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RESEARCH ARTICLE

# Microannelids (Enchytraeidae, Naididae) in the topsoil of periodically wet deciduous forests

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## Abstract

The topsoil is both a habitat for soil organisms and the product of their activity. Specific topsoil conditions are therefore linked to specific characteristics of the decomposer community. The aim of this study was to characterise the poorly studied aero-hydromorphic humus forms of periodically wet forest sites concerning the microannelid community. We collected vertically stratified samples at 64 sample points distributed across two forest sites on Stagnosols south-east of Münster (Northrhine-Westphalia, Germany). The microannelid community appeared to be adapted to periodic waterlogging, including species preferring well drained conditions as well as species indicating wet conditions. Of these, the most common were *Cognettia glandulosa* s.l., *Marionina simillima*, *Marionina filiformis*, *Marionina argentea* s.l., and *Cernosvitoviella atrata*. Species composition depended on humus form: Moist Moder hosted fewer moisture-indicating species than Moist Mull, as most of these species are acidity sensitive. Repeated sampling at two intensive measurement stations, where soil water tension was measured, showed high temporal variability of species composition. In April 2023, total abundance was significantly reduced after a five-month period of waterlogging compared to October 2022, and the population consisting mainly of wetness indicators. Another six months later, in October 2023, abundance as well as species number had recovered and dominance of wetness indicators decreased. Depending on soil moisture, vertical distribution of microannelids varied strongly over time. During waterlogging animals concentrated in the uppermost few centimetres of the topsoil profile, whereas during summer drought wetness indicators predominantly occurred in deeper layers. Linking the assessment of aero-hydromorphic humus forms with recording the microannelid community enables a more comprehensive description of the topsoil condition. Our results show that it is worthwhile to pay closer attention to aero-hydromorphic humus forms and their characteristic soil fauna, possibly also within the context of monitoring programs. In doing so, the specific characteristics of periodically wet soils should be taken into account when designing the sampling methodology.

**Keywords** Enchytraeids | aero-hydromorphic humus forms | forest floor | indicator species | waterlogging | potworms

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# 1 Introduction

Soil life is fundamentally connected to the topsoil, which is affected by environmental conditions such as soil properties, vegetation, climate and soil water regime. Anthropogenic impacts, including land-use intensity, eutrophication, acidification, and climate change further determine the formation of topsoil horizons. The topsoil, comprising organic surface layers plus mineral topsoil, is classified as humus form. Current classification systems of humus forms recognize the role of soil animals by using traces of their activity for the description of humus horizons (Wachendorf et al. 2023). Mull humus forms are characterized by a high activity of soil organisms incorporating dead organic matter into the mineral soil, whereas moder and mor humus forms are characterized by the accumulation of highly decomposed dead organic matter above the mineral soil in the form of an OH horizon (Ponge 2003). The increasing thickness of organic surface horizons within the series Mull - Moder - Mor indicates decreasing bioturbation due to decreasing soil animal activity and diversity.

The formation of the organic layer is strongly influenced by the soil water regime and thus the prevalence of oxic or anoxic conditions (Erber & Broll 2005, Frank et al. 2023). In aeromorphic humus forms, oxic conditions prevailing in the topsoil support litter decomposition by aerobic soil organisms. In hydromorphic humus forms, anoxic conditions predominate due to groundwater being near the soil surface more or less permanently. Here, organic matter decomposition is limited, causing the formation of peat. Conditions with groundwater or stagnant water occurring periodically up to the soil surface (mostly in winter / spring), alternating with periods with a drying out topsoil (during growing season), support the development of aero-hydromorphic humus forms (Wachendorf et al. 2023). In these soils, the periods of water saturation are too short to allow for the formation of peat, but due to the temporarily anoxic conditions, litter decomposition is slowed down and the thickness of the humus layer is often increased. Further, litter components often take on a greyish-black colour and subsoil horizons show hydromorphic features such as mottles (Frank et al. 2023). The term “Moist” is prefixed to the names of aero-hydromorphic humus forms, e.g. “Moist Moder” (AG Boden 2024).

Enchytraeids contribute substantially to organic matter decomposition and can reach considerable abundance especially in acid forest soils (Abrahamsen 1972, Kapusta et al. 2003, Makulec 1983, Schaefer & Schauermann 1990). They are also involved in the formation of micro-structures and pores (Didden 1990, Schrader et al. 1997). While enchytraeids avoid permanently dry soils due to their lack of significant protection against desiccation, it is well known that they can inhabit permanently waterlogged habitats such as bogs and fens (Healy & Bolger 1984, Schenková et al. 2018, Standen 1973). They have also developed strategies to cope with periodically wet and dry soils, such as vertical migration to soil layers with adequate conditions (Lagerlöf & Strandh 1997, Plum & Filser 2005, Springett et al. 1970). The ability to survive extreme conditions, such as waterlogging or acidification, varies greatly depending on the species. For a number of enchytraeid species, tolerance or preference of wet soils is well documented (Healy & Bolger 1984, Beylich & Graefe 2002). Especially in wet soils, species of other families of the Annelida, e.g. Naididae, are frequently found using the standard method for collecting enchytraeids. As these species are partly included in the data presented here, we will in the following use the term microannelids instead of enchytraeids.

