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Does carcass decomposition affect soil-dwelling enchytraeids?

Jiří Schlaghamerský[1,*] and René Krawczynski[2]

[1] Masaryk University, Faculty of Science, Department of Botany and Zoology, Kotlářská 2, 611 37 Brno, Czech Republic
[2] Brandenburg University of Technology, Faculty of Environmental Sciences and Process Engineering, Chair of General Ecology, Siemens-Halske-Ring 8, 03013 Cottbus, Germany
* Corresponding author, e-mail: jiris@sci.muni.cz

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Abstract

Carcass decomposition causes substantial changes in the humidity and chemistry of adjacent soil. Its potential effect on Enchytraeidae (Annelida: Clitellata) has, hitherto, not been studied. This pilot study on the effect of a large vertebrate carcass on enchytraeids was conducted in temperate grassland with sandy soil close to Cottbus (Germany). Soil cores for enchytraeid extraction were taken in June 2013 along four transects of 2.5 m length from the original centre of the carcass. By that time the carcass, exposed in September 2012, had almost entirely decomposed. Soil had been sampled along the transects in February and May 2013 for measurement of chemical characteristics. Enchytraeids were extracted by the wet funnel method (without heating) and identified alive to species. In total, 715 individuals and 8 species were recorded (including *Fridericia brunensis,* a species known from very few sites). Abundance means had a high variance, and apparent differences were not statistically significant. However, total abundance showed a distinct trend of increase with increasing distance from the carcass site, mostly due to high abundance and dominance of *Enchytronia parva*. Positive correlation with distance from the carcass was significant for enchytraeids as a group, *E. parva* and *Fridericia* spp. Enchytraeids in total and all species or genera tested except *Enchytraeus* spp. (predominantly *E. buchholzi* s.l.) had a negative correlation with conductivity. The latter, although not abundant, showed a clear peak at 0.5 m and had a positive correlation with soil pH. Further significant correlations were found between species or genera and pH, phosphate and humus content. In difference to some springtails, enchytraeids at the study site seemed to avoid the vicinity of carcasses, possibly due to high conductivity, ammonium and phosphate ion concentrations and pH of the affected soil. *E. buchholzi*, an opportunistic, stress-tolerant r-strategist, might be an exception.

Keywords Enchytraeidae | soil fauna | carrion | grassland

1. Introduction

Decomposition of carrion – dead animal bodies, also termed carcasses – is an integral part of nutrient cycles and thus the functioning of ecosystems. Fresh carrion is fed on by many large vertebrate scavengers (Gu et al. 2015); also many invertebrates are associated with carrion (Coljin 2014, Gu et al. 2014). Forensic entomology utilizes the identity and succession of insects developing in corpses to determine the time and place of death (Haskell 2015). Recent observations in Central Europe have shown that many more organisms make at least occasional use of carrion than generally assumed (Gu et al. 2014, 2015). Except of poor countries or wilderness regions, dead bodies of larger animals are generally removed and disposed of to protect human and animal health and for aesthetic reasons. In Europe, carrion has thus become a scarce resource with devastating effects on the populations of specialized scavengers, for instance vulture species. Handling of carcasses of larger animals is subject to rather stringent regulations, which makes scientific studies on their decomposition and the associated organisms (carrion ecology) difficult (Gu & Krawczynski 2012). What has been subject to very little research is the effect

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of carcass decomposition on the underlying and adjacent soil and organisms within. It is obvious that this process will change soil moisture and nutrient levels, potentially affecting the latter over a long time. It can be expected that effects will change in the course of the decomposition process both in terms of intensity and spatial patterns. Information on changes in soil chemistry, in particular nutrient levels, and vegetation has been published by Towne (2000), Danell et al. (2002), Melis et al. (2007), Carter et al. (2007) and Parmenter & MacMahon (2009). Their studies showed significant effects on soil, leading to 'cadaver decomposition islands' (Carter et al. 2007). Their persistence depends on the climatic region, original soil properties and presence / absence of large scavengers, wild boar and insect activity. Most significant changes can be observed in pH, conductivity, nitrogen and phosphorus content. Very little has been published about effects on soil fauna proper. Bornemissza (1957) observed reduced numbers of soil mesofauna –Acari and Collembola– under a decaying Guinea pig, whereas numbers of groups more or less directly associated with carrion, i.e. Calliphoridae (Diptera), Histeridae, Staphylinidae and Ptiliidae (all Coleoptera, the latter family feeding primarily on moulds) were increased. Recently, various effects of carrion, including such on soil and its fauna (Acari and Collembola) have been studied within the 'Necros Project' in a former military training area in south-eastern Germany (Klonowski et al., in press). We report on a pilot study from the same study area on the effect of a large vertebrate carcass on enchytraeids (Annelida: Clitellata: Enchytraeidae). Enchytraeids are in general considered to be saprophagous species with some, species-specific, ability to act as primary saprophages (digesting stable organic molecules, such as cellulose, of primarily plant origin), but also as secondary saprophages grazing on bacteria and fungal hyphae (Didden 1993). Some enchytraeid species are known to assemble at places with concentrations of dead organic matter of both plant and animal origin, such as compost heaps or shoreline tidal debris called wrack beds (e.g. Healy & Coates 1999). However, dead material of plant (algal) origin dominates these substrates. So far, no information on the effect of carcass decomposition on enchytraeids has been published.

