the Collembolan community in the 13 studied sites. This community was largely dominated in numbers of animals and species by poduromorphs, mainly belonging to the family Onychiuridae (Archaphorura, Hymenaphorura, Kalaphorura, Mesaphorura, Paratullbergia, Protaphorura). The second most abundant group was the family Isotomidae (Folsomia, Isotomiella, Parisotoma, Proisotoma, Pseudanurophorus, Pseudisotoma).

Table 2 Total number of Collembola collected over a 2×5-cm^2 area in the 13 beech stands

Code	Name	Beech samples												
		1	3	4	5	16	17	22	24	26	28	40	100	307
AAB	*Archaphorura absoloni*	0	0	2	0	0	0	26	0	0	0	0	0	3
AGR	*Anurida granulata*	3	2	0	0	0	0	0	0	0	4	1	1	1
CDE	*Ceratophysella denticulata*	0	0	1	0	0	1	13	5	0	1	0	0	1
DMI	*Dicyrtomina minuta*	0	0	0	0	1	4	0	0	0	0	0	0	0
ENI	*Entomobrya nivalis*	0	0	0	0	0	0	0	2	1	0	0	0	0
FMA	*Folsomia manolachei*	0	0	0	0	0	0	0	1	0	0	0	0	0
FQU	*Folsomia quadrioculata*	33	115	51	229	0	66	52	41	209	28	36	45	46
FTR	*Friesea truncata*	7	3	18	21	111	46	10	0	4	8	45	0	0
HSI	*Hymenaphorura sibirica*	0	0	0	0	0	0	0	0	0	6	0	0	0
IMI	*Isotomiella minor*	31	146	159	15	84	22	26	1	0	97	7	53	118
KFU	*Kalaphorura furcifera*	2	5	0	0	0	0	0	0	0	1	0	9	0
LLA	*Lepidocyrtus lanuginosus*	0	0	0	1	0	0	0	0	5	0	4	3	0
LLI	*Lepidocyrtus lignorum*	19	37	34	9	2	6	30	2	11	32	25	4	16
LLU	*Lipothrix lubbocki*	0	0	0	0	0	0	0	0	1	0	5	0	3
MMI	*Megalothorax minimus*	1	13	7	6	5	4	5	0	5	19	9	1	3
MBE	*Mesaphorura betschi*	0	0	0	0	0	0	0	0	2	0	2	0	0
MHY	*Mesaphorura hylophila*	0	0	0	0	0	0	0	0	0	6	0	0	0
MIT	*Mesaphorura italica*	0	7	0	0	0	0	0	0	0	0	3	0	0
MJE	*Mesaphorura jevanica*	0	7	59	19	46	20	0	8	0	3	21	0	33
MLE	*Mesaphorura leitzaensis*	0	0	0	0	5	0	0	0	0	16	3	0	0
MMA	*Mesaphorura macrochaeta*	0	1	61	25	4	166	50	3	5	74	82	1	62
MPO	*Mesaphorura pongei*	0	1	0	1	0	0	0	0	0	0	0	0	0
MTE	*Mesaphorura tenuisensillata*	1	11	52	40	98	78	4	22	0	11	0	1	26
MYO	*Mesaphorura yosii*	0	0	0	0	232	112	0	0	63	0	139	0	154
MFO	*Micranurida forsslundi*	0	0	0	0	0	0	0	0	0	0	0	0	3
MPY	*Micranurida pygmaea*	0	6	1	27	0	0	0	0	13	8	0	0	18
NMU	*Neanura muscorum*	0	0	0	0	1	0	0	0	0	0	0	0	0
PCA	*Paratullbergia callipygos*	20	0	0	2	0	3	14	5	0	6	0	8	21
PNO	*Parisotoma notabilis*	6	22	23	2	3	13	4	2	3	9	10	1	11
PFL	*Pogonognathellus flavescens*	0	6	0	2	1	0	1	0	1	3	6	2	7
PMI	*Proisotoma minima*	0	0	0	0	0	0	0	0	0	1	0	0	0
PEI	*Protaphorura eichhorni*	48	28	132	110	47	123	35	16	127	18	83	12	172
PBI	*Pseudanurophorus binoculatus*	0	0	0	0	0	0	0	2	1	13	0	0	0
PSE	*Pseudisotoma sensibilis*	0	0	0	12	0	1	0	0	0	0	0	0	1
PAL	*Pseudosinella alba*	0	0	0	0	0	2	0	0	0	0	5	0	0
PMA	*Pseudosinella mauli*	1	5	2	4	15	2	2	2	4	15	7	5	11
SWI	*Schaefferia willemi*	2	19	8	0	4	17	1	0	3	1	0	0	1
SAU	*Sminthurinus aureus*	0	0	0	0	0	0	0	0	0	0	1	0	0
SNI	*Sminthurinus niger*	0	0	0	0	0	0	0	0	0	1	0	0	0
SPU	*Sphaeridia pumilis*	0	0	0	0	0	0	0	0	1	0	1	0	0
WAN	*Willemia anophthalma*	1	0	22	1	2	3	14	25	4	21	0	0	5
WAS	*Willemia aspinata*	5	64	17	66	14	61	1	1	90	83	50	0	37
XTU	*Xenylla tullbergi*	0	0	0	0	0	0	0	0	0	1	0	0	0
XGR	*Xenylla grisea*	0	0	0	0	0	0	0	0	0	0	0	0	1
XAR	*Xenyllodes armatus*	0	0	0	0	0	0	0	0	0	0	1	0	0

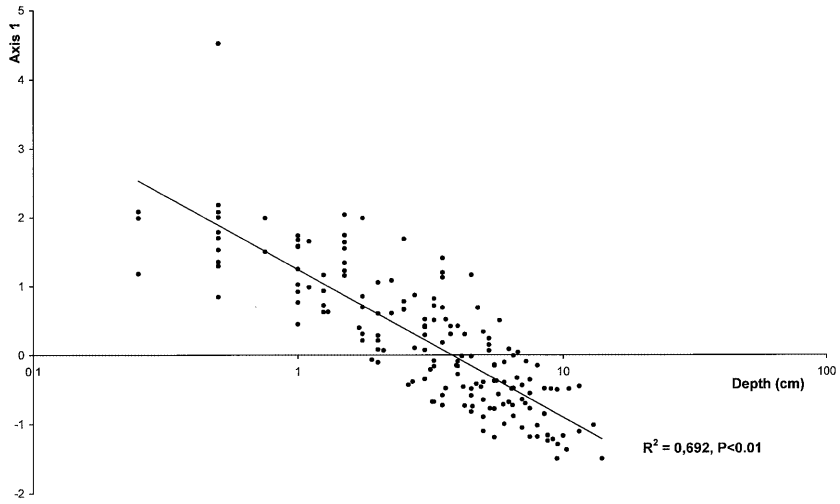

Fig. 1 Correlation between axis 1 of the correspondence analysis and depth

The first axis of the correspondence analysis was interpreted as the vertical distribution of both Collembolan species and micro-layers, revealing a vertical gradient in species composition. There was a significant logarithmic correlation ($P<0.01$) between depth and axis 1 (Fig. 1). The logarithmic rather than linear relation indicated that changes in species composition according to depth were more rapid in upper than in lower horizons, as shown by the distribution of depth classes along axis 1 (Fig. 2). Despite the low percentage of total variance explained by this axis (10% only), axis-1 coordinates can be used as reliable indices of the vertical distribution of Collembolan species. In the absence of other interpretable axes, in particular those indicating differences between humus forms, we considered that differences between sites can be neglected compared to differences according to depth.