Aero-hydromorphic humus forms recently receive more attention in the updated German field guide for soil mapping (AG Boden 2024). However, there is still limited knowledge of soil-biological properties in relation to these humus forms’ properties, although humus forms can be considerably affected by climate change with respect to water retention, carbon sequestration and habitat function (Lang et al. 2026). Within the project BioFeuchtHumus, relations between topsoil parameters, vegetation and the decomposer community were studied in periodically wet deciduous forest stands in Northwestern Germany (Frank et al. 2024). These sites can be characterized as moderately well-drained (Tab. 1), with soil water being removed

**Table 1**. Drainage classes (according to Soil Survey Staff 2024), corresponding soil properties and associated humus form.

| Natural drainage class | Soil properties | Humus form |
|---|---|---|
| well drained | water is removed from soil readily; wetness does not inhibit growth of mesophytic plants | aeromorphic |
| moderately well drained | water is removed from soil somewhat slowly; soil is wet for only a short time within rooting depth, but growth of mesophytic plants can be affected | aero-hydromorphic |
| poorly drained to varying degrees | soil is wet at shallow depths for significant periods; growth of mesophytic plants is restricted | hydromorphic |

from the rootzone slowly for limited periods due to low hydraulic conductivity (Soil Survey Staff 2024). Thus, waterlogging here is the effect of high precipitation on soil with subsoil layers of low water permeability. These moderately well drained forest sites, with their aero-hydromorphic humus forms, are not considered wetlands because periods with well-aerated conditions in the topsoil prevail. They represent a transitional situation between well drained sites and poorly drained wetland sites, such as carrs and fens.

Periodically wet deciduous forests might be particularly affected by climatic change (Fornfeist et al. 2024, Frank et al. 2024). In order to identify possible changes in the topsoil condition in these forest ecosystems, it is necessary to understand the typical features of aero-hydromorphic humus forms. To contribute to the characterization of the decomposer community in aero-hydromorphic humus forms, we (1) assessed the species composition of microannelids and (2) investigated the vertical distribution as well as (3) temporal variation of microannelid occurrence.

# 2 Material and Methods

## 2.1 Study area

The study was carried out in the Münsterland region, in the federal state of Northrhine-Westphalia (Germany). In this region, two deciduous forest sites, 12 km apart, were chosen for investigation: 1. Inkmannsholz (WGS84: 51.8584, 7.6009; 4 ha) and 2. Wolbecker Tiergarten (WGS84: 51.9030, 7.7411; 22 ha). The elevation of the study sites was 53–61 m a.s.l. (Geobasis NRW). Mean annual precipitation was about 782 mm, mean annual temperature was 9.9°C (long-term average 1981–2010; DWD 2026, weather station Münster Airport, situated 25 to 30 km from the study sites). The soil-forming substrate of both study sites consists of quaternary sediments of at least 3 m depth, with sandy sediments overlying clayey-loamy sediments. Due to the low water permeability of the latter, moderately well drained soils (Stagnosols) are prevailing on these sites. Mean pH($CaCl_2$) values were 4.6 for Moist L Mull, 4.00 for Moist F Mull, and 3.4 for Moist Moder. Dominating tree species were *Quercus robur* (pedunculate oak) and *Carpinus betulus* (common hornbeam), the phytosociological vegetation class being a *Stellario-Carpinetum* (Fornfeist et al. 2024). In our study, the focus was on the differences between moist humus forms, not between the two sampling sites. Thus, the results from both forest sites were pooled and not analysed separately.

## 2.2 Sampling set-up

In the initial phase of the project, humus forms were mapped on the study sites to locate spots with aero-hydromorphic humus forms (Frank et al. 2024). Based on this mapping, 56 sampling points with aero-hydromorphic humus forms were selected, distributed over the two study sites (Site 1: n = 36, Site 2: n = 20). The unequal number of sampling points reflects the natural spatial distribution and patch density of aero-hydromorphic humus forms, which occurred in a tighter mosaic at Site 1 and were more dispersed and scarcer at Site 2. At these 56 sampling points, samples for recording the microannelid community were taken once within the years 2022 and 2023, in spring or autumn. Sampling all points at the same date was not possible, as species determination requires live worms. The aim was to store the soil samples for no longer than 4–6 weeks to minimize mortality and hatching during storage (Didden 2002, ISO 23611-3:2019). In addition, there were further 8 sampling points at two intensive measurement stations (IMS), with one station set up in each study area to measure soil water tension (pF) and soil temperature. Each of the two IMS comprised four measurement points for water tension (distance between points of each station: maximum 100 m), at which also microannelid samples were taken, totalling in 64 (56 + 8) soil fauna sampling points. Only the 8 sampling points next to the intensive measurement stations were sampled repeatedly for microannelids (October 2022 / April 2023 / October 2023) in order to cover temporal variability, including water-saturated as well as dry conditions, and to relate zoological data to pF measurements. The studied forest sites show a small-scale pattern of varying humus forms, vegetation, soil moisture and terrain elevation. Note that our primary objective was not to compare the two forest sites as independent treatments, but rather to analyse the microannelid communities inhabiting these specific humus forms across their natural gradient of occurrence. Consequently, the proportional representation per site is a result of mapping reality rather than an experimental site comparison.

Sampling was done by a soil corer with a diameter of 5 cm to a depth of 15 ± 3 cm (depending on soil resistance), divided into 4–5 vertical sub-samples of 3–5 cm thickness, depending on thickness of humus horizons, to assess the vertical distribution of microannelids. At each sampling point, one sample was taken. Each sample profile was recorded and photographed for documentation (Figs S1–S3). Soil samples were kept cool (4–10 °C) until extraction. Microannelids were extracted from each vertical sub-sample separately, using a wet funnel extraction method without heating (ISO 23611-3:2019), for 48 h, with the sample being transferred to fresh water

once after 18–24 h. Individuals were identified alive with a light microscope with differential interference contrast (DIC), using the keys by Schmelz (2003) and Schmelz and Collado (2010).

## 2.3 Data analyses

The 64 sampling points were divided into three groups according to their humus form: Moist L Mull, Moist F Mull and Moist Moder. The data were analysed predominantly in relation to these three humus form groups. IMS' are represented by one sampling date only (April 2023) in the comparisons of humus form types so as not to give these locations undue weight. Statistical analysis was executed with *jamovi* (version 2.6.26.0, module jmv; The jamovi project 2024). Checking for differences in species richness between the three humus form types was done by ANOVA (with Tukey Post hoc test). Differences in abundance between the three humus form types were tested using the Kruskal-Wallis Test (with Dwass-Steel-Critchlow-Fligner Post-hoc-test) as data were not normally distributed. This test was also applied for checking differences between the data of the three samplings dates at the IMS (temporal variability), and for checking differences of dominance depending on humus form for six species.

