Soil Organisms 98 (SI 2) 2026

pp. 39–56
DOI 10.25674/515

RESEARCH ARTICLE

Microannelids (Enchytraeidae, Hrabeiellidae) of the eastern part of Podyjí National Park (Czechia)

Daniel Dusík[1] & Jiří Schlaghamerský[1,*]

[1] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic
* Corresponding author, email: jiris@sci.muni.cz, ORCID: https://orcid.org/0000-0002-0614-8140

Received 9 June 2026 | Accepted 8 September 2026 | Published online 10 November 2026

Abstract

Soil microannelid fauna (Enchytraeidae, *Hrabeiella periglandulata*) was studied in the Podyjí National Park, situated in southern Moravia, Czechia. We focused on the easternmost part of the national park, where we sampled several sites, representing either a single habitat or including several micro- or mesohabitats. In spring and autumn 2021 we sampled two acidophilous, thermophilous oak forests near the villages Popice and Hnanice, where we studied the effect of coppice restoration on microannelids. To supplement the obtained data, we sampled six additional meso- or microhabitats in the same area in spring and autumn 2023. These were: the Havraníky heathland, shallow soil on granite rocks (partially emerging from soil) in the Hnanice oak forest, alluvial soil of Daníž brook valley, soils on the north-facing slope ca 20 m from Daníž brook, dead wood from the alluvium and also, additionally, the bottom of the dried-out brook. We found 36 microannelid species in total. Microannelid mean densities ranged from 7 800 ind./m^2 to 69 200 ind./m^2 in the forests of Daníž valley, microannelids were more abundant in alluvial soils, in the oak forest, mean densities ranged from 10 300 ind./m^2 to 48 500 ind./m^2. Mean densities in Havraníky heathland reached up to 18 000 ind./m^2. The dead wood contained a relatively large number of individuals in the spring (92.0 ± 35.4 ind./sample, or 0.225 ind./cm^3), but low amounts in the autumn (3.2 ± 1.5 ind./sample, or 0.006 ind./cm^3). The most dominant species was *Fridericia brunensis*, except in the alluvium soil and dead wood. *H. periglandulata* reached relatively high abundance in the Popice oak forest. *Marionina clavata*, *Mesenchytraeus pelicensis* and *Bryodrilus ehlersi* preferred dead wood to the alluvial soil in the spring. Assemblages from the alluvial soil were more similar to those in dead wood collected in the alluvium than to those from soil on the slope.

Keywords Soil fauna | oak forest | coppice | heathland | dead wood

1 Introduction

The term soil-dwelling microannelids refers to terrestrial annelids of small body size, thus belonging to soil mesofauna (Swift et al., 1979), whereas earthworms and the few terrestrial leeches are larger and are classified as soil macrofauna. Most soil-dwelling microannelids are Enchytraeidae (potworms). Another clitellate family with soil-dwelling species is Naididae, but also several non-clitellate annelids are found in soils, including soils of temperate Europe (Aeolosomatidae, Hrabeiellidae: *Hrabeiella periglandulata* Chalupský and Pižl, 1994, Parergodrilidae: *Parergodrilus heideri* Reisinger, 1925). Enchytraeids are one of the three most abundant

© 2026 by the author(s), licensed by Senckenberg Gesellschaft für Naturforschung. This article is published under a Creative Commons Attribution 4.0 International License (CC BY 4.0).

groups of soil mesofauna together with springtails and mites (Schaefer, 1991). They are present in all humus forms and reach highest relative and total abundance in acidic soils, with mean annual population densities up to 150 000 ind./m^2 (Didden, 1993; Graefe and Schmelz, 1999; Huhta et al., 2005). Enchytraeids are involved in soil processes, taking part in decomposition of soil organic matter (Petersen and Luxton, 1982; Laurén et al., 2012), improving the soil structure with their faeces (van Vliet et al., 1993; Schrader et al., 1997), influencing soil porosity (van Vliet et al., 1993; Serbource et al., 2025) and interacting with soil microorganisms (Persson et al., 1980). Our knowledge on other soil-dwelling microannelids is mostly a by-product of research on enchytraeids. One can assume that their ecological function in soil is similar, but due to their often smaller body size and more sporadic occurrence, mostly as single species with rather low densities (although these can sometimes be high, see Schlaghamerský and Šídová, 2009), their overall ecological importance is usually assumed to be much lower.

Faunistic records of enchytraeids up to 1987 in what was then Czechoslovakia were summarized in a checklist by Chalupský (1988). To that date, records from Czechia were mostly available from central and northern Bohemia and the Jeseníky mountains in northern Moravia. From Slovakia, data were mainly available from the northern parts of central Slovakia and todays Bratislava and Trnava regions in western Slovakia.

Our area of interest for this study was the southernmost part of Moravia, close to the Austrian border. Only a single study that is more recent than the checklist is available from this region (Schlaghamerský, 2007), presenting data on the terrestrial microannelid assemblage of a floodplain forest on the Dyje (Thaya) river at the village Lednice (ca 60 km east of our study area). The closest records north(easterly) from the present study area are from the city of Brno, again in ca 60 km distance. The research there was relatively thorough and can be divided into two main topics; the fauna and ecology of enchytraeids and earthworms of the city parks (Pižl and Schlaghamerský, 2007; Schlaghamerský and Pižl, 2009; Schlaghamerský et al., 2009; Pižl et al., 2009) and the microannelid fauna of a municipal forest, serving partially as a game reserve, on the north-western margin of the city (Šídová and Schlaghamerský, 2007; Schlaghamerský and Šídová, 2007; Schlaghamerský and Šídová, 2009). Further to the east, in south-eastern Moravia, microannelids were studied in the Czech (Moravian) part of the White Carpathians, a mountain range, which is part of the Western Carpathians and stretches along the border between Czechia and Slovakia. Here, microannelid assemblages were studied in several grasslands (Schlaghamerský and Kobetičová, 2005, 2006; Schlaghamerský et al., 2007) and forests (Schlaghamerský, 2010), with the closest study site situated in ca 100 km distance from our study area. To the west of our study area, the closest records are from a similar distance as the White Carpathian sites in the east (ca 110 km), i.e., from the town of České Budějovice and its close vicinity in South Bohemia (e.g., Chalupský, 1989, 1991, 1994). Finally, from Austria in the south, microannelid records are almost exclusively from the Alps (e.g., Nurminen, 1977). The single exception is a study by Bauer (2002), who reported in her paper about supercooling temperature of potworms also on the composition of an enchytraeid assemblage from an oak forest in the vicinity of Vienna.

Even though the southernmost part of Moravia is a biogeographically interesting region, with many species of animals and plants reaching their northern or north-western border of distribution there (Rothröckl and Škorpík, 2008; Chytrý, 2012), terrestrial microannelids were studied only sparsely (as mentioned above). One of the most interesting areas in the region, both faunistically and geologically, is the Podyjí National Park on the border of South Moravia and (Lower) Austria. The Czech term Podyjí can be translated as lying along the river Dyje (Thaya in German) or, in a more narrow sense, as the valley of the river Dyje (thus Thayatal in German, which is also the name of the smaller Austrian national park (13 km^2), established in 2000, adjacent to the Czech one along the southern banks of the river). With 63 km^2 the Podyjí NP is the smallest Czech national park and covers only a rather short stretch of the Dyje river (40 km) in an area, where the river has created a deep meandering river canyon (up to 220 m deep). While there are some alluvial meadows at the bottom and beech forest on the lower parts of the slopes, the upper slopes and the adjacent plateau are mainly dominated by sessile oak woodlands, sometimes rather open due to rock outcrops.

The NP was established in 1991, shortly after the fall of the communist regime and thus the removal of the "physical iron curtain" along the border. However, it had been already protected since 1979 as a Protected Landscape Area (103 km^2, most of the area that did not become part of the NP serves now as its buffer zone). Being part of the guarded border zone to the "capitalist West" had made the Czech part almost inaccessible to the public, including researchers, for over 40 years. Even farming and forestry were limited because of access restrictions, but also because much of the local German-speaking population was expelled in the aftermath of World War II. Historically, many forests in this area had been managed by coppicing (trees are cut to near ground level to stimulate growth of new shoots, these are harvested in a regular rotational cycle for fire wood and other material) for hundreds of years; the oldest coppiced

stool was estimated to be over 800 years old (Vrška et al., 2017). Due to grazing, many now afforested areas were also much more open forests, brushlands and grasslands, in particular on the slopes towards the river (Miklín et al., 2016). There are still several heathlands of high nature conservation value along the eastern edge of the NP. After World War II coppicing and grazing ceased and while some coppices were transformed into high forest, many remained neglected, with very little management. Since 2016, the national park's administration has been gradually restoring coppicing in forests along the park's eastern edge in the vicinity of the villages Popice and Hnanice, creating every year at least one small clearing in both of these areas (this was also the area where we conducted our research).

From the point of view of geomorphology, the Podyjí NP is located on the south-eastern edge of the Bohemian-Moravian Highlands, with its eastern-most part extending into the Dyje-Svratka Valley. It should be noted that the Pannonian biogeographical region also extends from the south-east to the national parks eastern edge. The bedrock are mainly metamorphic rocks of the Moravicum (a zone of slightly metamorphic rocks along the eastern border of the Bohemian Massif). These are predominantly acidic (granitoids, gneisses, and schists), but in places also more basic amphibolites and marbles occur. In the south-eastern part, relevant to our study, the bedrock is covered by unconsolidated Miocene sediments and loess. Cambisols are the predominant soil type (Chytrý and Vicherek, 1995; Czech Geological Survey, 2026).

Podyjí NP was extensively studied by both zoologists and botanists in the past, including some research on soil fauna. Soil macrofauna (millipedes, centipedes, terrestrial isopods and earthworms) has been investigated there thoroughly during the last 20 years (Tajovský et al., 2024). Further, epigeic spiders were studied in the dry oak forests in the eastern part of the national park in context of the coppicing restoration (Hamřík et al., 2023). We also studied the impact of the restoration of coppicing on microannelids in forests along the eastern border of the NP (Dusík et al., 2026) and decided to complement this study by exploring microannelid assemblages of some additional meso- and microhabitats in the same area. For this we chose specific sites within the woodland, but also including the open area of a protected heathland. Our objective was to obtain a more comprehensive idea of the microannelid fauna of this area, but also to understand better the environmental factors shaping their assemblages. To provide a full picture, we also present assemblage data for the coppice sites, but in a different way than in the above-mentioned paper, giving species composition and representation for the two general sites, without distinguishing between neglected and restored coppices.

2 Materials and Methods

2.1 Study area

The study was conducted in the eastern part of the Podyjí National Park. The daily mean annual air temperature for the period 1961–2021 was 9.1 °C and the mean annual precipitation 363.3 mm. The mean annual temperature for the years 2020 to 2023 (the period covering one year before our first sampling and up to the year when the last sampling was conducted) was 10.4, 9.5, 10.8, and 11.3 °C, respectively. The mean annual precipitation for the same years was 563.5, 465.5, 411.9, and 516.3 mm, respectively. The above data were measured at

Table 1. Soil chemistry and texture (proportion of soil particles) in the studied habitats. T = total, av = available, — = not measured. For both oak forests the values are means for all measured plots. For more detailed information on stand level see Dusík et al. (2026) and on plot level see Edaphobase (Schlaghamerský, 2023a–d). Data on the other meso- and microhabitats are based on composite samples, all taken on the same day (13 June 2023). All values rounded to two decimal places.