Species were arranged along a vertical gradient, depicted by axis 1 (Fig. 2). From the positive to the negative side of axis 1 we observed a succession from litter-dwelling to soil-dwelling species. Symphypleona, represented by *Dicyromina minuta*, *Sphaeridia pumilis*, *Sminthurinus niger* and *Sminthurinus aureus*, lived preferentially near the surface. This was also the case for most Entomobryida, namely *Entomobrya nivalis*, *Lepidocyrtus lanuginosus*, *Pogonognathellus flavescens*, *Lepidocyrtus lignorum*, except *Pseudosinella mauli* and *Pseudosinella alba* which were found deeper. Species found at the deepest levels were onychiurids, together with the neanurid *Friesea truncata* (FTR).

The projection of sub-horizons onto axis 1 (Fig. 2) indicated a high degree of overlapping between OL, OF, and OH horizons, and no significant change in species composition between OH and A horizons. For instance, the species composition in the OL3 sub-horizon (when it existed) was not discernible from that of an OF2 sub-horizon, and the same was true for OF3 and OH1 sub-horizons. This suggested that depth explained a little better the vertical distribution of Collembolan species than the stage of decomposition of the beech litter. Nevertheless it should be remembered that the nomenclature of horizons was achieved by observing humus profiles with the naked eye, before any laboratory investigation of micro-layers under a dissecting microscope. Discrepancies between field nomenclature and laboratory investigations using the dissecting microscope have been discussed in a previously published paper (Ponge 1999).

The common distribution of Collembolan species and litter/humus components is shown in Fig. 3. Only a selection of 14 among 185 components which had been recognized (Appendix 1) has been shown on this figure. Species found in the top 2 cm (Symphypleona, Entomobryida, Poduromorpha of the genus *Xenylla*) were living in a habitat derived from beech leaves of varying decomposition stages. At this depth Collembola were in contact with micro-algae, faeces of litter-consuming animals such as slugs and woodlice, caterpillar frass, and pollen grains. At a lower depth (2–4 cm), mostly in the upper part of the OF horizon, springtail species were in contact with skeletonized leaves and plant organs (bark, twigs) tunnelled by mesofauna. In the lower part of the OF horizon, in the OH and in the top of the A horizon (4–8 cm or below, according to thickness of organic horizons), animals were in contact with enchytraeid faeces (free then compacted) and feeder roots of beech (long roots and mycorrhizae).

Figure 4 shows that gut content categories varied according to the vertical gradient depicted by axis 1. Pollen grains were present in the guts of species which were found near the surface. The position of this component closely resembled that of the corresponding litter/humus component (Fig. 3). Micro-algae, which were placed just beyond pollen grains along the depth gradient, were not registered during our observation of litter/humus components, due to their small size and transparency. We can conclude at this first step of our analysis that Collembolan species found in the first 2 cm ate mainly pollen grains and micro-algae, and not the main component of their habitat, i.e. beech leaves