Species were assigned indicator values for soil moisture and soil reaction according to Graefe & Schmelz (1999) and Beylich & Graefe (2002). The species were grouped according to their indicator values (reaction figure: three categories, moisture figure: two categories; Tab. 2). Concerning indicators of wetness, a fairly broad group was defined, ranging from species preferring constantly moist soils to species tolerating permanently wet soils with at least periodically oxygen deficiency, and including aquatic species. We considered this broad range reasonable, as information on soil moisture in the context of soil zoological studies is often much more vague than information on soil reaction (pH) which makes the moisture indicator values of species subject to a higher degree of uncertainty. Further, the species complexes of *Cognettia glandulosa* s.l and *Marionina argentea* s.l. can be considered to fit in here despite the missing determination of the cryptic species (see section 2.4).

## 2.4 Taxonomic notes

We do not follow Schmelz & Collado (2010) concerning *Enchytronia parva* Nielsen & Christensen, 1959 sensu lato including *Enchytronia minor* Möller 1971. Instead we tentatively distinguished *E. parva* (2 preclitellar nephridia, intestinal diverticula distally attached to intestine) from *E. minor* (3 preclitellar nephridia, intestinal diverticula larger and distally not attached to intestine), since these differences between the two variants were striking in the specimens examined. We regard this distinction as provisional and are aware that it is open to criticism, as the original descriptions do not specify the number of preclitellar nephridia.

The evidence of *Buchholzia simplex* was based on a single specimen. The occurrence of this species in Northwestern Germany should be confirmed by further studies.

For practical reasons (reduction of workload) the species complexes of *Cognettia sphagnetorum*, *Cognettia glandulosa* and *Marionina argentea* were

**Table 2.** Indicator values for soil moisture and soil reaction according to Graefe & Schmelz (1999) and Beylich & Graefe (2002). Even numbers for intermediate levels. For grouping of wetness indicators, reference is made to drainage classes according to table 1.

| R | Reaction figure | grouping | M | Moisture figure | grouping |
|---|---|---|---|---|---|
| 1 | Indicator of extreme acidity | R 1–3: Indicators of strong acidity | 5 | Indicator of well-aerated soils, mainly on moderately moist soils | M 5: Indicators of well drained soils |
| 2 | | | 6 | | M 6–11: Indicators of moderately well drained to very poorly drained, moist to wet soils |
| 3 | Acidity indicator, mainly in acid soils, but exceptionally up to the neutral range | | 7 | Moisture indicator, mainly on constantly moist, but not wet soils | |
| 4 | | R 4–6: Indicators of moderate acidity | 8 | | |
| 5 | Indicator of moderate acidity, only occasionally in strongly acid or neutral soils | | 9 | Wetness indicator, often on water-saturated, badly aerated soils | |
| 6 | | | 10 | | |
| 7 | Indicator of slightly acid to slightly alkaline conditions | R 7: Indicators of slight acidity to neutral conditions | 11 | Aquatic species; in soils indicator of subaqueous conditions | |
| x | Broad amplitude regarding soil acidity or unknown behaviour | | x | Broad amplitude regarding soil moisture or unknown behaviour | |

determined on the sensu lato (s.l.) level only in this study. In the following, we consider the restraints on the application of indicator values assigned to these species complexes.

*Cognettia glandulosa* sensu lato was shown by Martinsson et al. (2015a, b) to consist of two until then cryptic species: *Cogn. glandulosa* sensu stricto (s. str.) and *Cogn. varisetosa*. However, the authors admit that no characters completely separate the species, or in other words: "These two species overlap morphologically, and their identification may not always be possible using morphology alone" (Martinsson 2019). Based on this statement, we decided to dispense with this distinction. This also seemed reasonable to us in the context of our approach, which is based on distinguishing between species indicating well drained soils as opposed to species indicating moist to wet soils. As far as is known, *Cogn. varisetosa* occurs mainly in moist to wet soils while *Cogn. glandulosa* s. str. can be regarded as an aquatic species. Thus, both species fall in the broad group of species indicating wetness to some extent (Tab. 2). Discriminating between the two species would not have made a significant difference for this approach.

*Cognettia sphagnetorum* s.l. was split up into four species: *Cogn. sphagnetorum* s. str., *Cogn. pseudosphagnetorum*, *Cogn. chlorophila* and *Cogn. chalupskyi* (Martinsson et al. 2015a). The former two are a "cryptic species pair that can only be separated using molecular methods" (Martinsson 2019). However, the limitation to *Cogn. sphagnetorum* s.l. introduces a degree of uncertainty into the indicator approach as *Cogn. chlorophila* seems to be much less moisture dependent than the other three species of the complex. This is probably the reason why *Cogn. sphagnetorum* s.l. was reported to be tolerant of a wide range of soil moisture levels by many studies, resulting in Graefe & Schmelz (1999) assigning it a moisture indicator value of "x." The findings in this study regarding *Cogn. sphagnetorum* s.l. in relation to soil moisture should therefore be viewed in the light of this caveat.

In contrast to the *Cognettia* species, *Marionina argentea* s.l. was split up into four species without support by molecular data (Rota 2013). From our experience, the combination of discernible characters quite often does not correspond satisfactorily with one of Rota's descriptions nor those of another similar species, *Marionina sambugarae*, described by Martin et al. (2015), so that determination remains somewhat dubious. As habitats hosting the species mentioned by Rota (2013) are restricted to moist, damp, wet and littoral sites, and *Mar. sambugarae* is a stygobiont species, we consider all these species falling into the broad group of "indicators of moist to wet soils" according to our approach. We therefore considered it acceptable to refrain from distinction within the *Marionina argentea* s.l. complex.