Habitat	pH (H_2O)	C_{org} [%]	N_T [%]	P_{av} [mg/kg]	K_{av} [mg/kg]	Na_T [mg/kg]	Mg_T [mg/kg]	Ca_T [mg/kg]	Clay [%]	Silt [%]	Sand [%]
Heathland	5.32	4.34	0.37	31.38	2437.05	125.20	2181.25	4149.68	2.65	15.69	81.66
Oak forest (Popice)	4.53	7.95	0.4	24.35	201.19	—	—	—	7.09	49.80	43.15
Oak forest (Hnanice)	4.34	7.20	0.39	27.15	191.64	—	—	—	4.64	41.23	54.54
Rock (Hnanice)	4.53	20.47	1.12	58.45	2462.99	160.56	1509.60	2638.56	6.32	37.09	56.58
Alluvial soil	3.99	9.55	0.62	6.55	1902.52	129.60	1618.29	1588.77	4.97	47.04	47.99
Slope	4.31	3.49	0.17	5.04	1686.34	116.02	1651.83	933.69	10.84	49.50	39.66
Dead wood	4.34	48.41	1.64	39.35	1989.99	151.55	930.93	5335.34	—	—	—

Kuchařovice, a meteorological station ca 8 km north of our study area (Czech Hydrometeorological Institute, 2026). Measured chemical and physical properties of soil (or dead wood) are given in Table 1. Data on soil (or rotten wood) properties were measured in one composite sample for each sampled plot or microhabitat, for a brief methodology of the analyses see Dusík et al. (2026) and Edaphobase (Schlaghamerský, 2023a–d).

We studied several sites, representing a single habitat or including several micro- or mesohabitats (Fig. 1, Figs S1–26).

2.1.1 Popice coppice (oak forest)

An acidophilous, thermophilous oak forest (*Quercus petraea* agg.) near the village of Popice, traditionally managed by coppicing. Management had been neglected for over 60 years and has been gradually re-established since 2016, leading to the presence of clearings of different age (with different stages of succession, including re-sprouting tree stumps) within a matrix of neglected coppice. Other tree species such as Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*)

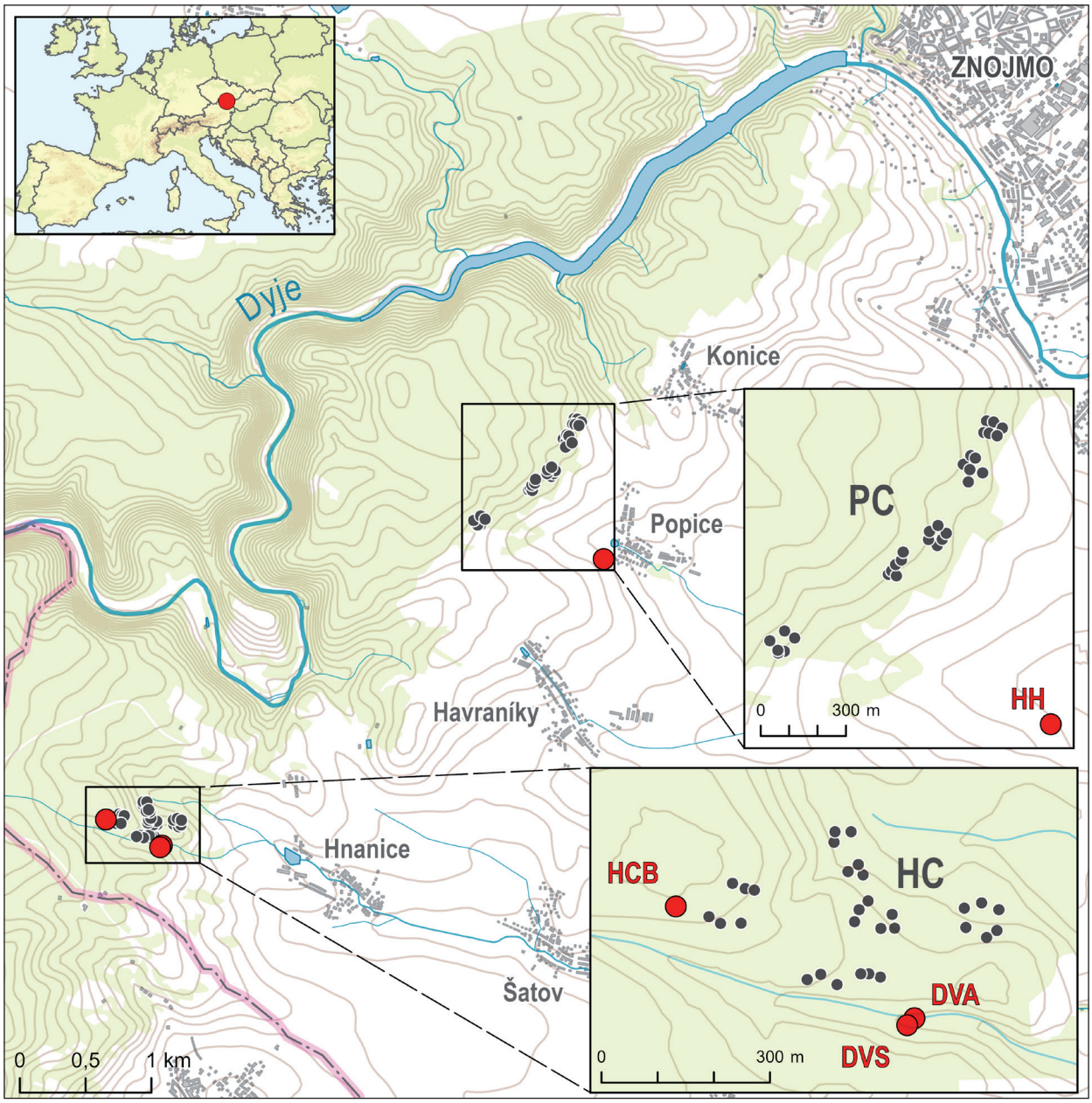


Figure 1. Map of study area and sampling sites. PC – Popice coppice; HC – Hnanice coppice; HCB - Hnanice coppice: rocks (boulders) with shallow soil; HH – Havraníky heathland; DVS – Daníž valley slope; DVA –Daníž valley alluvium (including samples of soil, dead wood, and samples of the dried-out brook bottom); small black dots – individual sampling plots in the coppices (oak forests). Dash-dot-dash line, underlaid in pink, in the lower left corner – Czech-Austrian border.

and the invasive black locust (*Robinia pseudoaccacia*) were locally interspersed in the stands within or close to our sampling plots. Dominant herbaceous plants were *Avenella flexuosa*, *Festuca ovina*, *Melampyrum pratense*, *Poa nemoralis*, and *Convallaria majalis*. The bedrock at the site was biotite-rich granite, soils were various subtypes of Cambisols (Czech Geological Survey, 2026). Elevation ranged from 333 m to 358 m a.s.l.; the approximate centre of the site was at 48°49‘38.6“N, 16°0‘25“E. Soil samples were taken in five clearings of different age (the oldest logged in early 2016) with resprouting oak stumps (the forest stands had been logged to restore coppice management) and in the neglected coppices adjacent to each of these clearings.

2.1.2 Hnanice coppice (oak forest)

Forest composition, soil and bedrock types, history and management as in the Popice coppice (but with some larger stands of planted Scots pine that had been recently logged). The Hnanice coppice was significantly less acidic than the Popice coppice and had a significantly higher soil moisture (gravimetric measurement, based on a few sampling dates only and thus to be interpreted with care). The approximate centre of the Hnanice site was at 48°48‘12.2“N, 15°57‘53“E, the site’s elevation range was 320−369 m a.s.l. As at the Popice site, soil samples were taken in five clearings of different age (again, the oldest logged in early 2016) with resprouting oak stumps and in the neglected coppices adjacent to each of these clearings. The dominant vegetation was the same as in the Popice coppice. See Dusík et al. (2026) for more information on coppicing restoration ecology and methodology of soil chemistry measurement for both oak forest habitats.

Typical for this area were granite boulders and rocky outcrops, often flat on top and partially emerging from soil, sometimes being present in clusters (less abundant at the Popice site). We chose one of these boulder fields and sampled, as a specific microhabitat, soil on top of these rocks. The soil was shallow, generally not deeper than 10–14 cm (often less), mostly covered by moss, less often by grasses. The centre of the sampling site with boulders was at 48°48‘13.4“N, 15°57‘43.48“E. To the south, the Hnanice coppice was bordered by the incised valley of a brook called Daníž, see further below.

2.1.3 Havraníky Heathland

This dry heathland, named after the Havraníky village to the south (though our sampling site was close to Popice, see Fig. 1) was mainly covered by two vegetation types: the *Carici humilis-Callunetum* and the *Potentillo arenariae-Agrostietum vinealis* (Sedláková and Chytrý, 1999). The bedrock of the site was biotite-rich granite and the dominant soil types of the heathland were Cambisols and shallow, Ranker-type, Leptosols (Czech Geological Survey, 2026). This site has most likely been deforested since the Neolithic. The heathland was used for grazing of livestock since then, but most pastures were abandoned at the end in the 19th century. The open character of the site was later maintained by occasional grazing, accidental fires and usage of some parts for military training. Nature conservation management began in the early 1990s (Chytrý et al., 2008).

We sampled a plot of ca 16 m^2 with its centre at 48°49‘14.3“N 16°0‘46.9“E at an elevation of 305 m a.s.l. This area had grasses and mosses as its dominant vegetation cover, with interspersed *Rosa* sp. and *Calluna vulgaris,* bordered by a small stand of *Genista pilosa* and a small Scots pine.

2.1.4 Daníž brook valley

The sampling site (48°48‘6.4“N, 15°57‘47.6“E) was situated south of the Hnanice coppice, in the valley of a small brook called Daníž at an elevation of 330 m a.s.l. The bedrock was biotite-rich granite but there was a layer of sediments in the alluvium. Soil was Cambisol, gleyic along the brook (Czech Geological Survey, 2026). The area was covered by high forest, the dominant tree species along the brook being common alder (*Alnus glutinosa*), while sycamore maple (*Acer pseudoplatanus*) and lime (*Tilia* sp.) were abundant both in the alluvium and on the slopes. Further interspersed tree and shrub species were aspen (*Populus* sp.), hazel (*Corylus avellana*), sessile oak (*Quercus petraea*) and also Scots pine (*Pinus sylvestris*), which was abundant on the north-facing slope. Dominant species of the herb layer, generally richer on the slope, were *Impatiens parviflora*, *Convallaria majalis*, *Dryopteris carthusiana*, and *Stellaria holostea*, with *Hieracium murorum*, *Myelis muralis* and *Geranium robertianum* being also rather abundant (geobotanical data from the Havraníky Heathland and Daníž brook valley are based on our observation, matched with cited literature and consulted with an expert botanist). We investigated microannelids in soil of three mesohabitats: the alluvial soil next to the brook, the north-facing slope ca 20 metres away from and ca 3 m above the brook, and, with lower intensity (see below), the bottom of the brook at times when this was dried-up. Furthermore, we sampled decomposing woody debris in the alluvium as a specific type of microhabitat that was rather abundant at this site.