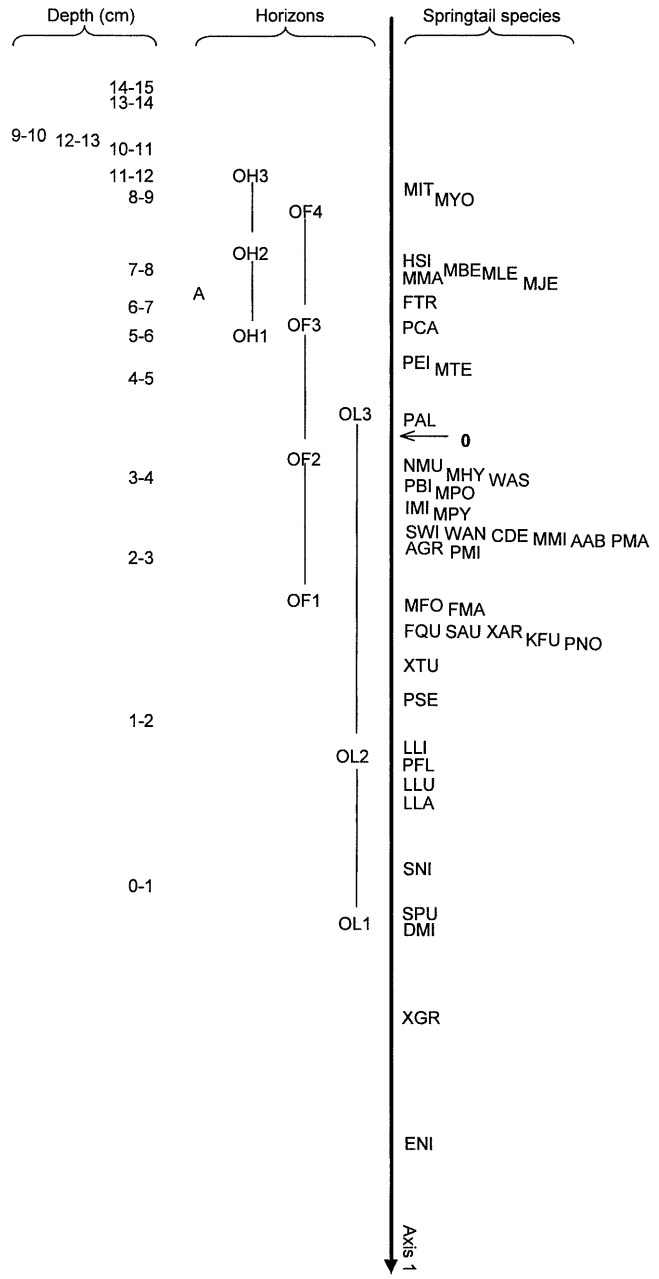

Fig. 2 Correspondence analysis. Projection of main variables (*Collembolan species*) and some additional variables (*horizons and depth classes*) on axis 1 of the correspondence analysis. *OL* Entire leaves, *OF* fragmented leaves, *OH* holorganic faeces, *AAB Archaphorura absoloni, AGR Anurida granulata, CDE Ceratophysella denticulata, DMI Dicyrtomina minuta, ENIEntomobrya nivalis, FMA Folsomia manolachei, FQU Folsomia quadrioculata, FTR Friesea truncata, HSI Hymenaphorura sibirica, IMI Isotomiella minor, KFU Kalaphorura furcifera, LLA Lepidocyrtus lanuginosus, LLI Lepidocyrtus lignorum, LLU Lipothrix lubbocki, MMI Megalothorax minimus, MBE Mesaphorura betschi, MHY Mesaphorura hylophila, MIT Mesaphorura italica, MJE Mesaphorura jevanica, MLE Mesaphorura leitzaensis, MMA Mesaphorura macrochaeta, MPO Mesaphorura pongei, MTE Mesaphorura tenuisensillata, MYO Mesaphorura yosii, MFO Micranurida forssslundi, MPY Micranurida pygmaea, NMU Neanura muscorum, PCA Paratullbergia callipygos, PNO Parisotoma notabilis, PFL Pogonognathellus flavescens, PMI Proisotoma minima, PEI Protaphorura eichhorni, PBI Pseudanurophorus binoculatus, PSE Pseudisotoma sensibilis, PAL Pseudosinella alba, PMA Pseudosinella mauli, SWI Schaefferia willemi, SAU Sminthurinus aureus. SNI Sminthurinus niger, SPU Sphaeridia pumilis, WAN Willemia anophthalma, WAS Willemia aspinata, XTU Xenylla tullbergi, XGR Xenylla grisea, XAR Xenyllodes armatus*

at an early stage of decomposition. At a lower depth (2–4 cm depth) springtails ate mainly fungal material, hemorganic and holorganic humus. Gut contents of the species living at the lowest depth were mostly composed of mycorrhizae and higher plant material. Even though more precise identification of the plant material was impossible, we can postulate that it was mainly made of root rather than of leaf tissues. The position of the mycorrhizal gut content category was similar to that of mycorrhizae found in the soil matrix at the same depth (Fig. 3). Likewise, the position of humus in guts closely resembled that of free enchytraeid faeces [the dominant fauna (Ponge et al. 1997)]. The latter result indicated that enchytraeid faeces were ingested when still in a fresh state, rather than when aged and compacted (see the position of compacted enchytraeid faeces on Fig. 3).

Although correspondence analysis provided information on general dietary preferences of animals and corresponding distributions of their gut content categories, it did not indicate the distribution of the sources of the different gut content categories with respect to the vertical distribution of animals. Figure 5 showed a wide range of food categories in Collembolan guts. In particular, holorganic humus and fungal material dominated the food bolus in bulked Collembola, even in animals found in the first top 2 cm. Mycorrhizal tissues were found in animals living at a greater depth.

We analysed the co-occurrence of gut content and litter/humus components by comparing the scores they obtained over the whole sample of micro-layers and distributing them among depth classes (Table 3). It can be seen that the distribution of pollen grains along a mean humus profile decreased abruptly from the soil surface to a depth of 6 cm, closely resembling that of pollen grains in springtail intestines ($r=0.95$). An even closer fit was observed ($r=0.98$) when comparing the distribution of holorganic faeces and that of holorganic humus in Collembolan guts. This result allowed us to conclude that holorganic humus in guts was derived from the ingestion of holorganic faeces. The distribution of fungal material in guts followed that of fungal mycelia in the environment ($r=0.91$), but fungal mycelia peaked in the depth class of 3–4 cm, while the score of fungal material in guts levelled off at a depth of 1–7 cm. This was probably due to the fact that fungal material was not perceptible under the magnification of the dissecting microscope when not in the form of rhizomorphs or mycorrhizal sheaths (around ectomycorrhizal roots). The distribution of mycorrhizal material

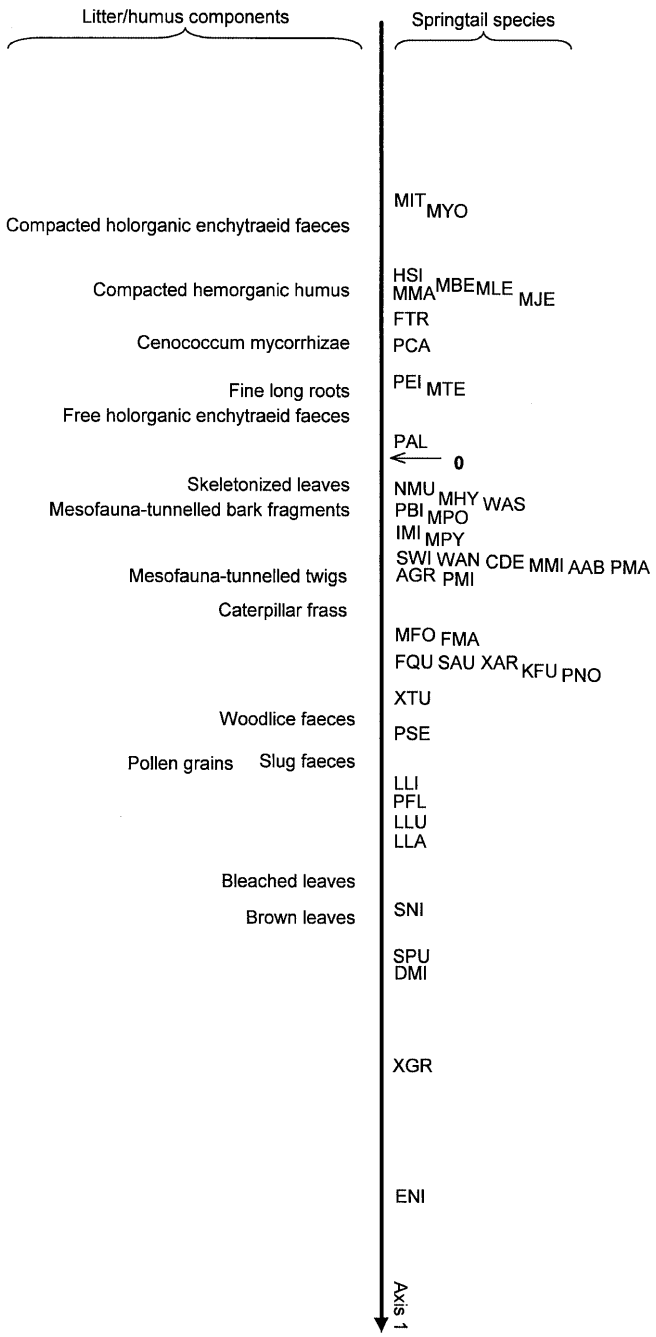

Fig. 3 Correspondence analysis. Projection of main variables (*Collembolan species*) and some additional variables (*selection of components of the immediate environment*) on axis 1 of the correspondence analysis. For abbreviations, see Fig. 2