Regarding soil acidity, no indication of different habitat requirements of the newly established species of the above mentioned species complexes was given by the corresponding authors (Martinsson et al. 2015a, b, Rota 2013). Furthermore, several species from a species complex have been recorded at the same location on some occasions (e.g. *M. argentea* s.l.: Toschki et al. 2021; *Cogn. sphagnetorum* s.l.: own unpublished data). Therefore, we assume that limiting the determination to species complexes (s.l.) will have no substantial impact on the conclusions drawn concerning the acidity indicator groups.

## 3 Results

The total number of species recorded, including all plots and sampling dates, was 55. Naididae were represented by *Rhyacodrilus falciformis* and at least one other species of *Rhyacodrilus* (unidentified juvenile specimen). Species

**Table 3.** Microannelid species number and dominance of indicators of wetness and indicators of strong acidity, differentiated according to humus form. Different superscript letters indicate significant differences with $p \leq 0.05$. Basic statistics see table S1.

| Parameter | | Moist L Mull | Moist F Mull | Moist Moder |
|---|---|---|---|---|
| | | n = 28 | n = 17 | n = 19 |
| Microannelid species (total) | | 31 | 39 | 24 |
| Microannelid species (per sampling point) | mean | 7.1 [a] | 8.1 [a] | 4.9 [b] |
| | sd | 3.2 | 2.4 | 2.9 |
| Microannelid abundance (individuals per sampling point) | mean | 66.1 [a] | 110.7 [b] | 127.6 [ab] |
| | sd | 65.7 | 79.9 | 128.4 |
| Microannelids: Indicators of wetness (dominance %) | | 48.1 | 26.7 | 10.0 |
| Microannelids: Indicators of strong acidity (dominance %) | | 33.9 | 60.0 | 87.8 |

**Table 4**. Frequency of species shown for the total number of sampling points (n = 64) and for the three humus form types separately. R: Reaction figure, M: Moisture figure (see table 2). *: Juveniles, not identified to species level; **: Species not yet formally described.

| Species, ordered according to indicator values | M | R | Frequency (%) | | | | |
|---|---|---|---|---|---|---|---|
| | | | Total | Moist L Mull | Moist F Mull | Moist Moder | |
| *Achaeta brevivasa* Graefe, 1980 | **5** | **1** | 1.6 | | 5.9 | | Indicators of strong acidity |
| *Marionina clavata* Nielsen & Christensen, 1961 | **5** | **1** | 12.5 | | 11.8 | 31.6 | |
| *Achaeta gemmata* Schmelz, Chen & Jozefowska, 2024 | **5** | **2** | 3.1 | | 5.9 | 5.3 | |
| *Cognettia sphagnetorum* s.l. (Vejdovský, 1878) | **x** | **2** | 79.7 | 67.9 | 88.2 | 89.5 | |
| *Achaeta aberrans* Nielsen & Christensen, 1961 | **5** | **3** | 25.0 | 7.1 | 41.2 | 36.8 | |
| *Achaeta camerani* (Cognetti, 1899) | **5** | **3** | 18.8 | 14.3 | 23.5 | 21.1 | |
| *Achaeta danica* Nielsen & Christensen, 1959 | **5** | **3** | 20.3 | 17.9 | 23.5 | 21.1 | |
| *Mesenchytraeus pelicensis* Issel, 1905 | **5** | **3** | 4.7 | | 5.9 | 10.5 | |
| *Mesenchytraeus sanguineus* Nielsen & Christensen, 1959 | **9** | **3** | 1.6 | | | 5.3 | |
| *Achaeta* sp. (affi) ** | **5** | **4** | 3.1 | | 5.9 | 5.3 | Indicators of moderate acidity |
| *Cognettia cognettii* (Issel, 1905) | **x** | **4** | 3.1 | | 5.9 | 5.3 | |
| *Oconnorella cambrensis* (O'Connor, 1963) | **5** | **4** | 6.3 | 3.6 | 5.9 | 10.5 | |
| *Enchytraeus norvegicus* Abrahamsen, 1969 | **5** | **5** | 3.1 | 3.6 | 5.9 | | |
| *Marionina simillima* Nielsen & Christensen, 1959 | **6** | **5** | 62.5 | 57.1 | 88.2 | 47.4 | |
| *Achaeta* sp. (circ) ** | **7** | **5** | 6.3 | | 11.8 | 10.5 | |
| *Marionina filiformis* Nielsen & Christensen, 1959 | **9** | **5** | 32.8 | 17.9 | 29.4 | 57.9 | |
| *Enchytronia parva* Nielsen & Christensen, 1959 | **5** | **6** | 7.8 | 7.1 | 11.8 | 5.3 | |
| *Oconnorella tubifera* (Nielsen & Christensen, 1959) | **5** | **6** | 1.6 | | 5.9 | | |
| *Marionina vesiculata* Nielsen & Christensen, 1959 | **7** | **6** | 12.5 | 14.3 | 23.5 | | |
| *Cognettia glandulosa* s.l. (Michaelsen, 1888) | **9** | **6** | 60.9 | 71.4 | 70.6 | 36.8 | |
| *Achaeta* sp. (dzwi) ** | **5** | **7** | 1.6 | | 5.9 | | Indicators of slight acidity to neutral conditions |
| *Enchytronia minor* Möller, 1971 | **5** | **7** | 1.6 | 3.6 | | | |
| *Enchytronia pygmaea* Graefe & Schmelz, 2017 | **5** | **7** | 1.6 | | | 5.3 | |
| *Stercutus niveus* Michaelsen, 1888 | **5** | **7** | 7.8 | 7.1 | 17.6 | | |
| *Achaeta unibulba* Graefe, Dózsa-Farkas & Christ., 2005 | **6** | **7** | 40.6 | 75.0 | 29.4 | | |
| *Enchytronia* sp. (omni) ** | **6** | **7** | 17.2 | 35.7 | 5.9 | | |
| *Fridericia cylindrica* Springett, 1971 | **6** | **7** | 15.6 | 17.9 | 23.5 | 5.3 | |
| *Marionina argentea* s.l. (Michaelsen, 1889) | **8** | **7** | 31.3 | 57.1 | 23.5 | | |
| *Rhyacodrilus falciformis* Bretscher, 1901 | **8** | **7** | 15.6 | 21.4 | 17.6 | 5.3 | |
| *Rhyacodrilus* sp. juv. * | **9** | **7** | 14.1 | 10.7 | 29.4 | 5.3 | |
| *Mesenchytraeus armatus* (Levinsen, 1884) | **9** | **7** | 7.8 | 10.7 | 5.9 | 5.3 | |
| *Enchytraeus buchholzi* Vejdovský, 1879 | **x** | **7** | 31.3 | 50.0 | 35.3 | | |
| *Enchytraeus dichaetus* Schmelz & Collado, 2010 | **x** | **7** | 1.6 | 3.6 | | | |
| *Fridericia benti* Schmelz, 2002 | **x** | **7** | 9.4 | 17.9 | 5.9 | | |
| *Fridericia bulboides* Nielsen & Christensen, 1959 | **x** | **7** | 3.1 | 7.1 | | | |
| *Fridericia galba* (Hoffmeister, 1843) | **x** | **7** | 7.8 | 14.3 | 5.9 | | |
| *Fridericia perrieri* (Vejdovský, 1878) | **x** | **7** | 1.6 | 3.6 | | | |
| *Fridericia striata* (Levinsen, 1884) | **x** | **7** | 1.6 | | 5.9 | | |
| *Fridericia ulrikae* Rota & Healy, 1999 | **x** | **7** | 3.1 | 7.1 | | | |
| *Fridericia* sp. juv. * | **x** | **7** | 37.5 | 46.4 | 52.9 | 10.5 | |
| *Henlea perpusilla* Friend, 1911 | **x** | **7** | 9.4 | 14.3 | 11.8 | | |
| *Cernosvitoviella atrata* (Bretscher, 1903) | **8** | **x** | 28.1 | 17.9 | 35.3 | 36.8 | Indifferent |
| *Achaeta* sp. (trin) ** | **x** | **x** | 1.6 | | 5.9 | | |
| *Achaeta* sp. juv. * | **x** | **x** | 4.7 | | 5.9 | 10.5 | |
| *Buchholzia simplex* Nielsen & Christensen, 1963 | **x** | **x** | 1.6 | | 5.9 | | |
| *Mesenchytraeus gaudens* Cognetti, 1903 | **x** | **x** | 3.1 | | 11.8 | | |
| *Mesenchytraeus* sp. juv. * | **x** | **x** | 1.6 | 3.6 | | | |