Figure 1. Decomposing red deer carcass covered by larvae of Diptera (maggots).

2. Materials and methods

2.1. Study site

The study was conducted in the former military training area Lieberoser Heide, 30 km north of Cottbus (Brandenburg, Germany). A fresh red deer carcass had been placed in a grassland at the end of September 2012. The study site was the area of an old landfill (10 ha) that had been reclaimed by covering it with soil from the region, consisting mainly of sand, but also demolition waste. It was the only site within the former military training area where soil samples could be taken as anywhere else the risk of finding buried ammunition was considered too high. It was covered by grassland vegetation consisting of a mosaic of vegetation patches ranging from *Corynephorus canescens* to *Calamagrostis epigejos* stands, with some interspersed bushes and tree saplings. The grassland is neighboured by pine forest on three sides and scrubland (as the result of succession on a formerly open ground) in the north.

2.2. Carcass exposure and soil characteristics

On 25 September 2012 a fresh red deer carcass (73 kg) was exposed at the site. No measures to exclude scavengers were taken, as their impact was part of a wider study. Although large carcasses may be relocated by large scavengers or by wild boar digging at the carcass site for larvae (Gu et al. 2015) this was not the case here. The carcass was monitored by automatic cameras, showing only limited action by two smaller scavenger species, i.e. red fox and raven (Lepaleni et al. 2013). A large carcass consumed fast by large scavengers affects the soil only marginally. In the given case, carcass decomposition was slow and mainly executed by maggots (Fig. 1). Therefore its effects on soil characteristics were substantial. By 1 February, i.e. after four months of exposure, only a few bones and a spot devoid of live herb layer remained at the carcass site. Soil characteristics were taken from Shihepo (2013) as no additional soil analyses parallel to enchytraeid sampling could be run (for details about the soil analyses see there). Soil for the analysis of soil chemistry was sampled on 1st of February and the 3rd of May 2013 (Fig. 2). In February, 15 soil cores (8 cm in diameter) to 5 cm depth were taken in the four cardinal directions, resulting in 60 samples plus one taken exactly in the centre. The soil cores along each transect were taken adjacent to each other, except the last one in each transect, which was taken in 5 m distance from the preceding (14^{th}) one. Thus a distance of 1.12 m from the centre was covered by continuous data, with an additional data point at 6.12 m serving as a control (not depicted in Fig. 2). In May, another 60 soil cores were taken, extending each transect by another 15 cores (starting adjacent to the positions of the 14th soil cores of the February sampling). The most outward soil cores of this second sampling were taken in 1 m distance from the preceding ones. Thus 2.24 m in each cardinal direction from the initial centre of the carcass were covered altogether, plus additional isolated data points at 3.24 m and 6.12 m. All soil samples were placed in plastic bags and stored frozen at ca. -9 °C until they were analysed. The effect of the carcass decomposition on soil was rather high (Shihepo 2013): soil pH, conductivity, phosphorus (as phosphate), and nitrogen (both as nitrate and ammonium) levels were elevated under the carcass and decreased with increasing distance from it (Figs 3 and 4); an anaerobic zone was found directly under the carcass. Humus content, of potentially high importance for the distribution of soil animals, did not show any clear spatial distribution pattern but was somewhat higher further away from the carcass in three of four transects (Fig. 5).