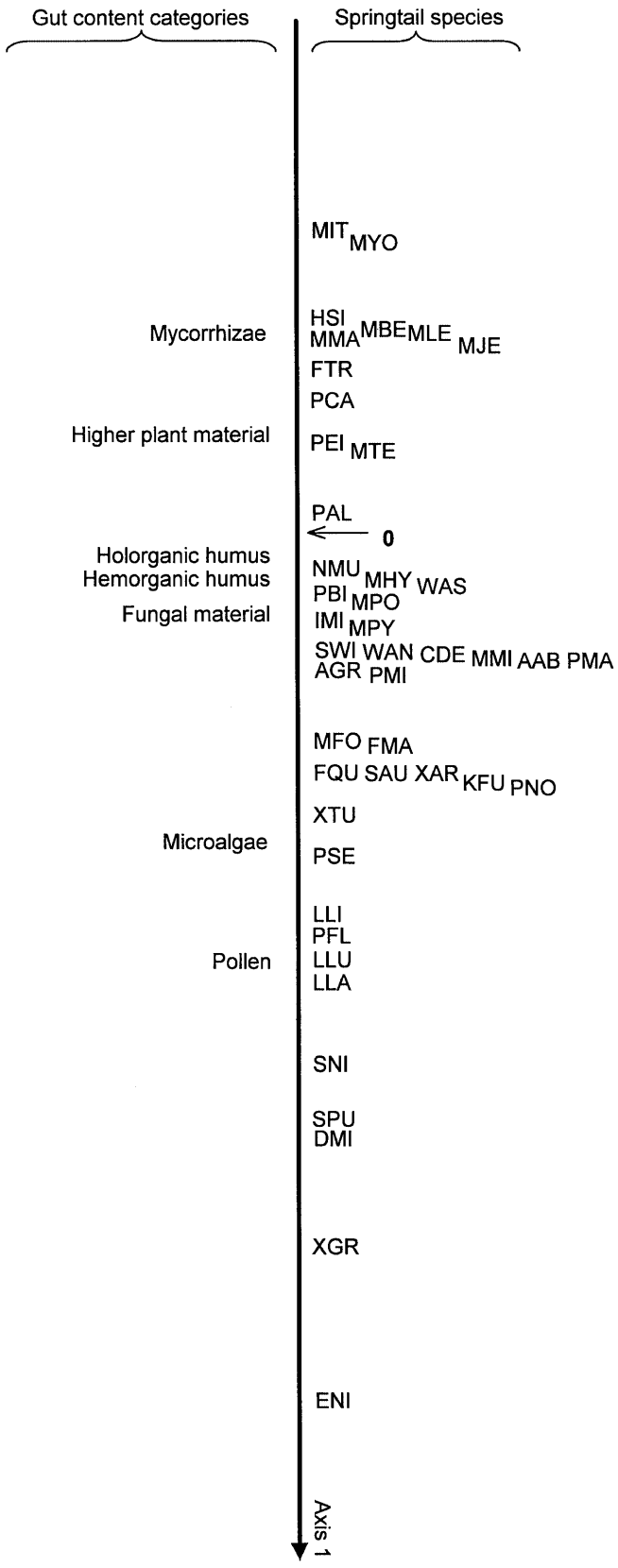

Fig. 4 Correspondence analysis. Projection of main variables (*Collembolan species*) and some additional variables (*gut content categories*) on axis 1 of the correspondence analysis. For abbreviations, see Fig. 2

in guts followed that of mycorrhizal roots ($r=0.84$), but the curve of gut contents peaked at a position 1 cm deeper than that of mycorrhizae. This indicated that animals probably ate aged rather than freshly formed ectomycorrhizae.

The results presented above concern the bulked Collembola. This may mask strong discrepancies between species. For this reason ten Collembolan species

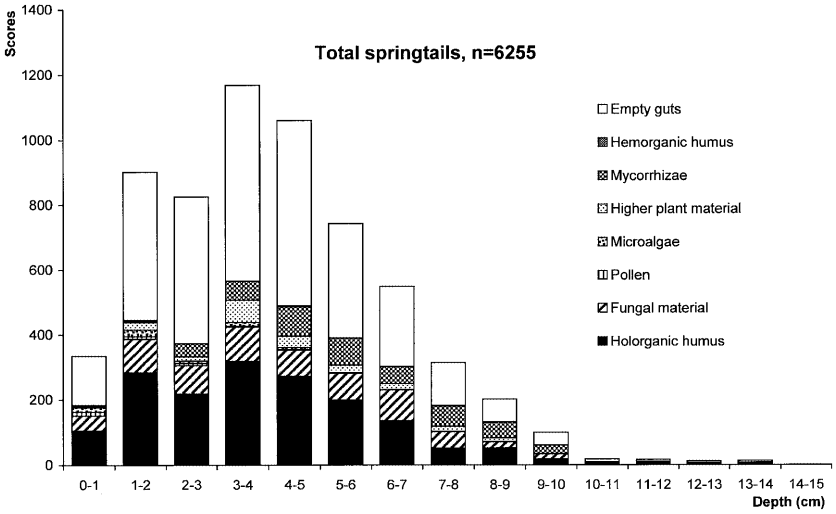

Fig. 5 Distribution of gut content categories according to depth in bulked Collembolan species

were studied in detail (Table 4). The distribution of individuals and gut contents of *Lepidocyrtus lignorum* was typical for epigeic species. The density of animals decreased abruptly from the soil surface to 6 cm depth, with a food bolus often made of pollen and micro-algae (see also Fig. 4). Fungal material was not dominant in the first top centimetres, but became so underneath. Holorganic humus was negligible. About half of the guts were empty. The composition of the food bolus reflected that of the immediate environment of these animals, with the exception of beech leaves which were not consumed at all.

Among endogeic species some had specialized food habits. *Isotomiella minor* ate only holorganic humus, probably derived from holorganic faeces found in the immediate environment (see Table 3). About half of the animals had empty guts, with the exception of those from the depth class of 0–1 cm, which was poorly populated but where guts were never empty. The other abundant isotomid species, *Folsomia quadrioculata*, had similar food habits, but with a higher rate of empty guts, reaching 80%, and a smaller content of fungal material. Here too the 0–1 cm depth class exhibited a lower rate of empty guts than underlying depth classes. *F. quadrioculata*, although widely distributed in lower organic horizons, was a little more abundant near the surface than *I. minor*. The onychiurid *Mesaphorura tenuisensillata* had also a gut content mainly made up of holorganic humus, but with a fairly high amount of fungal material compared to *F. quadrioculata*. About half of the animals had empty guts, like *I. minor*. Very few individuals were found in the 0–1 cm depth class, but none of them had empty guts; *M. tenuisensillata* was more abundant at deeper levels than *I. minor* (see also Fig. 2).