richness of microannelids increased along the sequence from Moist Moder to Moist L Mull to Moist F Mull (Tab. 3). The mean number of species per sampling point increased in the same order, with Moist Moder showing a significantly lower species number than the mull humus forms. The abundance of microannelids was increasing from Moist L Mull to Moist Moder. The dominance of indicators of moist to wet soils was lowest in Moist Moder and highest in Moist L Mull, whilst the indicators of strong acidity showed the opposite trend.

Regarding all 64 sampling points, highest frequencies were reached by *Cognettia sphagnetorum* s.l., a species indicating strong acidity (Tab. 4). The wide range of tolerance with regard to soil moisture conditions is likely due to the fact that the species within the complex *Cognettia sphagnetorum* s.l. were not distinguished here. Most other species showing a frequency of > 25 % were indicators of wetness. Considering the three types of humus forms, it becomes obvious that the frequency of wetness indicators was lower in moder humus forms than in mull humus forms (Moist Moder: 84 %, Moist F Mull: 100 %, Moist L Mull: 96 %). Indicators of strong acidity were less frequent or missing in Moist L Mull, while indicators of slight acidity were present to a very limited extent only in Moist Moder. Indicators of wetness were distributed unevenly regarding the reaction figure of the species: *Mesenchytraeus sanguineus* was the only species indicating wetness and simultaneously strong acidity. On the other hand, among the species indicating moderate to slight acidity, several indicators of moisture or wetness according to Tab. 2 occurred (*Cognettia glandulosa* s.l., *Marionina argentea* s.l. *Marionina filiformis, Achaeta unibulba, Marionina simillima*).

Figure 1 shows the dominance of six frequent species in relation to the respective humus forms. *Marionina argentea* s.l., being acidity sensitive, did not occur in Moist Moder at all. *Cognettia glandulosa* s.l. in contrast showed similar median dominance values for the two Moist Mull humus forms, but in Moist Moder the relative abundance was much lower, as this species complex belongs to the indicators of moderate acidity. As one of the few species that appears to be indifferent to soil acidity, *Cernosvitoviella atrata* showed no significant differences in dominance among the three humus forms. *Marionina simillima* and *Marionina filiformis*, although both considered indicators of moderate acidity, showed a contrasting behaviour: While the dominance of *Mar. simillima* decreased from Moist L Mull to Moist Moder, *Mar. filiformis* showed a significantly higher dominance in Moist Moder than in Moist L Mull, whilst overall dominance of this species was comparatively low. The species complex of *Cognettia sphagnetorum* s.l., indicating strong acidity, showed a strong increase in dominance from Moist L Mull to Moist Moder.