2.3. Enchytraeid sampling and sample processing

On 10 June 2013 a total of 21 soil cores (ca 48 cm^2 surface area, 15 cm depth) for enchytraeid extraction were taken by the second author. The soil cores were placed in the centre of the initial carcass location and at 0.5 m intervals along transects of 2.5 m length from the centre towards the four cardinal directions (Fig. 2). The soil cores were placed in plastic bags and shipped to the first author. Upon receipt they were stored at ca. 5 °C and subsequently subjected to wet funnel extraction without heating for 48 hours, with retrieval of extracted specimens after 24 hours (including replacement of water in the funnels) and at the end of the extraction period. The extraction method was based on Graefe's extraction method without heating while using a water-filled funnel as originally proposed by O'Connor (Dunger 1989, Kobetičová & Schlaghamerský 2003). The lower parts of the battery of funnels (i.e. the attached collection tubes) were cooled by a cold water bath as ambient temperature was high. Another measure to minimize enchytraeid mortality was using water adjusted to pH 5, thus being closer to the soil pH at the study site. Extracted enchytraeids from individual samples were stored in water-filled Petri dishes at ca. 5 °C and identified alive to species or genus (juveniles or damaged specimens) using an optical transmission microscope (Olympus BX 51; magnification max. 500x) with differential (Nomarski) interference contrast.

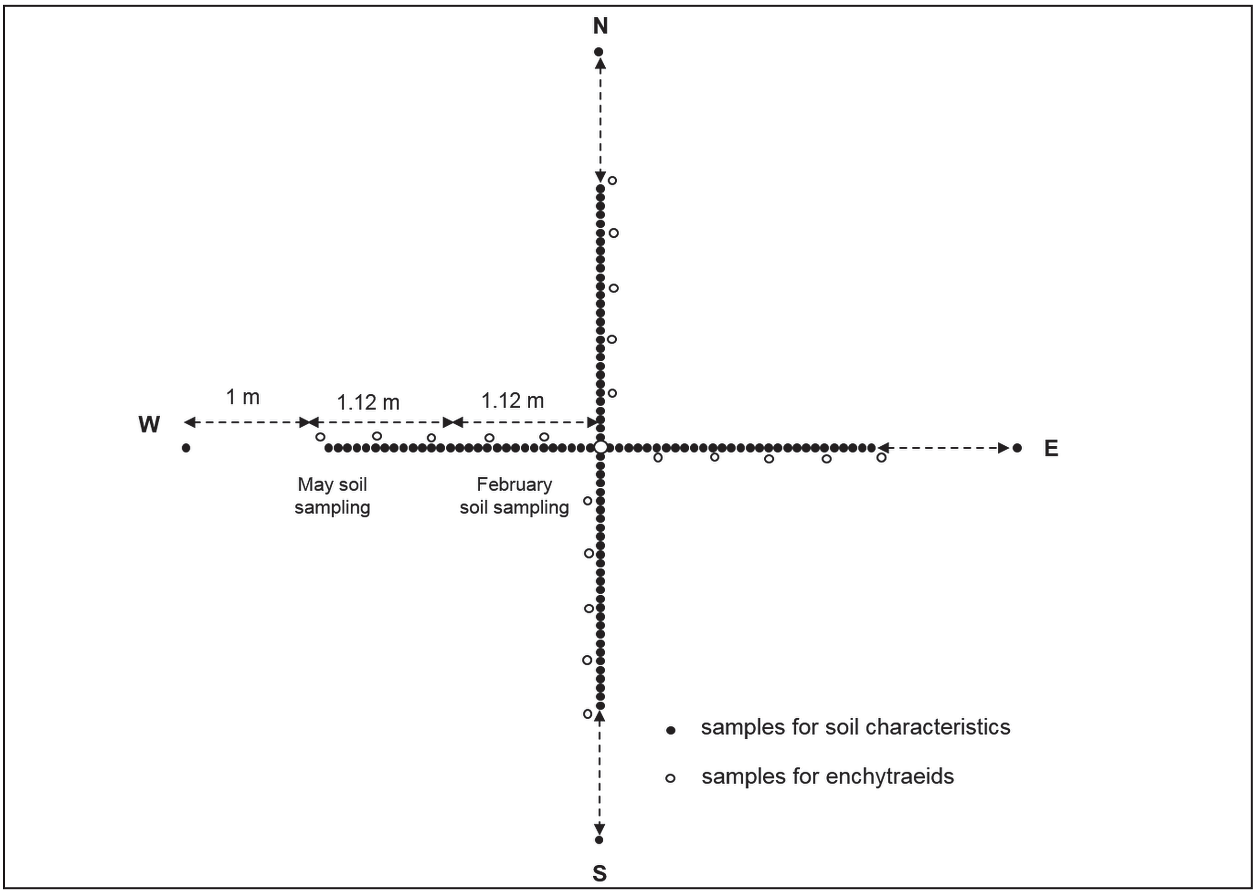

Figure 2. Positioning of sampling points for soil characteristics and enchytraeids along transects from the original centre of a red reed carcass.