The gut contents of *Willemia aspinata* were exclusively made of fungal material, and more particularly of comminuted hyaline hyphae. About 60% of individuals had empty guts, but only 50% in the 0–1 cm depth class, where they were far less abundant. No recognizable gut content was found in *Friesea truncata*, but the genus *Friesea* is known to eat micro-fauna, eggs and moults of small animals, and in most cases animal prey was completely digested (Singh 1969).

Four endogeic onychiurid species, namely *Protaphorura eichhorni*, *Mesaphorura yosii, Mesaphorura macrochaeta* and *Mesaphorura jevanica*, were found to ingest a wide array of food categories. Although holorganic humus was dominant in *M. jevanica* and *M. macrochaeta*, mycorrhizae made a significant contribution to the gut contents in all four species. In addition to holorganic humus, fungal material, and mycorrhizae, higher plant material (probably from roots) made a significant contribution to the gut contents in *P. eichhorni*.

Possible shifts according to soil depth in the gut contents of individual species were hard to discern, given prominent background noise in the data. Testing can be achieved only on those species occupying a wide vertical range of habitats with variable feeding habits. This was the case of the onychiurids *M. macrochaeta*, *M. yosii* and *P. eichhorni*. Table 5 shows that some significant shifts could be demonstrated. A decrease with depth in the gut levels of holorganic humus and fungal material was observed in *M. macrochaeta*. A decrease with depth in the percentage of empty guts and an increase with depth in the percentage of mycorrhizae were observed in *P. eichhorni*.

Discussion

The absence of clear trends relating the species composition of Collembolan communities to factors other than depth was expected given the strong acidity of the soil in all sites investigated; indeed the water pH was <5 in all samples (Ponge et al. 1997). Ponge (1993) de-

Table 3 Distribution of scores obtained by main components of Collembolan gut contents over the whole sample (food items at the same depth between parentheses)

Gut contents	0–1 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	5–6 cm	6–7 cm	7–8 cm	8–9 cm	9–10 cm	10–11 cm	11–12 cm	12–13 cm	13–14 cm	14–15 cm
Empty guts	4.9[a]	14.7	14.6	19.4	18.4	11.4	8.0	4.3	2.2	1.2	0.3	0.2	0.2	0.2	0.0
Pollen	38.8 (27.0)	26.3 (31.1)	20.3 (19.0)	7.3 (7.8)	4.2 (9.7)	1.6 (3.9)	0.0 (1.4)	0.8 (0.0)	0.8 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Micro-algae	22.3	32.8	11.0	19.0	9.7	2.4	0.9	0.9	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Higher plant material	1.3	10.6	6.5	31.6	16.4	11.0	8.7	7.4	5.5	0.5	0.1	0.2	0.1	0.1	0.1
Mycorrhizae	0.0 (1.1)	1.1 (10.6)	8.5 (10.3)	12.2 (17.8)	19.1 (15.6)	17.5 (13.0)	11.0 (10.6)	13.2 (8.1)	10.0 (7.4)	5.5 (3.5)	0.5 (0.4)	0.5 (1.0)	0.4 (0.2)	0.5 (0.3)	0.1 (0.2)
Fungal material	6.6 (3.7)	15.0 (12.7)	12.6 (13.4)	15.4 (20.5)	11.8 (14.7)	12.0 (11.4)	13.7 (7.8)	7.4 (5.8)	2.8 (6.2)	2.3 (2.8)	0.2 (0.4)	0.1 (0.6)	0.1 (0.0)	0.1 (0.0)	0.0 (0.0)
Holorganic humus	6.3 (6.8)	17.0 (15.5)	13.1 (15.5)	19.1 (18.5)	16.3 (13.2)	11.9 (11.0)	8.1 (9.6)	3.0 (3.7)	3.1 (2.4)	1.0 (1.8)	0.3 (0.9)	0.4 (0.4)	0.2 (0.3)	0.2 (0.3)	0.0 (0.1)
Hemorganic humus	26.9	7.7	0.0	7.7	19.2	7.7	7.7	7.7	15.4	0.0	0.0	0.0	0.0	0.0	0.0

[a] Data are percentages of total scores obtained over the whole studied profile

monstrated that soil-dwelling Collembolan communities were insensitive to humus form provided soil pH remained either below or above this threshold value.

Although the distribution of Collembolan gut content categories closely paralleled that of components of humus profiles, thereby suggesting indiscriminate feeding, this global trend masked strong disparities between individual species. Deeper-living species mostly found in the OH horizon, such as *Mesaphorura tenuisensillata*, *Protaphorura eichhorni*, *Friesea truncata*, *Mesaphorura jevanica*, *Mesaphorura macrochaeta*, and *Mesaphorura yosii*, exhibited quantitative differences in their food regimes. If we except the predatory neanurid *F. truncata*, all these species were members of the same family if not of the same genus. *M. tenuisensillata* ingested almost only holorganic humus which, given the depth range where this species was commonly found (Table 4, see also Fig. 3), was probably composed of enchytraeid faeces only. Although living at similar deep levels, *M. macrochaeta*, *M. yosii* and *M. jevanica* ingested a noticeable amount of mycorrhizal and higher plant material, which was intimately mixed with enchytraeid faecal material to form the bulk of OH horizons and upper parts of A horizons (Ponge 1999) (see also Fig. 3). Differences in body size, and thus in the size and mechanical power of mouth parts (Chen et al. 1996), cannot be invoked to explain these discrepancies, since the rank order of size of *Mesaphorura* species is: *M. macrochaeta*> *M. yosii*=*M. tenuisensillata*>*M. jevanica*. *P. eichhorni*, the size of which was at least three-fold that of *M. yosii*, exhibited quite similar feeding habits, with a dominance of root-fungal material over enchytraeid faeces.

Onychiurid and isotomid species exploited a wide spectrum of food resources contrary to predatory *Friesea* spp. or mycetophagous *Willemia* spp. Different onychiurid and isotomid species seemed to have different food sources. It is not easy to understand why *Mesaphorura* species, which only differ by some tiny anatomical characters (Rusek 1971), exhibited quantitative differences in their feeding habits. We have no proof that the observed differences were either species-specific or were the result of differences in the composition of horizons from site to site. Differences between the composition of OH horizons of moder and that of A horizons of mull were observed to occur in the studied sites (Ponge 1999). However, constant associations of Collembolan species with humus forms were not observed, and this precludes the formation of a hypothesis of any decisive influence of the latter on the former. Nevertheless, Table 2 shows that some common species were totally absent from some sites, while they were abundant in others, without clear reasons (background noise). Therefore, we cannot definitely conclude that quantitative differences actually exist among neighbouring species living in the same horizons and feeding on similar food components, as has been demonstrated on three onychiurid species sampled in the vicinity of an ant nest by McMillan (1975).