Even for the species that are generally dominant in a given humus form, the degree of dominance varies considerably. The samples taken next to the IMS at three occasions allow the assessment of variability at the same spot over time. The three samplings for the IMS occurred under very different soil moisture conditions. For this analysis, humus forms were not differentiated due to the low number of sampling points (n = 8). After a summer drought in 2022, microannelid abundance per sampling point and total species numbers were not exceptionally low, despite a still rather high mean soil tension of pF 3.10 (sampled on 25 October 2022) (Tab. 4). However,

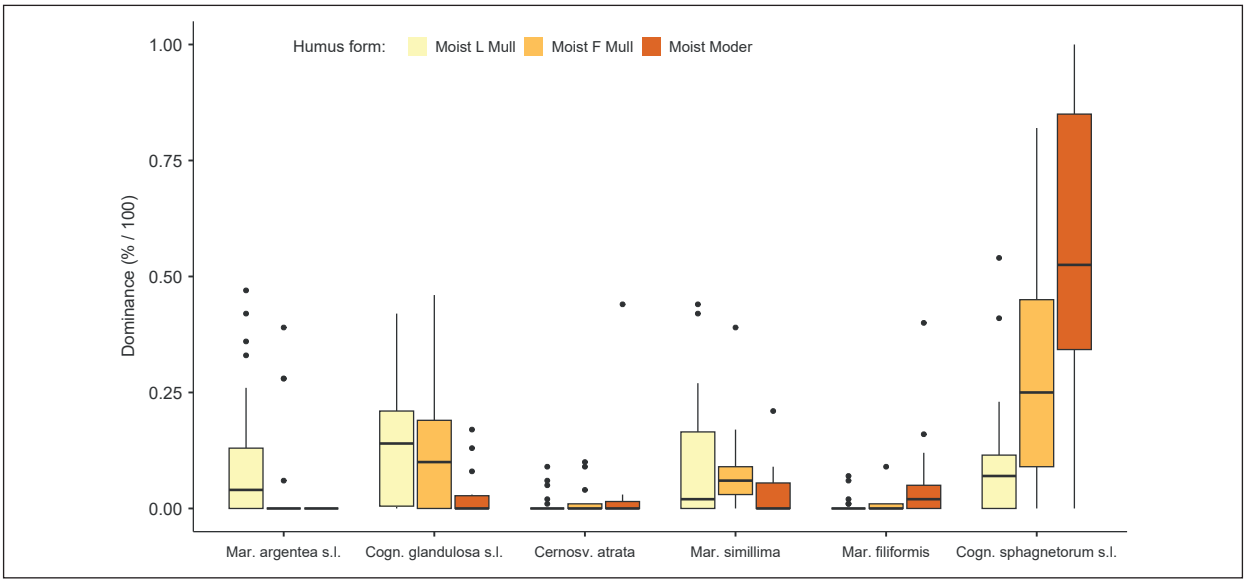



**Figure 1**. Dominance (mean relative abundance per sampling point) of six selected enchytraeid species, for the three humus forms (n = 62). Different superscript letters indicate significant differences for each species with p ≤ 0.05. For indicator values of the species, see table 4. Basic statistics see table S2.

the sampling conditions with highest water potential in October 2022 coincided with the lowest proportion of wetness indicators and the highest dominance of indicators of well drained soils. Total species number and species number per sampling point were lowest after a five-month period of soil water saturation (pF(mean) = 0.00; 26 April 2023). Indicators of wetness were prevailing while species indicative of strong acidity occurred in small numbers only. Further, abundance was significantly lower at this date compared to the October samplings. Highest abundance was found in October 2023, after a period neither waterlogged nor extremely dry (pF(mean) = 0.35; 23 October 2023).

Furthermore, the vertical distribution of microannelids in total and of indicator groups in particular shifted over time. Figure 2 illustrates the situation at measuring station A2. During the wet and the moderately wet period, microannelids reached their highest abundance in the top three centimetres. Conversely, in the dry period (October 2022) hardly any microannelids were found in the uppermost layer, and indicators of wet soils concentrated below 8 cm. On the other hand, indicators of well drained soils were mostly found above 8 cm depth. They were entirely missing at the sampling date with water saturation (April 2023). Although the picture of vertical distribution was different for the 8 sampling points of the IMS, IMS A2 can serve well as an example here, illustrating the high variability of vertical distribution of the total microannelid population as well as for indicator groups with time (Tab. S5).

## 4 Discussion

Our results show that some established differences between aeromorphic L Mull, F Mull and Moder humus forms regarding the decomposer community also apply to the corresponding aero-hydromorphic humus forms. Studies on microannelids in well-drained forest ecosystems often showed Moder or Mor humus forms with very low pH (< 4) related to a low species number, often ranging between 3 and 10, combined with a high absolute and relative abundance of a few acidity tolerating species, especially *Cognettia sphagnetorum* s.l. (Graefe et al. 2001, Jans & Funke 1989, Makulec 1983, Römbke 1989, Ventins & Melecis 2025). In contrast, Mull humus forms were generally characterized by considerably

**Table 5.** Mean abundance of microannelids for three sampling dates (n = 8 for each date). Indicators for wetness: moisture figure M > 5. Different superscript letters indicate significant differences with p ≤ 0.05. Basic statistics see table S3.

| Parameter | | Oct 2022 | April 2023 | Oct 2023 |
|---|---|---|---|---|
| | | n = 8 | n = 8 | n = 8 |
| Microannelid species (total) | | 30 | 14 | 23 |
| Microannelid species (per sampling point) | mean | 6.9 [a] | 3.9 [a] | 7.8 [a] |
| | sd | 4.88 | 3.04 | 4.03 |
| Microannelid abundance (individuals per sampling point) | mean | 38.00 [a] | 15.25 [b] | 76.25 [a] |
| | sd | 17.90 | 12.00 | 54.13 |
| Microannelids: Indicators of wetness (dominance %) | | 39.5 | 72.1 | 59.0 |
| Microannelids: Indicators of strong acidity (dominance %) | | 39.1 | 13.1 | 26.4 |