2.4. Statistics

Potential differences between enchytraeid abundances at different distances from the carcass centre were tested using the Kruskal-Wallis test (non-parametric ANOVA, two-tailed, $\alpha = 0.05$; software: GraphPad InStat 3). Correlations of enchytraeid abundances and soil parameters were tested using Spearman's Rho (software: IBM SPSS Statistics 22). The outmost enchytraeid sampling points at 2.5 m distance were beyond the 2.24 m covered by continuous sampling for soil parameters, so that these closest but less well associated data points had to be used for the correlation analysis (Tab. 1).

3. Results

3.1. Enchytraeid assemblage, abundance and correlation with soil variables

In total, 715 enchytraeid individuals of eight species were found, of which 78 percent belonged to *Enchytronia parva* s.l. (Tab. 2), a species of small body size. Almost no enchytraeids were found along the northern and eastern transects (Fig. 6). Therefore, abundance means had a high variability (Fig. 7), and apparent differences among them were not statistically significant (tested for Enchytraeidae in total, *Enchytronia parva*, *Enchytraeus* spp., *Achaeta* spp., and *Fridericia* spp.; Kruskal-Wallis test). Nevertheless, total enchytraeid abundance showed a distinct trend of increase with increasing distance from the carcass location, mostly due to the high abundance of *E. parva* at the farthest sampling points (2.5 m from carcass centre) along the southern and western transects (382 and 81 individuals, respectively). Correlation analysis revealed several significant correlations (Tab. 3). For all enchytraeids taken together there was a significant positive correlation to distance. *E. parva* s.l. showed significant positive correlations to distance and humus content and significant negative correlations to conductivity, pH and phosphate. Also the negative correlation to ammonium was almost significant. *Achaeta* spp. made up for 11 percent of all enchytraeids. They showed significant negative correlations to conductivity and phosphate, and an almost significant negative correlation to pH. The genus was represented by *Achaeta abulba* (subadult and adult specimens made up for 6.8 % of all enchytraeids) and at least one other species, but juveniles could not be assigned to species (see taxonomic notes below). The abundance of *Fridericia* spp. was positively correlated with distance from carcass; also its positive correlation with humus content was almost significant. It was negatively correlated with conductivity and phosphate. On the other hand, *Enchytraeus* spp. (*E. buchholzi* s.l. and *E. dichaetus*, the latter represented by two specimens only), although generally not abundant, showed a distinct peak at 0.5 m from the carcass centre (Tab. 2). The only significant correlation for *Enchytraeus* spp. was a positive one with pH. A single enchytraeid individual (*E. buchholzi* s.l.) was found in the soil core taken at the initial centre of the carcass.

3.2. Taxonomic and faunistic notes

Achaeta spp.: The genus was apparently represented by at least two species, that is *A. abulba* and another species (or several ones?) of unclear identity. The latter had also only dorsal pyriform glands, which were large, possibly also a single, small, ventral pair in V; 2–4 pairs of preclitellar nephridia at VI/VII, VII/VIII and sometimes also in VII/IX and even in IX/X; dorsal vessel originating in VII behind the 3rd pair of primary

Table 1. Values of soil variables (Shihepo 2013) used in the correlation analysis, i.e. along transects in the four cardinal directions at the sampling points closest to the enchytraeid sampling points. Data from the North transect sampled at 0.08 cm from the carcass centre were arbitrarily used to include the single corresponding enchytraeid sample in the correlation analysis, the other values from this distance are given for comparison only.

Variable	Transect	Distance from carcass					
		0.08 m	0.48 m	0.96 m	1.52 m	2.00 m	2.40 m
Conductivity [µS/cm]	N	119.8	145.3	116.4	22.8	59.4	33.2
	E	148.2	95.4	52.9	27.3	45.1	17.8
	S	141.8	147.9	69.6	39.2	50.8	39.0
	W	155.3	125.8	50.2	22.4	49.6	38.9
pH	N	6.25	6.25	5.51	4.66	5.60	5.60
	E	5.98	6.13	4.82	4.11	3.96	4.40
	S	6.23	6.13	4.68	4.81	4.75	4.45
	W	6.38	6.25	5.77	4.65	5.34	5.53
Humus content [%]	N	2.76	1.97	2.33	2.96	4.64	4.14
	E	2.64	1.57	3.82	2.42	3.45	3.88
	S	3.31	3.25	4.23	2.22	3.86	3.50
	W	1.86	3.69	3.77	3.07	3.53	4.27
NH_4^+ [µg/g DM]	N	82.21	56.8	2.45	0.20	0.55	0.54
	E	124.20	45.97	7.75	0.95	0.45	1.95
	S	84.13	72.82	14.82	13.35	10.39	1.01
	W	86.83	74.98	9.69	3.07	1.16	1.35
NO_3^- [µg/g DM]	N	7.69	7.31	18.09	5.08	8.42	6.09
	E	6.94	7.15	8.22	3.79	5.60	5.56
	S	10.59	9.77	11.48	10.44	7.45	6.24
	W	7.63	19.67	13.75	7.50	8.52	9.23
PO_4^{3-} [µg/g DM]	N	10.10	22.50	2.70	1.80	1.90	1.80
	E	9.5	7.1	3.5	1.7	1.7	1.4
	S	11.0	16.4	2.3	3.0	5.4	2.2
	W	18.6	15.5	2.3	1.0	1.4	1.8