2.2 Data collection

2.2.1 Microannelid sampling

All soil samples were taken by a soil corer of 17 cm^2 surface area, down to the depth of 12 cm (if possible). Each soil core was immediately divided into 3-cm-layers, to allow for the analysis of vertical distribution. The samples of dead wood were taken by hand. All samples were then put into plastic bags, transported to the lab in a cooling bag and kept cool in a refrigerator (4 °C) until extraction, using a modified O'Connor wet funnel method (no heating from above but cooling by water bath from below; pH of extraction water adapted to approximate the sites' soil pH) for 48 h with catch retrieval every 24 h (Graefe, 1984; Kobetičová and Schlaghamerský, 2003).

Sampling dates were meant to represent the more favourable conditions of spring and autumn, i.e., after warming up and before the onset of frost and avoiding too dry conditions. The samples from the thermophilous oak forests (Hnanice and Popice coppices) were obtained on the 21 May and 10 November 2021 at Popice, and 28 May and 17 November 2021 at Hnanice. We took 30 samples per site and sampling date, one half from neglected coppices and the other half from the restored ones.

We sampled the other sites with their selected meso- and microhabitats on the 13 June and 20 December 2023. For the sake of simplicity, we call these spring and autumn as well, though this is strictly speaking only correct in the astronomical sense. After a very dry and warm onset of spring, we waited for more favourable conditions and finally did the sampling after a rainy spell in mid-June. In autumn, there was little precipitation before the end of October; for logistic reasons we could not sample in November and then had to wait for warmer temperatures after a cold spell with frost (down to -11 °C) between 30 November and 10 December, after which temperatures rose again substantially (with up to 11 °C far above average for the season) until our sampling date (data from the hydrometeorological station in Retz, Austria, 5 km south of our Daníž brook site). On each date we took six replicates from every (micro)habitat. For the samples of decomposing wood, we took samples by hand from six different objects:

a and **b)** smaller pieces of rotten alder wood,

c) dead alder snag,

d) organic material, including but not limited to dead wood, accumulated in the fork where three alder trunks were growing out of a common stool,

e) big rotten aspen log,

f) rotten stump (tree species not identified).

The volumes of the individual wood samples ranged from ca 290 to 725 cm^3 (with mean volume of 410 cm^3 for spring and 556 cm^3 for autumn) and their mass ranged from 93 to 250 g. Volumes were assessed based on the volume and number of cylindric extraction strainers used (145 cm^3 each), which were filled with the woody debris up to the brim with no pressure applied.

The bottom of the brook, during times when it had fallen dry, was sampled in a less systematic way and therefore we provide only qualitative data. We took one soil core on 20 December 2023. Additional five soil cores were taken on 4 July 2025 during the excursion to Podyjí NP, which was part of the 15th Symposium on Enchytraeidae held in Brno. These samples were partially used in the workshop on enchytraeid identification at the end of the symposium, partially processed later.

2.2.2 Microannelid identification incl. molecular barcoding

Identification was based on live specimens examined under a compound microscope (Olympus CX 31, in more critical cases Olympus BX 51 with Nomarski contrast), primarily using the key by Schmelz and Collado (2010). The non-enchytraeid clitellates were identified using the key by Hrabě (1981) or directly by R. M. Schmelz during the ISE 2025 identification workshop.

Specimens of doubtful species identity were subjected to molecular barcoding, analysing mitochondrial markers, i.e., parts of the gene for 16S rRNA (16S) and the cytochrome oxidase c subunit I (COI) gene. The sequences obtained were compared with barcodes in both private and public databases (BOLD; GenBank; Erseus et al. – unpublished; own sequences) to verify the species identity. The process of molecular barcoding was as follows.

DNA isolation: The samples for isolation stored in 80 % ethanol absolute ethanol diluted by high grade purified water or in buffer TL from the isolation kit mentioned below. Genomic DNA was extracted using E.Z.N.A. Tissue DNA Kit (Omega Bio-Tek, USA) according to the manufacturer's protocol. When ethanol was used for storage, this was evaporated before extraction, using the Eppendorf vacuum concentrator (Eppendorf, Germany) and specimens were rinsed in common PBS buffer before using the TL lysing buffer. The process was modified with overnight lysing incubation and the final elution volume was reduced to 30 µl.

PCR amplification: PCRs (20 µl total volume) were performed using modified primers for COI, based on the barcoding primers (Simon et al., 1994) LCO (5'CAACATTTATTTTGATTTTTTGG) and enCOIr (5'ACTTCWGGGTGYCCAAAYAATC 3'). The reaction mixture contained in the final concentration: 1x PCRBIO HiFi buffer, 0.15 U/µl of PCRBIO HiFi polymerase (PCR Biosystems Ltd., UK), 0.2 µM of the primers mentioned, 1 mg/ml BSA, 50 ng of DNA

template and PCR-grade dH_2O up to the final volume of PCR. The PCR amplification profile was set on thermocycler Eppendorf ProS (Eppendorf, Germany) as follows: 95 °C/3 min; 35x (95 °C/45 s, 50 °C/45 s, 72 °C/1.25 min); 72 °C/5 min; 4 °C/∞.

In the case of unsuccessful amplification of the COI marker, the 16S mitochondrial region was amplified. The reaction mixture was set as previously but containing primers 16SAR-L (5′CGCCTGTTTATCAAAAACAT3′) and 16SBRH (5′CCGGTCTGAACTCAGATCACGT3′) (Palumbi et al., 1991 in Martinsson et al., 2017). The amplification profile of the PCR reaction for this marker was modified as follows: 95 °C/5 min; 35x (95 °C/30 s, 56 °C/30 s, 72 °C/1 min); 72 °C/8 min; 4 °C/∞.

Sequencing and sample identification: The PCR products were enzymatically purified using the ExoSAP-IT reagent (Affymetrix Inc. by Thermo Fisher Scientific, USA) following the manufacturer's protocol. Sanger sequencing was outsourced at Macrogen Europe (Netherlands) or carried out in-house. In the latter case, the sequencing reactions were prepared using the BigDye Terminator v3.1 Ready Reaction Cycle Sequencing Kit, purified by the BigDye X Terminator Kit, following exactly the recommendations of the manufacturer, and run on an ABI 3130 Genetic Analyzer (Applied Biosystems via Thermo Fisher Scientific, USA) under the appropriate module. Raw data were analysed by Sequencing Analysis Software v.5.3.1 supplied with the device. All sequences were trimmed, aligned, assembled and inspected in Sequencher 5.0 software (Gene Codes Corporation, USA).

The percentage of homology with the databases' releases in obtained sequences was checked using the online BLASTn tool (Sayers et al., 2025).

2.3 Data processing

All calculations and visualisations were done in R software (R core team, 2025) with the packages *ggplot2* (Wickham, 2016) and *vegan* (Oksanen et al., 2025). We calculated mean population densities and their standard errors for each (micro)habitat (except the stream bed of Daníž brook) separately for the spring and autumn sampling. We also calculated the mean relative abundance of each species in each (micro)habitat, where it was found (by calculating the relative representation within each replicate, and then the mean for all replicates taken in the given (micro)habitat). The more traditional percentage representation (dominance) as a ratio of the number of individuals of a given species and the total number of all microannelid specimens in a given sample (set of replicates) can be easily computed from the presented abundance data. The relative mean vertical distribution at a given depth was calculated as the mean of the relative vertical distribution percentages (number of individuals in a given layer, divided by the number of individuals in the whole sample), across all samples from a given habitat and sampling period (autumn and spring).

For the three microhabitats in the Daníž brook valley for which quantitative data were obtained (alluvial soil, soil on the slope in 20 m distance from the brook, dead wood) we used Bray-Curtis Principal Coordinates Analysis (log-transformed abundance data; empty replicates and doubtful species were omitted) to visualize the difference between the assemblages within a small area. Wood samples were standardized by volume (for more information on standardization and quantification of microannelids extracted from wood in general see Discussion).

3 Results

In total, we found 33 enchytraeid species, *Hrabeiella periglandulata, Nais communis* Piguet, 1906, and *Stylodrilus heringianus* Claparède, 1862. Both relative and absolute abundances of the recorded species, including their densities in spring and autumn, are presented in Table 2, together with the total number of species for each site or micro-/mesohabitat. The mean densities in dead wood samples calculated for the volume of substrate were 0.225 ind./cm^3 in spring and 0.006 ind./cm^3 in autumn. Densities on the autumn sampling date were generally lower. Relative mean vertical distributions of microannelids are shown in Table 3, separately for each meso- and microhabitat and each of the two seasons.

Comparing individual sites and habitats, we found the highest densities in the oak forests and in the alluvial soil along the Daníž brook. Species richness in these two habitats was also among the highest, but surpassed by the brook bottom, which also included aquatic species. Looking at the similarity of individual (micro)habitats in the Daníž valley (excluding the brook bottom for which we had no reliable quantitative data), PCoA (Fig. 2) showed assemblages in individual samples from the slope clustering apart from those in samples of alluvial soil and dead wood along the main gradient, with the latter two slightly overlapping.

3.1 Taxonomic, faunistic and ecological notes

Enchytraeidae

***Achaeta*:** We only found two species of this genus: *A. affinis* and *A. unibulba*. *A. affinis* is common in acidic

Table 2. List of microannelid species found at the individual sites and specific habitats with their total numbers, mean relative abundance and total densities. OF – oak forest, DW – dead wood, BB – dried-out brook bottom, ind./s. – individuals per sample. Mean volume of a dead wood sample was 410 cm^3 for spring and 556 cm^3 for autumn, volume of a soil core was 204 cm^3 (12 cm depth X 17 cm^2 surface area).