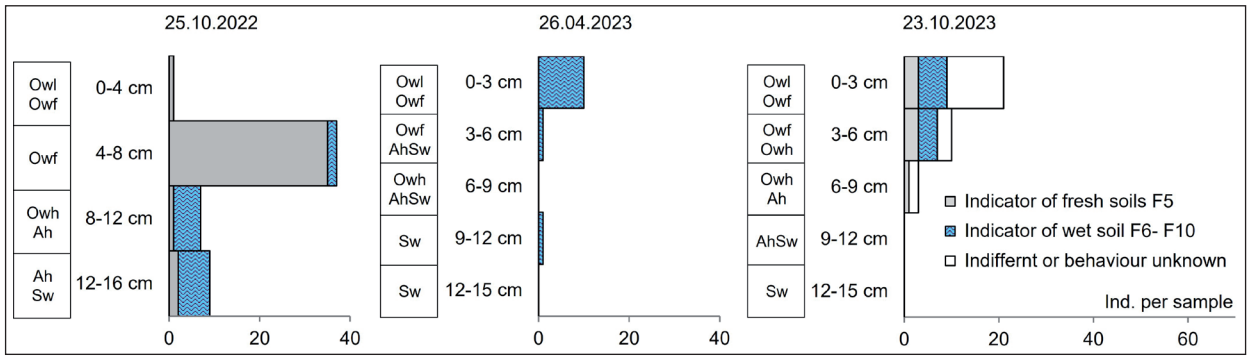



**Figure 2.** Vertical distribution of species groups according to their indicator values for soil moisture for three sampling dates (individuals per sample). Intensive Measurement Station A2, humus form: Moist Moder. Depth measurement from soil surface, including organic layers. Horizons as seen in the soil corer for microannelid sampling; nomenclature according to AG Boden (2024).

higher species numbers (Beylich & Graefe 2018, Mellin 1988, Schlaghamerský 1998, Schoch-Bösken & Greven 1987). Beylich & Graefe (2009) found that the average species number at forest sites with pH < 3.4 was lower than at sites with pH between 3.4 and 4.2. These findings are generally consistent with our results for the respective aero-hydromorphic humus forms. This is to be expected, as the typical decrease in pH from L Mull through F Mull to Moder, regardless of moisture levels, is a key factor influencing the occurrence of species in terms of their sensitivity to acidity.

The results of our study show that aero-hydromorphic humus forms on the other hand exhibit characteristics that distinguish them from the aeromorphic humus forms. Most striking is the occurrence of species indicating wet conditions with high frequency and dominance. Species such as *Cognettia glandulosa* s.l., *Marionina argentea* s.l., *Marionina filiformis,* and *Rhyacodrilus falciformis* are reported regularly from wet habitats such as fens and bogs (Beylich & Graefe 2002, Healy & Bolger 1984, Schenková et al. 2018), but in well drained forest ecosystems they tend to occur sporadically, in low numbers only or not at all (Ascher et al. 2012, Dusik et al. 2026, Toschki et al. 2021). However, there are some exceptions for which the cause might be attributed to (sub)soil conditions that were not accounted for in the respective studies (Mellin 1988, Schlaghamerský 1998). It should be noted here that comparison with earlier studies on this topic is constrained by the fact that the humus form and / or water regime are sometimes specified poorly or not at all and must be inferred from accompanying data (e.g. soil type, pH, vegetation). Anyhow, the fact that species indicating wet conditions are frequent and quite dominant in the moderately well drained forest ecosystems studied here demonstrates that these species are not restricted to open habitats.

Interestingly, species tolerating wet conditions come in addition to the species spectrum common in well drained forest topsoils. Species regarded as indicators of well drained soils according to Beylich & Graefe (2002) are still present in the temporarily wet sites investigated here. Generally, there are two main strategies for microannelids to cope with detrimental moisture conditions as drought or waterlogging: Migration to adequate microhabitats and survival as cocoons until conditions improve (Healy & Bolger 1984, Springett et al. 1970). These strategies are linked to the temporarily wet topsoil conditions in the study area by (a) the high temporal variability of soil moisture enabling species with various sensitivities concerning soil moisture to survive unfavourable conditions by vertical migration or survival as cocoons and (b) the high horizontal variability of relief and vegetation at a small scale, which provides horizontal escape routes to less moist microhabitats (Plum & Filser 2005). Thus, topsoils of periodically wet deciduous forests can support a comparatively high diversity of microannelids, as they provide a habitat for species with a wide range of habitat requirements concerning soil moisture. This is predominantly true for Moist Mull humus forms, while in Moist Moder the species richness is reduced due to acidification. The comparison of species tolerance concerning soil moisture and soil acidity shows that, in general, only very few species serve as both indicators of wetness and of strong acidity (Graefe & Schmelz 1999, Beylich & Graefe 2002). Hence, the low dominance of wetness indicators in Moist Moder (Tab. 3, Fig. 1) is likely attributable not to soil moisture conditions but to soil acidity.

Low soil moisture in summer months is a main reason for temporal fluctuations of microannelid abundances (Abrahamsen 1972, Dash & Cragg 1972, Nielsen 1955, Nowak & Pilipiuk 1997). Compared to other groups of mesofauna, microannelids are poorly protected against desiccation. pF values of > 4.0 were repeatedly reported to be fatal for single species in laboratory studies (*Cognettia sphagnetorum*: Abrahamsen 1971; *Fridericia galba*: Dózsa-Farkas 1977) or to reduce entire enchytraeid populations in the field to virtually zero (Gröngröft 1981, Nielsen 1955). In this context, the duration of the drought plays a role. Microannelids can cope with severe droughts by surviving as cocoons, unless the drought spell is extending for too long (Lagerlöf & Strandh 1997, Nielsen 1955). pF values of ≥ 4.0 were measured at some of the IMS, for a period of few days up to more than two months. At IMS A2, pF values above 4 were recorded for two weeks in August 2022 at 10 cm depth, but at the October 2022 sampling, the water potential was around pF 2.6 (Tab. S4), which has been shown to be suitable for microannelids survival and reproduction (Dozsa-Farkas 1977, Nielsen 1955). Apparently, after inadequate moisture conditions in August 2022, the population recovered to some extent after two months regarding overall abundance (Fig. 2). In October 2022, potential post-drought effects of August 2022 were more evident in the high dominance of indicators of well drained soils and in the vertical distribution of species. The collection of cocoons could provide further insights into survival strategies, but presents methodological challenges and was not within the focus of this study.