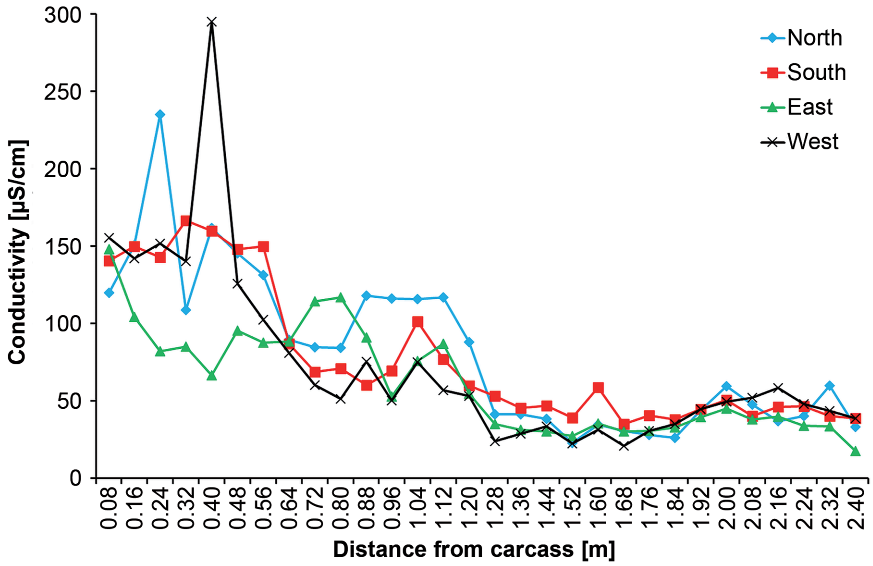

Figure 3. Conductivity in the upper 5 cm of soil along transects in the four cardinal directions from the original centre of a red deer carcass (based on measurements in 1st Feb. and 3rd May 2013, from Shihepo 2013).

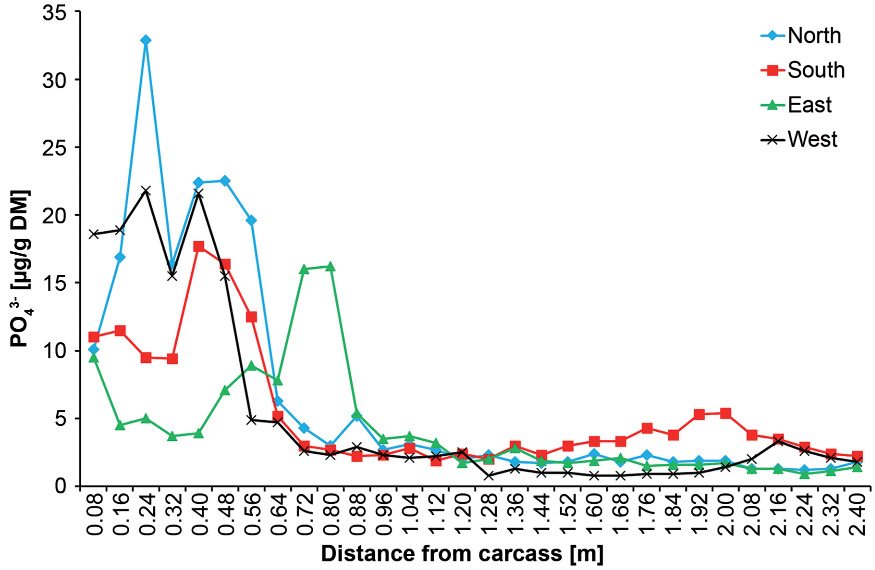

Figure 4. Phosphate content in the upper 5 cm of soil along transects in the four cardinal directions from the original centre of a red deer carcass (based on measurements in 1st Feb. and 3rd May 2013, from Shihepo 2013).