Species	Havraníky	Popice	Hnanice	Hnanice; Daníž valley				
	Heathland ind.] (%)	OF [ind.] (%)	OF [nd.] (%)	Rock [ind.] (%)	Slope [ind.] (%)	Alluvial soil [ind.] (%)	DW [ind.] (%)	BB
Achaeta affinis Nielsen & Christensen, 1959	–	1519 (15.6)	164 (7.8)	–	156 (68)	426 (38.9)	7 (5.8)	+
Achaeta unibulba Graefe, Dózsa-Farkas & Christensen, 2005	–	–	–	–	–	–	–	+
Bryodrilus cf. *diverticulatus* Černosvitov, 1929	–	6 (<1)	–	–	–	–	–	–
Bryodrilus cf. *ehlersi* Ude, 1892	–	–	–	–	–	–	8 (1)	–
Buchholzia appendiculata (Buchholz, 1863)	–	333 (9.8)	205 (12.7)	5 (<1)	–	–	–	+
Cernosvitoviella sp. Nielsen & Christensen, 1959	–	–	–	–	–	–	–	+
Cognettia chlorophila (Friend, 1913)	–	301 (6.8)	235 (13)	3 (3.2)	38 (13.9)	291 (33.9)	74 (14.2)	+
Cognettia sphagnetorum (Vejdovský, 1878)	–	–	–	–	–	6 (<1)	–	+
Enchytraeus buchholzi Vejdovský, 1878	1 (1.6)	5 (<1)	9 (<1)	–	–	–	9 (1.4)	+
Enchytraeus norvegicus Abrahamsen, 1969	–	–	–	–	–	6 (<1)	–	–
Enchytronia parva s.l. Nielsen & Christensen, 1959	4 (1.7)	44 (2.3)	48 (2.20)	1 (<1)	–	–	–	–
Enchytronia sp. Nielsen & Christensen, 1959	–	1 (<1)	–	–	–	–	–	–
Fridericia benti Schmelz, 2002	–	–	–	1 (<1)	–	15 (<1)	22 (3.4)	+
Fridericia bisetosa (Levinsen, 1884)	–	–	55 (4.4)	–	–	–	–	+
Fridericia brunensis Schlaghamerský, 2007	208 (91.5)	1258 (45.8)	684 (34.3)	91 (69)	36 (14.1)	–	–	–
Fridericia bulboides Nielsen & Christensen, 1959	1 (<1)	–	17 (1.8)	–	–	–	–	–
Fridericia connata Bretscher, 1902	–	50 (1.7)	9 (<1)	–	–	–	–	–
Fridericia cylindrica Springett, 1971	–	4 (<1)	28 (2.70)	–	–	–	–	–
Fridericia dura (Eisen, 1878)	–	33 (2.3)	15 (<1)	2 (8.5)	–	9 (<1)	1 (<1)	–
Fridericia cf. *larix* Schmelz & Collado, 2005	–	1 (<1)	–	–	–	–	–	–
Fridericia cf. *paranemoralis* Dózsa-Farkas, 1982	–	–	1 (<1)	–	–	–	–	–

Table 2 continued.

Species	Havraníky	Popice	Hnanice	Hnanice; Daníž valley				
	Heathland ind.] (%)	OF [ind.] (%)	OF [nd.] (%)	Rock [ind.] (%)	Slope [ind.] (%)	Alluvial soil [ind.] (%)	DW [ind.] (%)	BB
Fridericia paroniana Issel, 1904	–	20 (<1)	64 (3.60)	–	–	–	–	–
Fridericia perrieri (Vejdovský, 1878)	–	–	–	–	–	–	–	+
Fridericia ratzeli (Eisen, 1872)	–	–	2 (<1)	–	–	–	–	–
Fridericia semisetosa Dózsa-Farkas, 1970	3 (1.4)	7 (<1)	3 (<1)	4 (<1)	–	–	–	–
Fridericia sylvatica Healy, 1979	–	–	–	–	–	–	–	+
Fridericia cf. *tubulosa* Dózsa-Farkas, 1972	–	–	31 (<1)	–	–	–	–	–
Henlea perpusilla Friend, 1911	–	25 (<1)	9 (1.50)	–	–	–	–	+
Henlea ventriculosa (d'Udekem, 1854)	3 (1.9)	–	2 (<1)	–	–	–	–	–
Marionina argentea (Michaelsen, 1889)	–	–	–	–	–	–	–	+
Marionina clavata Nielsen & Christensen, 1961	–	–	–	–	–	133 (22.7)	326 (48.4)	–
Mesenchytraeus pelicensis Issel, 1905	–	76 (1.6)	2 (<1)	–	1 (<1)	2 (<1)	87 (19.7)	–
Oconnorella cambrensis (O'Connor, 1963)	–	–	750 (6.9)	–	4 (3)	19 (1.70)	–	–
Stercutus niveus Michaelsen, 1888	–	–	6 (<1)	–	–	–	–	+
Fridericia spp. Michaelsen, 1889	2 (1.7)	1 (<1)	16 (1.4)	1 (<1)	–	–	35 (5.4)	+
Enchytaeidae unidentified	–	6 (<1)	3 (<1)	2 (5.5)	1 (<1)	–	2 (<1)	–
Nais communis Piguet, 1906	–	–	–	–	–	–	–	+
Stylodrilus heringianus Claparède, 1862	–	–	–	–	–	–	–	+
Hrabeiella periglandulata Pižl & Chalupský, 1984	–	428 (10)	50 (2.8)	3 (8.3)	–	1 (<1)	–	–
Mean population density (Spring)	18 039 ± 4 578 ind./m²	48 464 ± 5 242 ind./m²	36 843 ± 12 570 ind./ m²	10 588 ± 8 293 ind./m²	15 294 ± 4 066 ind./m²	69 216 ± 18 868 ind./m²	92.0 ± 35.4 ind./s.	–
Mean population density (Autumn)	3 725 ± 2 327 ind./m²	23 647 ± 5 742 ind./m²	10 373 ± 01 646 ind./m²	490 ± 0 490 ind./m²	7 843 ± 3 442 ind./m²	20 000 ± 07 917 ind./m²	3.2 ± 01.5 ind./s.	–
Species in total	6	16	22	8	5	10	8	16

forest soils (Graefe and Schmelz, 1999, Römbke et al., 2013), it was present at all sites except the Havraníky Heathland and the shallow soils on the granite rocks in the Hnanice forest. The species is similar to *A. danica* Nielsen & Christensen, 1959, but lacks spermathecae. Among the more than 2000 individuals examined, we did not find a single adult with developed spermathecae, and the species identity was also confirmed by barcoding (COI).

A. unibulba was found in a single specimen in the dried-out bed of Daníž brook in one of the samples taken in July 2025 (the species is easy to identify based on morphology but was also confirmed by barcoding with COI 99% identity).

***Bryodrilus*:** The *Bryodrilus* specimens we found at the Popice site were morphologically difficult to identify, due to their low number and lack of adults. Barcoding using 16S, showed a 96–97% identity with a sequence assigned to *B. diverticulatus*, whereas the obtained COI sequences had no close matches, closest match: 86% *B. librus* (Nielsen & Christensen, 1959). *B. diverticulatus* is a species with an interesting distribution mostly in the northern Holarctic: Siberia (Christensen and Dózsa-Farkas, 1999), Spitsbergen or Svalbard (Birkemoe et al., 2000), Scandinavia (Martinsson et al. 2017), and Estonia (Schmelz et al., 2005). It was also found in Greenland and the Canadian Arctic Archipelago (Christensen and Dózsa-Farkas, 2006). Apart from that, it was also recorded far to the south in Korea (Felföldi et al., 2020). Its presence in a warm and dry central European oak forest is surely noteworthy. The closest place from which it could have theoretically spread is the Alps, where there is one record confirmed also by molecular methods (H3) from the Grossglockner massif in the Austrian Alps (Schlaghamerský, unpublished). The second recorded species was *B. ehlersi*. Molecular barcoding confirmed its identity (COI: 94% identity nearest match). It was found only in the dead wood samples (Objects *b* and *f*) taken in spring 2023. *B. ehlersi* is one of the few species already recorded from dead wood (Schlaghamerský, 2007; Dózsa-Farkas, 2019). The species is widespread in northern and central Europe, mostly in forests, bogs and peatlands, and has been also reported from Siberia and the Russian Far East (Piper et al. 1982; Nurminen, 1973, 1980; Degtyarev et al., 2020), Korea (Nagy et al., 2020), and North America (Schlaghamerský, 2013; Schlaghamerský et al. 2014).

Cognettia: We found two *Cognettia* species. The more common one, *C. chlorophila,* was only absent at the heathland site. It is one of the species recognized (re-established) since *C. sphagnetorum* s.l. was split into several more or less cryptic species (Martinsson at al., 2015). This species is morphologically well distinguishable, widespread, and particularly common in acidic forest soils, where it is often dominant (mostly in coniferous forests). It is likely that the species referred to as *C. sphagnetorum,* which has been reported as dominant from numerous forests, was most often *C. chlorophila*. Huhta et al. (2010) found *C. sphagnetorum* s.l. in samples from dead wood in Finland (together with *Enchytronia parva, Enchytraeus albidus* and *Fridericia callosa)*, this might well have been *C. chlorophila,* which was abundant in our dead wood samples.

The second recorded species was *C. sphagnetorum* s.str. It might have a narrower niche than *C. chlorophila,* preferring moister habitats (Schmelz and Collado, 2010; Martinsson at al., 2015; Rüdiger M. Schmelz, pers. comm.). We found it only in the alluvial soil and the dried-out bed of Daníž brook, which is consistent with its proposed preference for wet sites. Both species identities were confirmed by barcoding (COI, 16S).

***Enchytraeus*:** Our specimens of *E. buchholzi* (a species complex, see Schmelz and Collado, 2010) had all refractile granula in their coelomocytes. These granules were quite small and brown in transmitted light.

E. norvegicus, recorded in the alluvial soil along Daníž brook (6 specimens), had consistently three pairs of preclitellar nephridia only.

***Enchytronia*:** The found individuals had two elongate and quite conspicuous intestinal diverticula and two pairs of preclitellar nephridia in VII/VIII and VIII/IX. Lateral chaetae were missing in VIII-XII. Except having two instead of three pairs of preclitellar pairs of nephridia, these characters matched *E. christenseni*

Table 3. Relative mean vertical distribution of microannelids in studied meso- and microhabitats for the given season. Last row shows occurrence of empty samples in percent (n = 30 for oak forests, n = 6 for the rest). A – autumn, S – spring, OF – oak forest.

Depth	Havraníky		Hnanice OF		Rock		Popice OF		Daníž slope		Daníž alluvium	
[cm]	S [%]	A [%]	S [%]	A [%]	S [%]	A [%]	S [%]	A [%]	S [%]	A [%]	S [%]	A [%]
0-3	28.5	48.0	70.9	83.5	66.3	80.0	56.8	70.7	71.1	34.0	74.9	32.8
3-6	46.8	21.7	21.2	12.5	22.1	20.0	22.1	24.7	25.6	59.1	19.5	55.5
6-9	21.4	20.8	5.5	2.4	7.7	0	13.7	3.2	3.3	6.0	5.2	11.7
9-12	3.3	9.5	2.5	1.6	3.9	0	7.3	1.5	0	0.9	0.5	0
Empty [%]	0	50	0	3.33	16.67	83.33	0	16.67	0	16.67	0	0

Dózsa-Farkas, 1970. Molecular barcoding failed. In accordance with Schmelz and Collado (2010) we list these specimens as *E. parva* s.l.

***Fridericia*:** The most dominant species was *F. brunensis* (except in the Daníž valley). We already discussed the ecology of this species in Dusík et al. (2026), characterizing it as acidotolerant (uncommon for the genus) and with affinity to dry habitats. It was very dominant (92 %) in the non-forested Havraníky healthland and in shallow soil on the rocks (69 %). In the Daníž valley it was present only in the driest mesohabitat, i.e., soil on the slope. The Leptosols (ranker) of the heathland were quite shallow, and prone to drought, in line with the occurrence of xerophilous plant communities. Similarly, the soil on the rocks was shallow and prone to drying out. The very low population densities in autumn (only four individuals of the species were extracted) in the rock microhabitat might have been connected to the severe summer and autumn droughts, less pronounced in other (micro)habitats.

F. connata: Morphologically the identification was unambiguous. Molecular barcoding of one specimen showed 90 % identity with *F. connata* as the closest match for COI.