Table 4 Scores obtained by main gut content categories in the ten most abundant species collected at 15 different depths

	0–1 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	5–6 cm	6–7 cm	7–8 cm	8–9 cm	9–10 cm	10–11 cm	11–12 cm	12–13 cm	13–14 cm	14–15 cm
Lepidocyrtus lignorum ($n=227$)															
Empty guts	41	36	25	15	6	3	2	0	0	1	0	0	0	0	0
Pollen	8	8	4	1	1	1	0	0	0	0	0	0	0	0	0
Micro-algae	4	9	3	3	2	1	0	1	1	0	0	0	0	0	0
Higher plant material	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungal material	14	13	9	5	2	1	1	0	0	0	0	0	0	0	0
Holorganic humus	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Total (no. of individuals)	69	71	41	23	11	6	3	1	1	1	0	0	0	0	0
Isotomiella minor ($n=759$)															
Empty guts	3	55	57	103	61	23	16	2	0	0	0	0	0	0	0
Micro-algae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Higher plant material	0	4	2	1	0	0	1	0	0	0	0	0	0	0	0
Mycorrhizae	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
Fungal material	1	2	2	4	3	1	0	0	0	0	0	0	0	0	0
Holorganic humus	25	97	84	109	51	25	14	5	1	0	0	0	0	0	0
Hemorganic humus	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Total (no. of individuals)	32	159	146	217	115	50	31	7	1	0	0	0	0	0	0
Folsomia quadrioculata ($n=951$)															
Empty guts	78	197	140	159	75	54	29	11	1	0	0	0	0	0	0
Micro-algae	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Higher plant material	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungal material	2	9	2	15	4	4	0	0	0	0	0	0	0	0	0
Holorganic humus	40	66	21	14	12	7	7	2	1	0	0	0	0	0	0
Total (number of individuals)	120	275	163	188	91	65	36	12	2	0	0	0	0	0	0
Mesaphorura tenuisensillata ($n=344$)															
Empty guts	0	19	24	23	34	27	19	3	0	1	0	0	0	0	0
Micro-algae	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Higher plant material	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Mycorrhizae	0	0	1	3	2	1	0	0	0	0	0	0	0	0	0
Fungal material	0	3	5	4	3	0	1	0	1	3	0	0	0	0	0
Holorganic humus	3	20	16	30	38	32	20	3	2	1	0	0	0	0	0
Total (no. of individuals)	4	43	45	62	78	60	39	6	3	4	0	0	0	0	0
Willemia aspinata ($n=489$)															
Empty guts	11	40	58	51	52	43	43	10	3	2	0	0	0	0	0
Fungal material	10	32	30	21	26	29	18	6	5	1	0	0	0	0	0
Total (no. of individuals)	21	72	88	72	78	71	60	16	8	3	0	0	0	0	0
Friesea truncata ($n=273$)															
Empty guts	1	6	20	40	70	56	40	15	15	9	1	1	0	0	0
Total (no. of individuals)	1	6	20	40	70	56	40	15	15	9	1	1	0	0	0

Table 4 Continued

	0–1 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	5–6 cm	6–7 cm	7–8 cm	8–9 cm	9–10 cm	10–11 cm	11–12 cm	12–13 cm	13–14 cm	14–15 cm
Protaphorura eichhorni ($n=951$)															
Empty guts	3	24	53	86	115	60	24	11	6	0	1	0	0	0	0
Pollen	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Micro-algae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Higher plant material	1	10	11	38	24	13	12	6	3	0	0	0	0	0	0
Mycorrhizae	0	3	17	30	31	34	21	12	19	8	0	0	0	0	0
Fungal material	1	6	13	19	6	6	30	29	2	7	1	0	0	0	0
Holorganic humus	0	9	17	38	36	21	15	7	4	1	0	0	0	0	0
Hemorganic humus	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0
Total (no. of individuals)	4	51	112	211	215	136	102	65	35	16	2	1	0	0	0
Mesaphorura yosii ($n=700$)															
Empty guts	0	1	9	30	72	47	37	48	39	19	3	2	2	2	0
Micro-algae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Higher plant material	0	0	0	11	3	1	2	3	2	1	0	0	0	0	0
Mycorrhizae	0	0	4	6	27	18	13	29	22	14	1	1	1	1	1
Fungal material	1	8	2	11	11	3	7	9	7	4	0	0	0	0	0
Holorganic humus	2	4	5	18	48	24	16	11	25	11	1	1	1	1	0
Total (no. of individuals)	3	13	19	75	161	92	74	99	94	49	6	5	4	4	1
Mesaphorura macrochaeta ($n=534$)															
Empty guts	1	7	12	14	21	33	34	16	6	4	2	2	2	2	0
Micro-algae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Higher plant material	1	1	1	7	3	3	2	6	4	0	0	0	0	0	0
Mycorrhizae	0	2	11	13	23	21	15	16	3	3	1	1	1	1	0
Fungal material	1	3	3	4	5	4	2	2	1	0	0	0	0	0	0
Holorganic humus	1	13	22	36	35	43	36	8	8	3	2	2	2	2	0
Hemorganic humus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Total (no. of individuals)	4	26	49	74	87	103	89	47	22	10	6	6	6	6	1
Mesaphorura jevanica ($n=216$)															
Empty guts	0	2	9	17	23	15	9	7	1	0	0	0	0	0	0
Higher plant material	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Mycorrhizae	0	0	4	4	4	5	1	1	1	2	0	0	0	0	0
Fungal material	1	1	1	2	1	1	0	2	1	2	0	0	0	0	0
Holorganic humus	1	7	12	20	18	19	10	4	4	2	0	0	0	0	0
Total (no. of individuals)	2	10	26	43	47	40	20	13	7	6	1	1	1	1	0

Table 5 Vertical shifts in gut contents of three onychiurid species. Departures from theoretical expectations are indicated by + or − signs. *N.S.* Not significant

	1–2 cm	2–3 cm	3–4 cm	4–5 cm	5–6 cm	6–7 cm	7–8 cm	8–9 cm	9–10 cm	Run test
Mesaphorura macrochaeta										
Empty guts	−	−	−	−	+	+	+	−	+	N.S.
Micro-algae	−	−	−	+	+	−	−	−	−	N.S.
Higher plant material	−	−	+	−	−	−	+	+	−	N.S.
Mycorrhizae	−	+	−	+	−	−	+	−	+	N.S.
Fungal material	+	+	+	+	−	−	−	−	−	$P<0.05$
Holorganic humus	+	+	+	+	+	+	−	−	−	$P<0.05$
Hemorganic humus	−	−	+	+	−	−	−	−	−	N.S.
Mesaphorura yosii										
Empty guts	−	+	−	+	+	+	+	−	−	N.S.
Micro-algae	+	−	−	−	−	−	−	−	−	N.S.
Higher plant material	−	−	+	−	−	−	−	−	−	N.S.
Mycorrhizae	−	+	−	−	−	−	+	+	+	N.S.
Fungal material	+	−	+	−	−	+	−	−	−	N.S.
Holorganic humus	+	−	+	+	+	−	−	+	−	N.S.
Protaphorura eichhorni										
Empty guts	+	+	+	+	+	−	−	−	−	$P<0.05$
Pollen	−	+	−	−	−	−	−	−	−	N.S.
Micro-algae	+	+	−	−	−	−	−	−	−	N.S.
Higher plant material	+	−	+	−	−	−	−	−	−	N.S.
Mycorrhizae	−	−	−	−	+	+	+	+	+	$P<0.05$
Fungal material	−	−	−	−	−	+	+	−	+	N.S.
Holorganic humus	+	−	+	+	−	−	−	−	−	N.S.
Hemorganic humus	−	−	−	+	+	−	−	+	−	N.S.