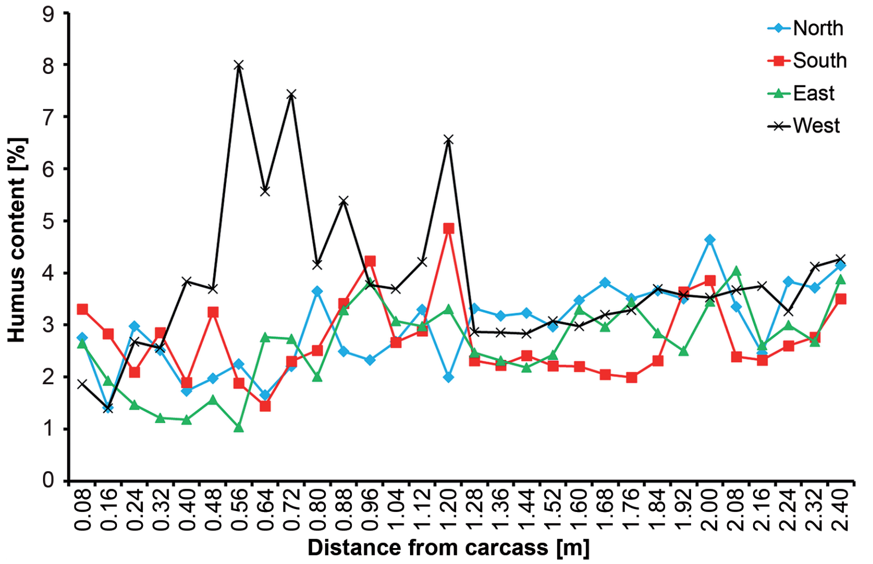

Figure 5. Humus content in the upper 5 cm of soil along transects in the four cardinal directions from the original centre of a red deer carcass (based on measurements in 1st Feb. and 3rd May 2013, from Shihepo 2013).

Table 2. List of enchytraeid species and numbers of individuals found at different distances from the original centre of a decomposed red deer carcass in a grassland within the Lieberoser Heide near Cottbus (Germany) in June 2013; zero distance represented by a single soil core of 48 cm^2, all other distances total values for four soil cores of identical size, i.e. 192 cm^2 (identical positions along four transects pooled); *Achaeta* spp. and *Fridericia* spp. represent either juvenile, injured or dead specimens that could not be identified to species.

Species	**Distance from carcass**	**0 m**	**0.5 m**	**1.0 m**	**1.5 m**	**2 m**	**2.5 m**	**Total**
Achaeta abulba Graefe, 1989					19	1		20
Achaeta sp. 1					2	2	9	13
Achaeta spp.					38	8	1	47
Enchytraeus buchholzi s.l. Vejdovský, 1879		1	27	1				29
Enchytraeus dichaetus Schmelz & Collado, 1989						1	1	2
Enchytraeus spp.			2				1	3
Enchytronia parva s.l. Nielsen & Christensen, 1959				3	5	84	464	556
Fridericia brunensis Schlaghamerský, 2007							19	19
Fridericia bulboides Nielsen & Christensen, 1959					1	8	6	15
Fridericia sp. (cf. *larix*) Schmelz & Collado, 2005							1	1
Fridericia spp.						1	9	10
Enchytraeidae, total		**1**	**29**	**4**	**65**	**105**	**511**	**715**

Table 3. Correlations between soil properties and enchytraeids along all four transects leading away from the carcass centre (each transect 2.5 m long, 24 sampling points altogether for both soil properties and enchytraeids); correlation coefficients (Spearman's rho) given above p-values, significant correlations bold.

	Enchytraeidae	***Achaeta* spp.**	***Enchytraeus* spp.**	***Enchytronia parva***	***Fridericia* spp.**
Distance	**0.573** **0.003**	0.335 0.109	-0.144 0.502	**0.632** **0.000**	**0.619** **0.001**
Conductivity	**-0.409** **0.047**	**-0.459** **0.024**	0.214 0.315	**-0.542** **0.006**	**-0.460** **0.024**
pH	-0.353 0.091	-0.401 0.052	**0.418** **0.042**	**-0.622** **0.001**	-0.234 0.271
Humus	0.372 0.073	0.175 0.414	-0.033 0.877	**0.429** **0.037**	0.393 0.058
NH_4^+	-0.295 0.161	-0.292 0.166	0.118 0.581	-0.403 0.051	-0.372 0.073
NO_3^-	-0.197 0.355	-0.105 0.626	0.113 0.599	-0.139 0.517	-0.101 0.638
PO_4^{3-}	-0.380 0.067	**-0.620** **0.001**	0.210 0.324	**-0.599** **0.002**	**-0.465** **0.022**

pharyngeal glands, no secondary pharyngeal glands; oesophageal appendage ('sponge-like') in V, with dorsal channel in IV; very long sperm funnels – ca 8x as long as wide; long spermathecae with ventral orifice of ectal duct; the largest specimen had ca 31 segments and was 7 mm long in vivo, despite missing its rear end). Due to the variability in characters, in particular the number and position of preclitellar nephridia, it was not entirely clear if one or several species (additional to *A. abulba*) were involved. For the juveniles even a separation of *A. abulba* and the other species was not possible.