Fridericia cf. *larix*: One subadult specimen was tentatively identified as *F. larix*: 50 segments, 10.1 mm long, body width (XI) 288 µm; chaetal formula: (1),2,(3)–2 : 2,3(VI–XI),(4)−3(XIII–XIV),2; chylus distinct, in XII−XIII (sometimes shifted forward to XI−XIII); 5 pairs preclitellar nephridia; oesophageal appendages short with one main branch reaching further to the back and a few thinner and shorter, branched ones at its base; brain 89 µm long, 46 µm wide, hind margin slightly incised; coelomo-mucocytes clear, without granules, 25−37 µm long, lenticytes 5−8 µm long, both types numerous; body wall (XI) 27 µm; no subneural glands; clitellum not well developed, no seminal vesicle; sperm funnel ca 100 µm long, 50 µm wide (not mature?, some spermatozoa attached to collar); bursal slit: only long transversal slit visible; spermathecae: each with two ear-like diverticula without sperm, ental ducts possibly merging at connection to oesophagus, ectal duct of medium length (not well visible), with tiny, sessile ectal gland. Barcoding (COI) did not yield any match (above 85 % identity) with sequences in the relevant databases. Size differences among chaeta of one bundle, typical of *F. larix*, were not observed.

Fridericia cf. *paranemoralis*: One subadult specimen was tentatively identified as *F. paranemoralis*: 35 segments, 6.5 mm, body width (XI) 365 µm; chaetal formula: (1),2,3−3,2 : 2,3,4 – 4,3,2; chylus in XII?; 5 pairs preclitellar nephridia; oesophageal appendage short, unbranched (?, not well visible); coelomo-mucocytes clear, without granules, 27−34 µm long, lenticytes 5–7 µm long; body wall (XI) 28 µm; no subneural glands; clitellum not well developed, no seminal vesicle; sperm funnel ca 115 µm long, 70 µm wide (not mature?, some spermatozoa attached to collar); bursal slit with transverse component, T-shaped; spermathecae: each with two ear-like diverticula (one with sperm), ental ducts connected separately with oesophagus, ectal duct of medium length, with large, floppy ectal gland; some transverse rows of brown epidermal gland cells in anterior segments. Barcoding did not yield any match (above 85 % identity) with sequences in the relevant databases (which do not include *F. paranemoralis*) in case of COI, however in case of 16S there was a 93 % identity with *Fridericia heliota* Zalesskaya, 1990.

Fridericia cf. *tubulosa*: One adult specimen (with one small yolky egg) was tentatively identified as *F. tubulosa*: 53 segments, 14 mm, body width (XI) 500 µm; chaetal formula: 2,3−3,2 : 4 – 4,3,2; chylus in XIII-XIV; oesophageal appendages not well visible, apparently a larger lumen of a basal part with some smaller basal branches present; coelomo-mucocytes without granules, ca 45 µm long, lenticytes 8 µm long; body wall (XI) 28 µm; no subneural glands (?); clitellum with +/- regular transverse rows; no seminal vesicle; sperm funnel ca 330 µm long, 250 µm wide, spermatozoa attached to collar ca 343 µm long, of those 170 µm sperm heads; bursal slit with transverse component, T-shaped; spermathecae: each with two ear-like diverticula with some sperm, ampullae broadly and separately connected to oesophagus (no proper ental ducts), ectal duct short, with one mid-sized sessile gland (possibly a second, smaller one present). Barcoding (COI) did not yield any match (above 84 % identity) with sequences in the relevant databases. Identity with the only COI sequence of *F. tubulosa* in an accessible database (BOLD: Process ID ENKDF143-11), collected in Hungary, identified by K. Dózsa-Farkas and thus highly trustworthy, was only 81.9 %.

***Marionina*:** *M. clavata* was only recorded in the alluvial soil and dead wood in the Daníž brook valley. This species is widespread and common in acidic forest soils (Graefe and Schmelz, 1999, Römbke et al., 2013). At our site, *M. clavata* had high relative abundances in the dead wood (almost 50 %), which suggests that the species preferred this microhabitat, at least in spring. However, enchytraeids in the sampled dead wood microhabitat were probably particularly affected by draught during the summer and/or frost in early December as we found almost no enchytraeids in our samples from mid-December (“autumn”).

Of three specimens identified as *M. argentea* and subjected to molecular barcoding two showed 99 % and one 93 % identity with *M. argentea* s. str. as the closest match (COI). We refer from considering the latter specimen as a different species.

***Mesenchytraeus pelicensis*:** We recorded only this species of the genus (barcoding of two specimens showed 100% identity in COI). It was quite rare in the forest soils, with a maximum relative abundance of just under 2%. On the other hand, it was relatively common in the wood samples (almost 20%), being present in all objects except *e*. However, its presence in dead wood was restricted to the spring samples, when it apparently preferred the dead wood compared to soil.

Naididae

***Nais communis*:** One juvenile specimen from the dried-out bottom of Daníž brook, confirmed by molecular barcoding (COI: 97% identity).

Lumbriculidae

***Stylodrilus heringianus*:** One juvenile specimen from the dried-out bottom of Daníž brook confirmed by molecular barcoding (COI: 99% identity). A second juvenile *Stylodrilus* specimen was tentatively identified as the same species by R. M. Schmelz.

Hrabeiellidae

***Hrabeiella periglandulata*:** The only non-clitellate microannelid recorded at the sites. It has been reported from forests and non-forested habitats, sometimes achieving high relative population densities (Schlaghamerský and Šídová, 2009; Dózsa-Farkas and Schlaghamerský, 2013). This was also the case in the Popice oak forest.

4 Discussion

Across all investigated assemblages, mean "population" densities (all microannelids together) were lower in the autumn period. This difference was most profound in two of the microhabitats, i.e., shallow soil on rocks and dead wood, where only very few individuals were found in the autumn samples (5 and 19, respectively). Interestingly, the spring samples of dead wood had on average less volume, yet much higher abundances. We know that enchytraeid abundance and survival are closely linked to soil moisture (Beylich and Achazi, 1999; Maraldo and Holmstrup, 2009; Coyle et al., 2017), and these two microhabitats would be very prone to drying out, but also to frost (relevant for our 2023 sampling in December). The worms encountered in the dead wood substrate might migrate into soil to wait out the unfavourable conditions and then return to the dead wood. However, in the shallow soils on rock the studied microhabitat

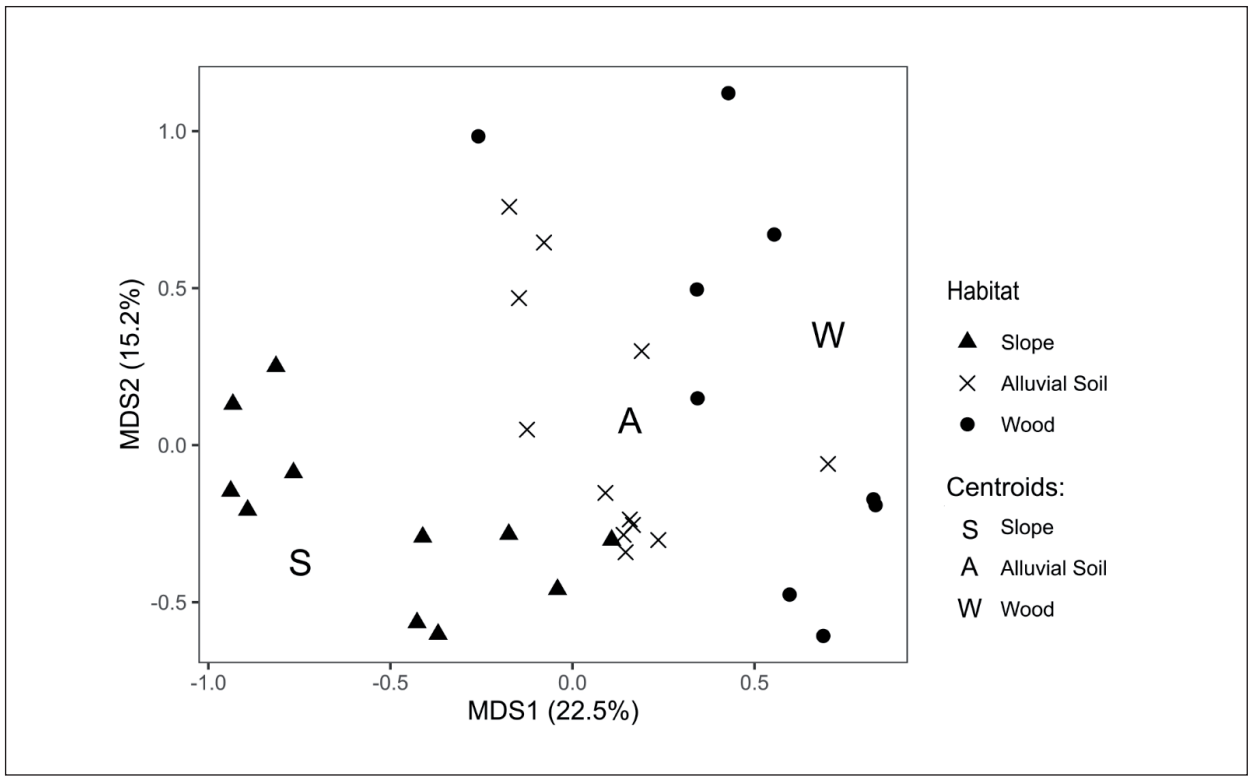


Figure 2. Principal Coordinates Analysis (PCoA) calculated with Bray-Curtis metric. Each triangle (slope), cross (alluvial soil) and full circle (dead wood) represents a microannelid assemblage from one sample (soil core or wood sample) taken in the Daníž brook valley in the specific meso- or microhabitat. Letters are centroids, passively projected into the figure, S = Slope, A = alluvial soil, W = dead wood

was isolated from the underlying and surrounding soil by the rock so that migration into deeper soil would be more difficult. Alternatively, microannelids could rely on drought-resistant stages (cocoons), to survive in such shallow soil (Nielsen, 1955; Lagerlöf and Strandh, 1997). In regard to the recorded vertical distributions and the seasonal differences between them, we cannot draw meaningful conclusions for the heathland and shallow soils on rock habitat due to many empty samples in the autumn period. In the soils of the Daníž brook valley, we found a higher proportion of microannelids in the 3–6 cm soil layer in the autumn compared to spring, supporting the hypothesis of migrations into deeper soil layers during dry periods or frost (Springett et al., 1970) or alternatively high mortality in the 0–3 cm layer. On the other hand, in the oak forests (both recently cut and neglected coppices) the majority of microannelids stayed in the upper layer both in the spring and autumn (with even higher percentages in the autumn), contradicting the above hypothesis. The weather in the two years (sampling in coppices was done in 2021 and in the Daníž brook valley in 2023) differed, 2023 being warmer by almost 2 °C on average and also the total precipitation being higher that year. This difference in precipitation was caused by higher rainfall in only four months (Table S1), but these were the periods directly preceding or even covering our sampling dates. Despite this, in autumn the majority of individuals in the soils of the Daníž brook valley was in the 3–6 cm layer, suggesting that their distribution was affected either by a long-term effect of the very dry conditions in September and October or by the sudden low temperatures in late November and early December (ending 10 days before the sampling as mentioned in the Methods). Another notable fact is that, except one sample of the shallow soil on rock habitat (which was the harshest one according to our results), all the other empty samples had been taken in autumn. This suggests that also the horizontal distribution was affected by the seasonality, resulting in microannelids being more clustered in horizontal space in the autumn, likely due to the same climatic factors.