In the present study we demonstrated that food resources were vertically distributed and that there was a good correlation between the gut contents of animals and the composition of their immediate environment, provided we did not take into account beech leaves or woody organs, which were seemingly not consumed by Collembola. If we compare species living at different depths, such as *Lepidocyrtus lignorum* and *Protaphorura eichhorni*, it can be ascertained that their gut contents reflected differences in the composition of their immediate environment. Nevertheless, this does not prove any clear-cut influence of food availability on the vertical distribution of these two species. Fungal material, which was ingested in abundance by *L. lignorum*, was present in even greater abundance at greater depth, where it was consumed by species which live at a greater depth (Table 3). Literature on diets of Collembola abounds in examples of food preferences or aversions observed in laboratory experiments. For instance, different Collembolan species may selectively eat different fungal strains or different organs of the same strain (Schultz 1991). It has even been demonstrated that they use odours as clues for finding their preferred food (Bengtsson et al. 1991). These mechanisms, observed in laboratory conditions, with as less background noise as possible, may be overwhelmed in field conditions by other influences, which force the animals to move vertically in the humus profile. Didden (1987) demonstrated that the onychurid *Onychiurus fimatus* moved to deeper levels when placed in a rotating artificial soil profile, even when the pore size distribution of deeper levels was unfavourable to its big size, and that this positive geotropism took place only in adults. Conversely, epigeic species were observed to climb towards aboveground substrates provided moisture conditions were favourable (Bauer 1979). From published literature it seems that a variety of physiological and environmental factors may determine or reinforce the vertical distribution of Collembolan species; among these factors there are food preferences, which may differ from species to species even in the absence of a strong specialization. That some species may optimize their food regime by composing a diet made of strongly attractive substrates and others, less attractive but favourable to either survival, growth and reproduction, may be thought a realistic view, in the light of laboratory studies by Verhoef et al. (1988), Chen et al. (1995) and Sadaka et al. (1998). This may explain why unspecialized feeders may nevertheless exhibit definite preferences in laboratory tests.

Despite difficulties that arise when testing such a hypothesis, we demonstrated that mycorrhizae as a food source increased with depth in the endogeic *P. eichhorni*. This increase was concomitant with a decrease in empty guts, suggesting that mycorrhizal material was the preferred food and that its abundance in the immediate environment increased with depth (also confirmed by the distribution of mycorrhizal tips), at least within the vertical range occupied by *P. eichhorni* at the time of sampling (Table 3). Conversely, the part played by fungal material and holorganic humus decreased with depth in the other endogeic species, *M. macrochaeta*, replaced by other components such as higher plant material (roots) and mycorrhizae, although no

significant trend was perceptible in these two food sources. Attraction by roots and strong interactions with rhizosphere fungi and bacteria have been already demonstrated in Collembola (Klironomos and Kendrick 1996), and it has been demonstrated that the vertical distribution of species was affected by manipulation of the root system of trees (Faber 1991). Our own results support the idea that some adaptation of the food regime could occur in root-fungal feeding species when moving up and down through the humus profile. Similarly, Hasegawa and Takeda (1995) observed a shift in the gut contents of some Collembolan species during the decomposition of pine needles placed in litter bags.

Beside species which are specialized on fungi, such as those belonging to the genera *Willemia* or *Pseudosinella* (Ponge 1991), or which show predatory behaviour such as the genus *Friesea* (Singh 1969), most species we studied were unspecialized feeders eating mainly animal faeces, roots and fungi, as seems to be a general case in soil ecosystems (Gunn and Cherrett 1993). The distribution of humus components in topsoil profiles was in good agreement with the distribution of gut contents of Collembola, but strong differences were shown to occur between species. Part of these differences could be attributed to the vertical distribution of species, but some residual variation was still perceptible between species living at the same depth, thus suggesting the existence of species-specific preferences even in the absence of food specialization. This was in agreement with the idea that plasticity and adaptability of the diet is a key factor in the coexistence of soil animal species with similar food requirements (Ponge 1985). In the same range of ideas, competition cannot be considered as a cause of speciation within soil animal communities but rather as one of the manifold causes of perpetually changing (but reversible) shifts observed in food regimes and the spatial distribution of animal species (Den Boer 1985; Ponge in Vannier 1985).

Appendix 1. Components of the litter/soil matrix identified under the dissecting microscope

Entire brown leaves of beech
Bundles of entire brown leaves of beech
Brown leaves of beech skeletonized by macrofauna
Bundles of brown leaves of beech skeletonized by macrofauna
Brown leaves of beech skeletonized by mesofauna
Bundles of brown leaves of beech skeletonized by mesofauna
Entire variegated leaves of beech
Bundles of entire variegated leaves of beech
Entire variegated leaves of beech skeletonized by macrofauna
Entire variegated leaves of beech skeletonized by mesofauna
Bundles of variegated leaves of beech skeletonized by macrofauna
Entire bleached leaves of beech
Bundles of entire bleached leaves of beech
Bleached leaves of beech skeletonized by macrofauna
Bundles of bleached leaves of beech skeletonized by macrofauna
Bleached leaves of beech skeletonized by mesofauna
Bundles of bleached leaves of beech skeletonized by mesofauna
Pits done by caterpillars in beech leaves
Nests done by foliage-consuming insects
Organo-mineral material smearing beech leaves
Holorganic faecal material smearing beech leaves
Intact petioles and nerves of beech
Petioles and nerves of beech tunnelled by fauna
Petioles and nerves of beech filled with enchytraeid faeces
Petioles and nerves of beech filled with faeces of *Adoristes ovatus* (oribatid mite)
Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites
Petioles and nerves of beech filled with faeces of sciarid dipteran larvae
Petioles and nerves of beech filled with grass roots
Petioles and nerves of beech brown and tough
Petioles and nerves of beech bleached
Sandwich material made of beech leaf fragments and holorganic enchytraeid faeces
Sandwich material made of beech leaf fragments and holorganic earthworm faeces
Sandwich material made of beech leaf fragments and holorganic oribatid faeces
Sandwich material made of beech leaf fragments and organo-mineral earthworm faeces
Sandwich material made of beech leaf fragments and organo-mineral enchytraeid faeces
Sandwich material made of beech leaf fragments and holorganic sciarid faeces
Skeletonized beech leaf fragments
Bundles of skeletonized beech leaf fragments
Brown beech leaf fragments untouched by fauna
Intact bud scales of beech
Bud scales of beech, entire but brown and soft
Strongly decayed bud scales of beech
Intact male inflorescences of beech
Brown decaying male inflorescences of beech
Pollen mass
Intact seed coats of beech
Seed coats of beech tunnelled by phthiracarid mites
Seed coats of beech tunnelled by enchytraeids
Seed coats of beech tunnelled by sciarid larvae
Seed coats of beech penetrated by roots
Intact fragments of beech burr
Soft fragments of beech burr
Soft fragments of beech burr tunnelled by oribatid mites
Soft fragments of beech burr tunnelled by enchytraeids