Enchytronia parva s.l.: The specimens were characterized by an abrupt transition between oesophagus and intestine with intestinal diverticula distinct but not extending into any truly everted pouches, and two pairs of preclitellar nephridia at segments VII/VIII and VIII/IX.

Fridericia brunensis: Its occurrence is noteworthy from a faunistic point of view as it has been hitherto reported only from a limited number of sites in northern Germany, south-eastern Czechia and Hungary (Schlaghamerský, 2007; Schmelz & Collado, 2010).

Fridericia sp. (cf. *larix*): A single subadult specimen belonged clearly to a third *Fridericia* species (additional to *F. brunensis* and *F. bulboides*) and was tentatively assigned to *F. larix* based on the observed character combination: 40 segments, ca 8 mm long (in vivo); chaetal formula: 2 (3) – 2 : 2, (4), (3), (1); dorsal vessel originating in XVII; chylus in XIII-XIV; no subneural glands; 5 pairs of preclitellar nephridia at VI/VII-X/XI; coelomo-mucocytes without refractile granules, lenticytes small; oesophageal appendages rather long, with few very short, knob-like branches; spermathecal ampullae communicating separately with oesophagus, each with two elongate diverticula with approximately globular chambers in their apical parts, long duct with small, sessile ectal gland; sperm funnel length : width = 2 : 1, length less than body width, bursal slit T-shaped).

4. Discussion

Rising enchytraeid numbers (in particular *E. parva*) with increasing distance from the carcass might have been the consequence of the preference of the respective species for lower pH and avoidance of disturbance. Extreme differences in enchytraeid abundances among the individual transects made it impossible to find statistically significant differences among distances

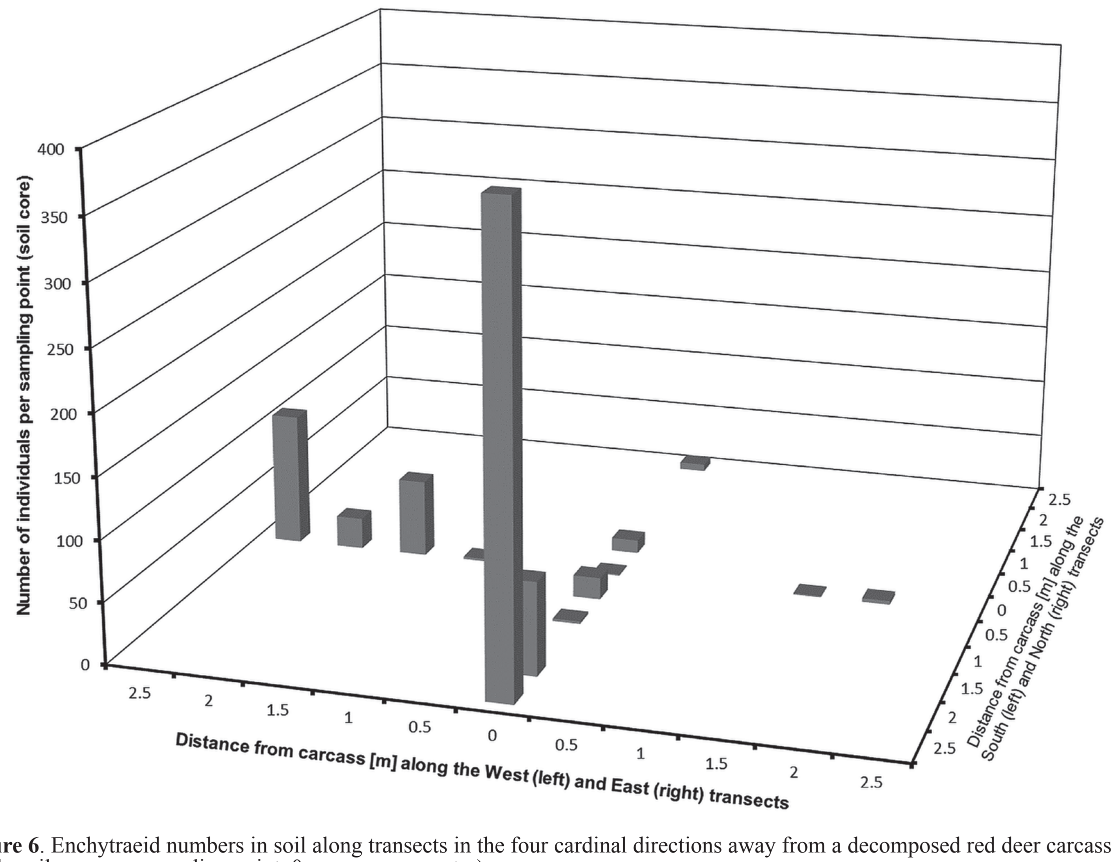

Figure 6. Enchytraeid numbers in soil along transects in the four cardinal directions away from a decomposed red deer carcass (based on single soil cores per sampling point, 0 m = carcass centre).