There is no general agreement yet on how to quantify and standardize dead wood samples. Huhta et al. (2010) sampled a standardized volume of dead wood (which was 100 cm^3), we chose a similar approach, by calculating the volume of each sample post-hoc. The only obvious alternative would be standardizing the samples by mass, which would mainly be a function of the concrete wood density, volume and the current water content (which would account for a significant part of the mass). Using volume directly avoids the need to measure these other values.

We cannot calculate the population densities of microannelids in the wood in the same way as in the soil, where giving the number of individuals per square metre is the standard (assuming a sampling depth sufficient to obtain the vast majority of individuals in the soil profile). It is easy to calculate the volume of individual soil cores based on the soil corer dimensions, and the mean number of individuals per soil core (= per volume of soil) is a value obtained during sample processing, but can also be calculated from the population density (presented in Table 2) using the surface area sampled by the soil corer (17 cm^2 in this case). This allows for some comparison of the microannelid assemblages in dead wood with those in soil (given in any paper with a well-described sampling design and providing quantitative data). However, the vertical distribution of microannelids in soil shows general preference for the upper layers (Didden, 1993; Graefe and Schmelz, 1999; Schmelz and Collado, 2010), whereas the spatial distribution of microannelids in dead wood is completely unknown and might very much depend on the character of the wood (e.g., stage of decomposition) and its position in the habitat (e.g., wood mould in a tree cavity vs rotten tree stump). Thus extrapolating abundance values obtained from a certain volume of woody debris is still problematic.

In our samples, at least three species (*M. clavata*, *M. pelicensis* and *B. ehlersi*) preferred the dead wood substrate to the soil (relatively speaking) in spring (in autumn, only a few *M. clavata, A. affinis* and *C. chlorophila* individuals were present). In addition to the studies already mentioned above (subchapter 3.1), Standen et al. (2009) also sampled dead wood for enchytraeids and found three *Fridericia* species (no numbers were reported).

We found quite different assemblages in the individual micro- (dead wood) and mesohabitats (soil in the alluvium and on the slope) in the Daníž brook valley (Fig. 2), although these were sampled within a relatively small area (ca 200 m^2). The assemblage of the driest habitat, the valley slope, was the most different. It had a rather low species richness and microannelid density and was also the only one of the Daníž meso- and microhabitats that included *F. brunensis.* The other two micro-/mesohabitats had more similar assemblages, clearly distinguished from that of the slope soil, with many species present both in alluvial soil and dead wood. This was likely caused by their close spatial proximity, the dead wood being present directly in the stretch of alluvium where also the soil was sampled. Both alluvial soil and dead wood were moister than the soil on the slope, but they differed by the character of the substrate, also reflected by its chemistry, namely by very different carbon, phosphorus and calcium contents (Tab. 1).

Dead wood as a habitat for microannelids is understudied, and the total abundances (at least at the time of the spring sampling) were high, while relative

abundances differed between soil and dead wood. Furthermore, at least two species, which were not found in the soil, were present in the wood. Therefore, including dead wood samples when assessing species diversity and ecological importance of microannelids might be worth doing in general (mainly in forests, but actually anywhere where some dead wood is part of the habitat) as the description of a site-related assemblage might be otherwise incomplete.

When comparing the species richness among the individual sites and micro-/mesohabitats, one has to bear in mind that much higher numbers (five-fold) of replicates (soil cores) were taken within the oak forest habitat at the Popice and Hnanice sites, than at the other sites or in special micro- and mesohabitats.

In conclusion, this is the only dataset concerning terrestrial microannelids in the Podyjí NP (only the data regarding restored and neglected coppices were already published, see Dusík et al., 2026), and one of few from southern Moravia. There are no data from the adjacent part of Austria. We mostly studied thermophilous deciduous forests on acidic soils. Studies on the microanelid fauna from thermophilous deciduous forests on various soils are mostly only qualitative and rather limited in number, coming from Hungary (Dózsa-Farkas, 1973, 1978, 1987, 1991, 1993), Czechia (Schlaghamerský, 2007; Schlaghamerský and Šídová, 2007; Schlaghamerský, 2010), Austria (Bauer, 2002) and Germany (Römbke, et al., 1991; Römbke and Beck, 2010; Römbke et al., 2013, Toschki et al., 2021) within Central Europe, from Italy (Rota, 1995; Rota et al., 2014), south-western France (Healy, 1980), Portugal (Römbke et al., 2018), Turkey (Rota, 1994), North Africa (Rota and Healy, 1994) in the Mediterranean, and also from the Caucasus (Degtyarev et al., 2023; Saifutdinov et al., 2025; Zaitsev et al., 2026). Our data are a significant contribution to the understanding of microannelid assemblage composition in forests, especially of the studied subtype. Together with the information on dead wood as an understudied substrate for microannelids and on the specific forest microhabitat of shallow soil on top of granite boulders, we present a robust dataset representing the microannelid fauna in the forests of the study area. Our data on the assemblage in a dry heathland also provide one of few sources of information on the microannelid fauna of this habitat type. So far, microannelids of dry heathlands have been only studied in Scandinavia (e.g., Maraldo et al., 2008, 2010; Holmstrup et al., 2012, 2015), and in the United Kingdom (Payne et al., 2012). The assemblages there were all dominated by *C. sphagnetorum* s.l. In contrast, we found a very different species composition, dominated by *F. brunensis* (same dominant species as in the close-by oak forests), showing that the microannelid fauna of dry heathlands might vary, possibly depending on the exact type of vegetation, soil parameters and geographical location (climatic conditions) of the heathland.

Acknowledgements

Jana Ilgová conducted the molecular barcoding and comparison with the relevant databases for critical specimens. We are further particularly thankful to Christer Erséus (University of Gothenburg, Sweden) for allowing us to use his unpublished database of enchytraeid molecular sequences (by now available in GenBank). We thank the Administration of the Podyjí National Park for supporting our research within the park. Gravimetric soil moisture data were kindly provided by Karel Tajovský, Institute of Soil Biology and Biogeochemistry, Biology Centre of the Czech Academy of Sciences. Data on soil chemistry and vegetation data from the oak forest coppices were provided by Radim Hédl from the Institute of Botany, Czech Academy of Sciences. Ondřej Hájek from our department kindly created Figure 1.

Supplementary Online Material

The supplementary online material includes Supplementary Table S1 and Supplementary Figures 1–26, available at https://doi.org/10.25674/515.

References

Bauer, R. (2002). Survival of frost and drought conditions in the soil by enchytraeids (Annelida; Oligochaeta) in Arctic, subalpine and temperate areas. *European Journal of Soil Biology*, 38(3–4), 251–254. https://doi.org/10.1016/S1164-5563(02)01154-8

Beylich, A., & Achazi, R. K. (1999). Influence of low soil moisture on enchytraeids. In Schmelz, R. M. & Sühlo, K. (Eds.) *Newsletter on Enchytraeidae No. 6. Proceedings of the 3rd International Symposium on Enchytraeidae, Osnabrück, Germany, 3. –4. July 1998* (pp. 49–58). Universitätsverlag Rasch, Osnabrück.

Birkemoe, T., Coulson, S. J., & Sømme, L. (2000). Life cycles and population dynamics of enchytraeids (Oligochaeta) from the High Arctic. *Canadian Journal of Zoology*, 78(12), 2079–2086.

Chalupský, J. (1988). Czechoslovak Enchytraeids (Oligochaeta, Enchytroeidae). II: Catalogue of species. *Věstník Československé společnosti zoologické*, 52(2), 81–95.

Chalupský, J. (1989). The influence of Zeazin 50 on Enchytraeidae (Oligochaeta) in an apple orchard soil. *Pedobiologia*, 33(5), 361–371.

Chalupský, J. (1991). Czech Enchytraeidae (Oligochaeta). III. Description of a new species of *Enchytronia* and notes on two species of *Marionina*. *Acta Societatis Zoologicae Bohemicae*, 55, 99–113.

Chalupský, J. (1994). Czech Enchytraeidae (Oligochaeta). IV. Description of *Enchytronia pratensis* sp.n. and a note on *Marionina communis*. *Acta Societatis Zoologicae Bohemicae*, 57, 167–172.

Christensen, B., & Dózsa-Farkas, K. (1999). *The enchytraeid fauna of the Palearctic tundra (Oligochaeta, Enchytraeidae)*. Biologiske Skrifter 52, Royal Danish Academy of Sciences and Letters.

Christensen, B., & Dózsa-Farkas, K. (2006). Invasion of terrestrial enchytraeids into two postglacial tundras: North-eastern Greenland and the Arctic Archipelago of Canada (Enchytraeidae, Oligochaeta). *Polar Biology*, 29(6), 454–466.

Chytrý, M., & Vicherek, J. (1995). Lesní vegetace Národního parku Podyjí/Thayatal. Die Waldvegetation des Nationalparks Podyjí/Thayatal [Forest vegetation of the Podyji/Thayatal National Park]. Academia, Praha. [In Czech and German]

Chytrý, M., Grulich, V., & Antonín, V. (2008). *Podyjí National Park: botanical excursion guide.* Department of Botany and Zoology, Masaryk University, Brno.

Chytrý, M. (2012). Vegetation of the Czech Republic: diversity, ecology, history and dynamics. *Preslia*, 84, 427– 504

Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., Mundepi, A., Phillips, C. A., & Callaham Jr, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, 110, 116–133. https://doi.org/10.1016/j.soilbio.2017.03.008

Czech Geological Survey (Access 2026–04–01): Půdní mapa 1: 50 000. [Soil Map 1: 50 000, in Czech]. https://mapy.geology.cz/pudy/

Czech Hydrometeorological Institute (Access 2026–04–01): Historical meteorological data in Czechia (open access). Opendata of CHMI. https://opendata.chmi.cz/meteorology/climate/historical_csv/data/yearly/

Degtyarev, M. I., Lebedev, I. M., Kuznetsova, K. G., & Gongalsky, K. B. (2020). A history of study and new records of terrestrial enchytraeids (Annelida, Clitellata, Enchytraeidae) from the Russian Far East. *ZooKeys*, *955*, 79–96. https://doi.org/10.3897/zookeys.955.53106

Degtyarev, M. I., Medvedev, D. A., Zvychaynaya, E. Y., & Korobushkin, D. I. (2023). Enchytraeidae (Annelida: Oligochaeta) from the North-Western Caucasus, Russia, with the Description of *Fridericia gongalskyi* sp. nov. *Diversity*, 15(1), 106. https://doi.org/10.3390/d15010106

Didden, W. A. M. (1993). Ecology of terrestrial Enchytraeidae. *Pedobiologia*, 37, 2–29. doi.org/10.1016/S0031-4056(24)00082-9

Dózsa-Farkas, K. (1973). Saisondynamische Untersuchungen des Enchytraeiden-Besatzes im Boden eines ungarischen Quercetum petraeae cerris. *Pedobiologia*, 13(5), 361–367.

Dózsa-Farkas, K. (1978). Die ökologische Bedeutung des Mikrohabitates für das Vorkommen einiger Enchytraeiden-Arten 1. *Pedobiologia*, 18(5–6), 366–372.