Soft fragments of beech burr tunnelled by sciarid larvae
Soft fragments of beech burr tunnelled by springtails
Soft fragments of beech burr penetrated by grass roots
Beech cupules tunnelled by fauna
Intact beech gallnuts
Intact twigs
Twigs decayed by white-rot
Twig fragments tunnelled by fauna
Bark remnants of twigs
Twigs filled with enchytraeid holorganic faeces
Twigs filled with enchytraeid organo-mineral faeces
Twigs filled with sciarid holorganic faeces
Twigs filled with oribatid holorganic faeces
Twigs penetrated by beech roots
Intact wood fragments
Decayed wood fragments
Wood fragments tunnelled by fauna
Wood fragments penetrated by grass roots
Wood fragments penetrated by beech fine roots
Intact bark fragments
Well-decayed bark fragments
Bark fragments tunnelled by enchytraeids
Bark fragments tunnelled by phthiracarid mites
Bark fragments tunnelled by sciarid larvae
Bark fragments penetrated by grass roots
Intact living fine long roots of beech
Living fine long roots of beech browsed by fauna
Intact dead fine long roots of beech
Dead fine long roots of beech tunnelled by fauna
Dead fine long roots of beech penetrated by grass roots
Dead fine long roots of beech, voided
Living woody roots of beech
Living woody roots of beech browsed by fauna
Decaying woody roots of beech
Living pale yellow creamy mycorrhizae of beech
Pale yellow creamy mycorrhizae of beech browsed by fauna
Dead pale yellow creamy mycorrhizae of beech
Living orange brown mycorrhizae of beech with woolly mycelium
Orange brown mycorrhizae of beech with woolly mycelium browsed by fauna
Dead orange brown mycorrhizae of beech with woolly mycelium
Living black mycorrhizae of beech (produced by *Cenoccum geophilum*)
Living black mycorrhizae of beech browsed by fauna
Dead black mycorrhizae of beech
Living yellow mycorrhizae of beech with woolly mycelium
Living shoots of *Polytrichum formosum*
Fragments of stems of *Polytrichum formosum*, red and tough
Fragments of stems of *Polytrichum formosum*, voided
Dead stem bases of *Polytrichum formosum*
Decaying stem bases of *Polytrichum formosum*
Living shoots of *Scleropodium purum*
Dead shoots of *Scleropodium purum*
Living shoots of *Leucobryum glaucum*
Dead shoots of *Leucobryum glaucum*
Dead moss, undetermined
Intact leaves of *Luzula forsteri*
Bleached leaves of *Luzula forsteri*
Living leaf bases of *Luzula forsteri*
Decaying leaf bases of *Luzula forsteri*
Intact leaves of *Deschampsia flexuosa*
Decaying leaves of *Deschampsia flexuosa*
Living leaf bases of *Deschampsia flexuosa*
Decaying leaf bases of *Deschampsia flexuosa*
Intact inflorescences of *Deschampsia flexuosa*
Decaying inflorescences of *Deschampsia flexuosa*
Living grass roots
Decaying grass roots
Intact grass stems
Fragments of grass stems browsed by fauna
Fragments of decaying grass roots
Intact leaves of *Vaccinium myrtillus*
Skeletonized leaves of *Vaccinium myrtillus*
Roots of *Vaccinium myrtillus*
Living rhizomes of *Vaccinium myrtillus*
Decaying rhizomes of *Vaccinium myrtillus*
Bleached leaves of *Oxalis acetosella*
Brown entire leaves of *Acer pseudoplatanus*
Brown leaves of *Acer pseudoplatanus* skeletonized by macrofauna
Bleached leaves of *Acer pseudoplatanus*
Bleached leaves of *Acer pseudoplatanus* skeletonized by macrofauna
Leaves of *Acer pseudoplatanus* skeletonized by mesofauna
Winged seed of *Acer pseudoplatanus* with intact wing
Winged seed of *Acer pseudoplatanus* with skeletonized wing
Wingless seed of *Acer pseudoplatanus*
Winged seed of *Fraxinus excelsior* with intact wing
Brown entire leaves of *Quercus petraea*
Leaves of *Quercus petraea* skeletonized by mesofauna
Intact unidentified fragments of seed wings
Skeletonized unidentified fragments of seed wings
Brown entire needles of *Picea abies*
Bleached entire needles of *Picea abies*
Needles of Picea abies browsed by fauna
Seed wings of *Picea abies*
Brown rhizomorphs
White rhizomorphs
Yellow rhizomorphs
Dead rhizomorphs of *Armillaria*
Dead rhizomorphs of *Armillaria* tunnelled by fauna
Sclerotia of *Cenoccum geophilum*
Lichens
Intact caterpillar faeces
Caterpillar faeces tunnelled by phthiracarid mites
Intact slug faeces
Slug faeces tunnelled by enchytraeids
Slug faeces tunnelled by sciarid larvae

Intact holorganic earthworm faeces
Holorganic earthworm faeces tunnelled by enchytraeids
Unidentified holorganic faeces
Intact organo-mineral earthworm faeces
Compacted organo-mineral earthworm faeces
Organo-mineral earthworm faeces tunnelled by enchytraeids
Holorganic woodlice faeces
Holorganic millipede faeces
Holorganic milliped faeces tunnelled by enchytraeids
Holorganic millipede faeces tunnelled by phthiracarid mites
Holorganic cranefly faeces
Intact holorganic sciarid faeces
Compacted holorganic sciarid faeces
Intact holorganic enchytraeid faeces
Compacted holorganic enchytraeid faeces
Organo-mineral enchytraeid faeces
Compacted organo-mineral enchytraeid faeces
Compacted organic-dominant organo-mineral material
Compacted organo-mineral material
Compacted mineral-dominant organo-mineral material
Unidentified mineral assemblages
Charcoal
Snail shells
Woodlice shells
Intact stones
Weathering stones
Weathering stones impregnated with organic matter

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