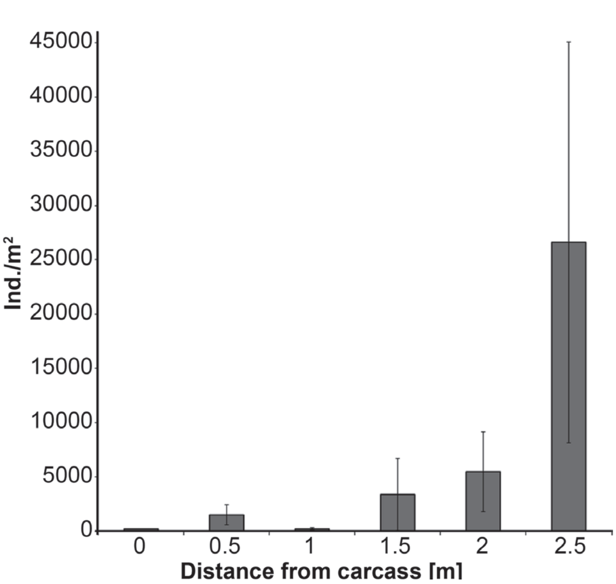

Figure 7. Enchytraeid density in soil with increasing distance from a decomposed red deer carcass (means ± SE from four transects away from the carcass, 0 m = carcass centre, single soil core).

from the carcass centre. The trend towards higher abundance of *Enchytraeus buchholzi* s.l. at 0.5 m could be explained by its tolerance to disturbance and elevated conductivity, but also preference for higher soil pH (Graefe & Schmelz 1999) and nutrient contents. Although statistically not significant, this finding is in line with the known stress and disturbance tolerant, opportunistic behaviour of *E. buchholzi* s.l. and some of its cogeners, which are considered typical r-strategists also utilizing accumulations of decomposing matter [though one has to bear in mind that this is a complex of species and possibly of strains reproducing by self-fertilization (Schmelz & Collado 2010)]. Humus content could be assumed a key factor affecting enchytraeid distribution along the transects. Close to the carcass it was only elevated along the West transects (at ca 0.5–1.2 m); along the other transect, there was a trend of humus content increase with increasing distance from the carcass (Fig. 5). However, higher numbers of enchytraeids were only found along the West and South transects (Fig. 6), in neither case copying the humus distribution. Nevertheless, the positive correlation between the most abundant species, *Enchytronia parva*, and soil humus content was significant. Any effect of carcass decomposition on soil parameters and soil fauna, including enchytraeids, will be changing in time. The present results are therefore a snapshot of enchytraeid distribution at a moment at which the decomposition of the carcass as such was already completed but its effects on the soil still persisted at rather high levels. The samples for soil analysis were taken at two different dates (one still in winter, the other in spring) almost five and two months prior to enchytraeid sampling. Whereas many of these parameters did probably not change much in-between these three sampling dates, this cannot be assumed for water content, which can be an important factor determining enchytraeid distribution. Therefore, water content was not included in the correlation analysis but might have also affected the observed enchytraeid distribution. At the same study site, the other two dominant groups of soil mesofauna, mites (Acari) and springtails (Collembola) had been studied at an badger carcass using a very similar sampling design (Klonowski et al., in press). Both groups were almost missing in the soil at the carcass centre but fairly well represented along the transects leading away from it (over 7000 individuals of either group had been collected). In Collembola, some 8 species were present, of which one –*Hypogastrura vernalis*– made up for 95 percent of all individuals and showed a strong positive correlation with nitrate and phosphate concentrations in soil, reaching highest densities at medium distances from the carcass. Acari were not identified and their total numbers showed a more even distribution along the transects. Thus the situation in springtails and enchytraeids seems rather comparable in terms of almost identical species numbers and a strong domination of their assemblages by a single species. However, in difference to the situation within the springtail assemblage, the by far most abundant enchytraeid species, *E. parva*, avoided soil affected by carcass decomposition.

5. Acknowledgements

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