Dozsa-Farkas, K. (1987). Effect of human treading on enchytraeid fauna of hornbeam-oak forests in Hungary. *Biology and Fertility of Soils*, 3(1), 91–93.

Dózsa-Farkas, K. (1991). Neue Enchytraeiden-Art aus tieferen Bodenschichten eines Hainbuchen-Eichenwaldes in Ungarn (Oligochaeta, Enchytraeidae). *Acta Zoologica Hungarica*, 37(1-2), 21–25.

Dózsa-Farkas, K. (1992). Über die vertikale Verbreitung der Enchytraeiden (Oligochaeta: Enchytraeidae) in einem Hainbuchen-Eichenwald Ungarns. *Opusc. Zool. Budapest*, 25, 61–74.

Dózsa-Farkas, K. (2019). *Enchytraeids of Hungary (Annelida: Clitellata, Enchytraeidae)*. Eötvös University Press, Budapest.

Dózsa-Farkas, K., & Schlaghamerský, J. (2013). *Hrabeiella periglandulata* (Annelida:‘‘Polychaeta’’) − do apparent differences in chaetal ultrastructure indicate the existence of several species in Europe? *Acta Zoologica Academiae Scientiarum Hungaricae*, 59(2), 143–156.

Dusík, D., Hédl, R., & Schlaghamerský, J. (2026). Microannelids (Enchytraeidae, Hrabeillidae) in acidic soils of oak coppices: restoration of coppicing increased soil moisture and microannelid density. *Applied Soil Ecology*, 217, 106576. https://doi.org/10.1016/j.apsoil.2025.106576

Felföldi, T., Dozsa-Farkas, K., Nagy, H., & Hong, Y. (2020). Three new enchytraeid species (Enchytraeidae, Annelida) from mountain soils of Korea and ten species new for the country. *Zootaxa*, 4896(1), 1–45. https://doi.org/10.11646/zootaxa.4896.1.1

Graefe, U. (1984). Eine einfache Methode der Extraktion von Enchytraeiden aus Bodenproben. In *Protokoll des Workshops zu Methoden der Mesofaunaerfassung (Moderation H Koehler) und zu PCP-Wirkungen auf Collembolen und andere Mesofauna-Gruppen, Bremen (Moderation Prof. L. Beck) 22.11.-23.11.84, in Bremen* (pp. 17–17).

Graefe, U., & Schmelz, R. M. (1999). Indicator values, strategy types and life forms of terrestrial Enchytraeidae and other microannelids. In R. M. Schmelz, & K. Sühlo, (Eds.) *Newsletter on Enchytraeidae No. 6. Proceedings of the 3rd International Symposium on Enchytraeidae, Osnabrück, Germany, 3.- 4. July 1998* (pp. 59–67). Universitätsverlag Rasch, Osnabrück.

Healy, B. (1980). Records of Enchytraeidae (Oligochaeta) from western France and the Pyrénées. *Bulletin du Muséum national d'histoire naturelle,* 2(2), 421–443.

Holmstrup, M., Sørensen, J. G., Maraldo, K., Schmidt, I. K., Mason, S., Tietema, A., Smith, A. R., Emmett, B., Schmelz, R. M., Bataillon, T., et al. (2012). Increased frequency of drought reduces species richness of enchytraeid communities in both wet and dry heathland soils. *Soil Biology and Biochemistry*, 53, 43–49.

Holmstrup, M., Schmelz, R. M., Carrera, N., Dyrnum, K., Larsen, K. S., Mikkelsen, T. N., & Beier, C. (2015). Responses of enchytraeids to increased temperature, drought and atmospheric CO2: results of an eight-year field experiment in dry heathland. *European Journal of Soil Biology*, 70, 15–22.

Hrabě, S. (1981). Vodní máloštětinatci (Oligochaeta) Československa [The freshwater Oligochaeta (Annelida) of Czechoslovakia]. *Acta Universitatis Carolinae – Biologica*, 1979: 1–167.

Huhta, V., Räty, M., Ahlroth, P., Hänninen, S. M., Mattila, J., Penttinen, R., & Rintala, T. (2005). Soil fauna of deciduous forests as compared with spruce forests in central Finland. *Memoranda Societatis pro Fauna et Flora Fennica*, 81, 52–70.

Huhta, V., Siira-Pietikäinen, A., Penttinen, R., & Räty, M. (2010). Soil fauna of Finland: Acarina, Collembola and Enchytraeidae. *Memoranda Societatis pro Fauna et Flora Fennica*. 86, 59–82.

Kobetičová, K., & Schlaghamerský, J. (2003). On the efficiency of three schemes of enchytraeid wet funnel extraction. In W. Didden, P. van Vliet (Eds.), *Newsletter on Enchytraeidae No. 8: Proceedings of the 5th International Symposium on Enchytraeidae, Wageningen, The Netherlands, 12–14 April 2002* (pp. 25–31). Wageningen University, Dept. of Soil Quality, Wageningen.

Lagerlöf, J., & Strandh, M. (1997). Hatching of Enchytraeidae (Oligochaeta) from egg cocoons in agricultural soil exposed to different drought regimes-a laboratory study. *Pedobiologia*, 41(4), 334–341. https://doi.org/10.1016/S0031-4056(24)00250-6

Laurén, A., Lappalainen, M., Saari, P., Kukkonen, J. V., Koivusalo, H., Piirainen, S., Setälä, H., Sarjala, T., Bylund, D., Heinonen, J., et al. (2012). Nitrogen and carbon dynamics and the role of Enchytraeid worms in decomposition of L, F and H layers of boreal mor. *Water, Air, & Soil Pollution*, 223(7), 3701–3719. https://doi.org/10.1007/s11270-012-1142-4

Maraldo, K., & Holmstrup, M. (2009). Recovery of enchytraeid populations after severe drought events. *Applied Soil Ecology*, 42(3), 227–235.

Maraldo, K., Schmidt, I. K., Beier, C., & Holmstrup, M. (2008). Can field populations of the enchytraeid, *Cognettia sphagnetorum*, adapt to increased drought stress? *Soil Biology and Biochemistry*, 40(7), 1765–1771.

Maraldo, K., Krogh, P. H., van der Linden, L., Christensen, B., Mikkelsen, T. N., Beier, C., & Holmstrup, M. (2010). The counteracting effects of elevated atmospheric CO2 concentrations and drought episodes: Studies of enchytraeid communities in a dry heathland. *Soil Biology and Biochemistry*, 42(11), 1958–1966.

Martinsson, S., Dózsa-Farkas, K., Rota, E., & Erséus, C. (2017). Placing the forgotten: on the positions of *Euenchytraeus* and *Chamaedrilus* in an updated enchytraeid phylogeny (Clitellata: Enchytraeidae). *Invertebrate Systematics*, 31(1), 85–90. https://doi.org/10.1071/IS16042

Martinsson, S., Rota, E., & Erséus, C. (2015). Revision of *Cognettia* (Clitellata, Enchytraeidae): re-establishment of *Chamaedrilus* and description of cryptic species in the *sphagnetorum* complex. *Systematics and Biodiversity*, 13(3), 257–277. https://doi.org/10.1080/14772000.2014.986555

Miklín, J., & Hradecký, J. (2016). Confluence of the Morava and Dyje Rivers: A century of landscape changes in maps. *Journal of Maps*, 12(4), 630–638. https://doi.org/10.1080/17445647.2015.1068714

Nagy, H., Dózsa-Farkas, K., Hong, Y., & Felföldi, T. (2020). Extending the geographic distribution of *Bryodrilus ehlersi* (Annelida, Enchytraeidae): morphological and molecular comparison of Korean and European specimens. *Acta Zoologica Academiae Scientiarum Hungaricae*, 66(4), 345–360. https://doi.org/10.17109/AZH.66.4.345.2020

Nielsen, C. O. (1955). Studies on Enchytraeidae 5. Factors causing seasonal fluctuations in numbers. *Oikos*, 6(2), 153–169.

Nurminen, M. (1977). Enchytraeidae (Oligochaeta) from the Grossglockner region of the Austrian Alps. *Annales Zoologici Fennici*, 14, 224–227.

Nurminen, M. (1973). Enchytraeidae (Oligochaeta) from the vicinity of the Lake Baikal, Siberia. *Annales Zoologici Fennici*, 10, 478–482.

Nurminen, M. (1980). Notes on the Enchytraeids (Oligochaeta) of the USSR. *Annales Zoologici Fennici*, 17, 175–179.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., et al. (2025). *vegan: Community Ecology Package (Version 2.7-2)* [R package]. https://CRAN.R-project.org/

Palumbi, S. R., Martin, A., Romano, S., Mc-Millan, W. O., Stice, L., & Grabawski, G. (1991). ‚The simple fool's guide to PCR, version 2.0.' Privately published, compiled by S. Palumbi,: University of Hawaii, Honolulu.Payne, R. J., Thompson, A. M., Standen, V., Field, C. D., & Caporn, S. J. (2012). Impact of simulated nitrogen pollution on heathland microfauna, mesofauna and plants. *European Journal of Soil Biology*, 49, 73–79.

Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B. E., & Sohlenius, B. (1980). Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. *Ecological Bulletins*, 32, 419–459.

Petersen, H., & Luxton, M. (1982). A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39(3), 288–388. https://doi.org/10.2307/3544689

Piper, S. R., MacLean, S. F., & Christensen, B. (1982). Enchytraeidae (Oligochaeta) from taiga and tundra habitats

of northeastern USSR. *Canadian Journal of Zoology*, 60(11), 2594–2609.

Pižl, V., & Schlaghamerský, J. (2007). The impact of pedestrian activity on soil annelids in urban greens. *European Journal of Soil Biology*, 43, S68–S71. https://doi.org/10.1016/j.ejsobi.2007.08.004

Pižl, V., Schlaghamerský, J., & Tříska, J. (2009). The effects of polycyclic aromatic hydrocarbons and heavy metals on terrestrial annelids in urban soils. *Pesquisa agropecuaria brasileira*, *44*(8), 1050–1055.

R Core Team. (2025*). R: A language and environment for statistical computing (Version 4.5.1).* [Computer software]. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Römbke, J. (1991). Estimates of the Enchytraeidae (Oligochaeta, Annelida) contribution to energy flow in the soil system of an acid beech wood forest. *Biology and Fertility of Soils*, 11(4), 255–260.

Römbke, J., & Beck, L. (2010). Ecotoxicological evaluation of selected forest plots in Baden-Württemberg (Germany): Influence of emissions of potential toxic substances from a highway on oligochaetes. In S. Schrader, & R. M. Schmelz (Eds.), *Newsletter on Enchytraeidae No 12. Proceedings of the 9th Internationa Symposium on Enchytraeidae*,*14-16 July 2010, Braunschweig, Germany* (pp 27–38). Landbauforschung – vTI Agriculture and Forestry Research, Special Issue 357.

Römbke, J., Bandow, C., Gerlach, A., Jaeschke, B., Schmelz, R. M., Natal-da-Luz, T., Sousa, J. P., Russell, D. J. (2018) Data on the Lumbricidae and Enchytraeidae from six forest sites in Germany and Portugal. *Opuscula Zoologica Budapest*, 48(2), 73–81.

Römbke, J., Jänsch, S., Höfer, H., Horak, F., Roß-Nickoll, M., Russell, D., & Toschki, A. (2013). State of knowledge of enchytraeid communities in German soils as a basis for biological soil quality assessment. *Soil Organisms*, 85(2), 123–146.

Rota, E. (1994). Enchytraeidae (Oligochaeta) of western Anatolia: taxonomy and faunistics. *Italian Journal of Zoology*, 61(3), 241–260.

Rota, E. (1995). Italian Enchytraeidae (Oligochaeta). I. *Italian Journal of Zoology*, 62(2), 183–231.

Rota, E., & Healy, B. (1994). The enchytraeid fauna of North Africa. *Hydrobiologia*, 278(1), 53–66.

Rota, E., Caruso, T., & Bargagli, R. (2014). Community structure, diversity and spatial organization of enchytraeids in Mediterranean urban holm oak stands. *European Journal of Soil Biology*, 62, 83–91.

Rothröckl, T., & Škorpík, M. (2008). Národní park Podyjí [The Podyjí/Thaya River Basin National Park]. *Ochrana přírody,* 2. 2–5. [In Czech, English Summary].

Saifutdinov, R. A., Degtyarev, M. I., Korobushkin, D. I., Artemieva, S. M., Byzov, P. S., Danilova, M. A., Dits, A. A., Ermokhina, K. A., Garibian, P. G., Gorbunova, A. Y. et al. (2025). Taxonomic diversity and abundance of enchytraeids (Annelida, Clitellata, Enchytraeida) in the Northern Palaearctic. 2. European Russia. *Biodiversity Data Journal*, *13*, e144992.

Sayers, E.W., Beck, J., Bolton, E. E, Brister, J. R., Chan, J., Connor, R., Feldgarden, M., Fine, A. M., Funk, K., Hoffman et al. (2025). Database resources of the National Center for Biotechnology Information in 2025. Nucleic Acids Res. 53(D1), D20–D29. doi: 10.1093/nar/gkae979

Schaefer, M. (1991). The animal community: diversity and resources. In E. Röhrig, & B. Ulrich (Eds.) *Ecosystems of the World 7: Temperate Deciduous Forests* (pp. 51–120). Elsevier Science, Amsterdam.

Schlaghamerský, J. (2007). The small annelids (Enchytraeidae, Tubificidae, Aeolosomatidae) of a South Moravian floodplain forest with disturbed water regime. In J., Schlaghamerský, (Ed.)*, Newsletter on Enchytraeidae No. 10: Proceedings of the 7th International Symposium on Enchytraeidae; May 25–28, 2006, Brno, Czech Republic* (pp. 123–133). Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia 110. Masaryk University, Brno.

Schlaghamerský, J. (2010). The small annelids (Annelida: Enchytraeidae, Rhyacodrilinae, Aeolosomatidae) in soils of three forests in the White Carpathians (Czech Republic). *Acta Societatis Zoologicae Bohemicae*, 74, 103–115.

Schlaghamerský, J. (2013). Enchytraeid assemblages (Annelida: Clitellata: Enchytraeidae) of two old growth forests in the Porcupine Mountains (Michigan, USA). *Soil Organisms*, 85(2), 85–96.

Schlaghamerský, J. (2023a). Enchytraeidae of neglected and reestablished coppices in Podyjí National Park, Czechia [Data set]. https://portal.edaphobase.org

Schlaghamerský, J. (2023b). Enchytraeidae of deciduous forest in valley of Daníž stream; Enchytraeidae of exposed stones in Quercus forest, Podyjí NP, Czechia [Data set]. https://portal.edaphobase.org

Schlaghamerský, J. (2023c). Enchytraeidae of Havraníky heathland, Podyjí NP Czechia [Data set]. https://portal.edaphobase.org

Schlaghamerský, J. (2023d). Enchytraeidae from dead wood in deciduous forest in Daníž stream valley, Podyjí NP Czechia [Data set]. https://portal.edaphobase.org

Schlaghamerský, J., & Kobetičová, K. (2005). A small annelid community (Enchytraeidae, Tubificidae, Aeolosomatidae) during meadow restoration on arable land and in a nearby well-preserved meadow. *Proceedings of the Estonian Academy of Sciences, Biology and Ecology*, 54(4), 323–330.

Schlaghamerský, J., & Kobetičová, K. (2006). The impact of cattle pasturage on small annelids (Annelida: Enchytraeidae, Tubificidae, Aeolosomatidae) in grasslands of the White Carpathians (Czech Republic). *European Journal of Soil Biology*, 42, S305–S309. https://doi.org/10.1016/j.ejsobi.2006.07.037

Schlaghamerský, J., & Pižl, V. (2009). Enchytraeids and earthworms (Annelida: Clitellata: Enchytraeidae,

Lumbricidae) of parks in the city of Brno, Czech Republic. *Soil Organisms*, 81(2), 145–173.

Schlaghamerský, J., & Šídová, A. (2007). On a species-poor enchytraeid community of peculiar composition. In J. Schlaghamerský (Ed.)*, Newsletter on Enchytraeidae No. 10: Proceedings of the 7th International Symposium on Enchytraeidae; May 25–28, 2006, Brno, Czech Republic* (pp. 183–192). Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia 110. Masaryk University, Brno.

Schlaghamerský, J., & Šídová, A. (2009). Dynamics and vertical distribution of a *Hrabeiella periglandulata* (Annelida) population in South Moravia, Czech Republic. *Pesquisa Agropecuária Brasileira*, 44, 917–921. https://doi.org/10.1590/S0100-204X2009000800017

Schlaghamerský, J., Eisenhauer, N., & Frelich, L. E. (2014). Earthworm invasion alters enchytraeid community composition and individual biomass in northern hardwood forests of North America. *Applied Soil Ecology*, 83, 159–169. https://doi.org/10.1016/j.apsoil.2013.09.005

Schlaghamerský, J., Khodabocus, J.B., & Pižl, V. (2009): Has *Tilia* x *euchlora* a detrimental effect on soil annelids in urban greens? In K., Tajovský, J. Schlaghamerský, & V. Pižl (Eds.), *Contributions to Soil Zoology in Central Europe III* (pp. 141–145). ISB BC AS CR, v.v.i., České Budějovice.

Schlaghamerský, J., Šídová, A., & Pižl, V. (2007). From mowing to grazing: Does the change in grassland management affect soil annelid assemblages? *European Journal of Soil Biology*, 43, S72–S78. https://doi.org/10.1016/j.ejsobi.2007.08.054

Schmelz, R. M., & Collado, R. (2010). A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta). *Soil Organisms*, 82(1), 1–176.

Schmelz, R. M., Arslan, N., Bauer, R., Didden, W., Dózsa-Farkas, K., Graefe, U.,Panchenko, I., Pokarzhevski, A., Römbke, J., Schlaghamerský, J., et al. (2005). Estonian Enchytraeidae (Oligochaeta) 2. Results of a faunistic workshop held in May 2004. *Proceedings of the Estonian Academy of Sciences,* 54(4), 255–270.

Schrader, S., Langmaack, M., & Helming, K. (1997). Impact of Collembola and Enchytraeidae on soil surface roughness and properties. *Biology and Fertility of Soils*, 25(4), 396–400. https://doi.org/10.1007/s003740050331

Sedláková, I., & Chytrý, M. (1999). Regeneration patterns in a Central European dry heathland: effects of burning, sod-cutting and cutting. *Plant Ecology*, 143(1), 77–87. https://doi.org/10.1023/A:1009807411654

Serbource, C., Sammartino, S., Cornu, S., Papillon, J., Adrien, J., & Pelosi, C. (2025). Enchytraeids: Small but important ecosystem engineers. *Geoderma*, 453, 117150. https://doi.org/10.1016/j.geoderma.2024.117150

Šídová, A., & Schlaghamerský, J. (2007). The impact of high game density on enchytraeids in a mixed forest. In K., Tajovský, J., Schlaghamerský, & V., Pižl (Eds.), *Contributions to Soil Zoology in Central Europe II* (pp. 147–152). ISB BC AS CR, České Budějovice.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H., & Flook, P. (1994). Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain-reaction primers. *Ann. Entomol. Soc. Am.* 87, 651–701. https://doi.org/10.1093/aesa/87.6.651.

Springett, J. A., Brittain, J. E., & Springett, B. P. (1970). Vertical movement of Enchytraeidae (Oligochaeta) in moorland soils. Oikos 21, 16–21.

Standen, V., Graefe, U., Schmelz, R. M., & Schlaghamerský, J. (2009). Diversity of Enchytraeidae (Annelida: Clitellata) in habitats within the Magnesian Limestone Plateau of County Durham, UK. *Soil Organisms*, 81(2), 137–143.

Swift, M. J., Heal, O. W., & Anderson, J. M. (1979). *Decomposition in Terrestrial Ecosystems.* Blackwell, Oxford.

Tajovský, K., Pižl, V., & Matějka, K. (2024). Structure and changes in the communities of millipedes (Diplopoda), centipedes (Chilopoda), terrestrial isopods (Oniscidea) and Earthworms (Lumbricidae) at selected localities in Podyjí National Park. *Thayensia*, 21, 21–73. [In Czech, English abstract].

Toschki, A., Burkhardt, U., Haase, H., Höfer, H., Jänsch, S., Oellers, J., Römbke, J., Roß-Nickoll, M., Salamon, J., Schmelz, R. M., et al. (2021). Die Edaphobase-Länderstudien: Synökologische Untersuchungen von Bodenorganismen in einem Biotop- und Standortgradienten in Deutschland 2014–2018. *Peckiana* 14, 1–367.

van Vliet, P. C. J., West, L. T., Hendrix, P. F., & Coleman, D. C. (1993). The influence of Enchytraeidae (Oligochaeta) on the soil porosity of small microcosms. In L. Brussaard, & M. J. Kooistra (Eds.), *Soil structure/soil biota interrelationships* (pp. 287–299). Elsevier Science, Amsterdam.

Vrška, T., Janík, D, Pálková, M., Adam, D., & Trochta, J. (2017). Below- and above-ground biomass, structure and patterns in ancient lowland coppices. *iForest Biogeosciences and Forestry*, 10, 23–31. https://doi.org/10.3832/ifor1839-00910.3832/ifor183

Vymazalová, P., Košulič, O., Hamřík, T., Šipoš, J., & Hédl, R. (2021). Positive impact of traditional coppicing restoration on biodiversity of ground-dwelling spiders in a protected lowland forest. *Forest Ecology and Management*, 490, 119084. https://doi.org/10.1016/j.foreco.2021.119084

Wickham, H. (2016). *ggplot2: Create elegant data visualisations using the grammar of graphics (Version 4.0.3)* [R package]. Springer-Verlag, New York. ISBN 978-3-319-24277-4. https://CRAN.R-project.org/package=ggplot2

Zaitsev, A. S., Degtyarev, M. I., Korobushkin, D. I., Saifutdinov, R. A., Danilova, M. A., Medvedev, D. A., Zvychaynaya, E. Y., & Gongalsky, K. B. (2026). Species richness of Enchytraeidae (Enchytraeidae: Clitellata: Annelida) in the center and east of northern Palaearctic. *Applied Soil Ecology*, 217, 106637.