Typically, topsoil conditions of periodically wet forests on Stagnosols oscillate between two extremes: drying out in summer and waterlogging in winter. The periods with water saturated soil (pF = 0) can extend over months at the studied sites (Frank et al. 2024). Microannelids can survive in water as long as there is no oxygen deficiency (Healy 1987). As temperature determines the $O_2$-solubility of water and survival of cocoons is only possible for a limited time, length of waterlogging period

and season are crucial for the survival of species. In 2023, a period of waterlogging was recorded at IMS A2 from the beginning of the year until the end of May 2023 (pF = 0 at 0–30 cm). The sampling in April 2023 at the IMS revealed a low abundance and a species spectrum consisting of a few wetness indicators only, suggesting mortality (or horizontal migration) of some species. Six months later, however, species richness and abundance had recovered significantly, suggesting that the five-month period of waterlogged soil had no lasting negative impact on the microannelid community (Tab. 5). During the five months period of waterlogging, temperatures never exceeded 10 °C. Dózsa-Farkas (1977) reported *Fridericia galba* to survive water saturation with temperatures between 9 and 13.5 °C for two months near the soil surface, while at 17 and 26 °C the worms died within a few days. This is consistent with the finding that at the end of the five months of water-saturated conditions at least some species survived in our study.

The vertical distribution of microannelid species reveals information about living conditions in different depths as microannelids are known to move vertically in soil and can cover a distance of several centimetres within hours (Springett et al. 1970). Figure 2 indicates that the effects of the drought in August 2022 were still present in October 2022, when the different indicator groups were clearly distributed across different depth levels: The uppermost centimetres were devoid of animals while immediately below a comparatively high number of microannelids, mainly indicators of well drained soils, were present (4–8 cm). Indicators of wetness predominantly occurred in deeper layers > 8 cm. This simultaneous decrease of microannelids in 0–4 cm and increase in 4–8 cm can be interpreted as an example of vertical migration rather than of increased mortality in the uppermost centimetres (Abrahamsen 1972, Dash & Cragg 1972). However, it remains unclear, if the wetness indicating species migrated to even deeper layers because of their higher requirements of soil moisture or due to increasing competition caused by the majority of microannelids moving downwards. It should be considered that downward vertical migration might be limited by decrease of food resources with increasing depth (Briones et al. 2007). In contrast to the dry periods, during water saturation, especially when higher temperatures cause $O_2$ deficiency, the topsoil is only inhabited in the uppermost centimetres, where $O_2$ levels are highest (Plum & Filser 2005). Figure 2 shows that microannelid activity was more or less absent below 3 centimetres at pF 0 and a temperature in 10 cm depth of about 9 °C (Tab. S4).

While vertical migration behaviour and survival strategies in general appear to vary between species, information on these traits and habitat requirements are known only for a few selected species, partly from laboratory studies. Vertical migration might be a survival strategy favoured by species that reproduce by fragmentation so that survival in the cocoon stage is not a viable option to cope with adverse moisture conditions. This was shown for *Cognettia sphagnetorum* s.l. by Springett et al. 1970 and Briones et al. 1997. On the other hand, *Cognettia glandulosa* and *Cognettia sphagnetorum*, i.e. species mainly reproducing by fragmentation, showed a higher proportion of sexually mature animals in temporally submerged areas of bogs, implying more frequent reproduction via cocoons as adaptation to waterlogging (Healy & Bolger 1984). However, as these species complexes (*Cogn. sphagnetorum* s.l., *Cogn. glandulosa* s.l.) are meanwhile considered to comprise four and two species, respectively, that probably differ to some extent concerning reproduction mode and behavioural traits, these findings will have to be checked within the light of the split up species complexes. Healy (1987) found several species increasing in numbers with the lowering of the water table in a pot experiment - indicators of wetness, such as *C. glandulosa* and *Marionina argentea*, as well as species indifferent to soil moisture, such as *Enchytraeus minutus*. However, *C. glandulosa* moved downwards with the lowering of the water table in this experiment, while *E. minutus* stayed near the surface, representing the different requirements of species concerning soil moisture. For the small, wetness indicating species *Cernosvitoviella atrata*, Briones et al. (1997) found no vertical migration in response to decreasing soil moisture, resulting in increased mortality. Very little information can be found on the behavioural characteristics of other wetness indicating species such as *Fridericia cylindrica*, *Marionina filiformis* and *Marionina simillima* or indeed of most Enchytraeidae species (Eisenhauer et al. 2024).

Currently, we encounter an increasing demand for indicators for soil health and thus the inclusion of soil organisms in monitoring programmes (Ballasus et al. 2024, Vidal et al. 2025). Microannelids are suitable as indicators of topsoil conditions (Graefe 2004, Pelosi & Römbke 2016, Rutgers et al. 2009). To monitor the long-term development of biodiversity and functionality of decomposer communities, it is essential to record the species composition of indicator groups as comprehensively as possible. It must be noted that wetness-indicating species not only tolerate wetness but are dependent on it. Already in 1997, Nowak and Pilipiuk (1997) showed that drainage of fen habitats caused the disappearance of wetness indicators such as *Cernosvitoviella atrata* and *Mesenchytraeus armatus*. Species occurring predominantly in (periodically) wet habitats can be expected to be particularly vulnerable to climate change due to the danger of desiccation of these

habitats (Carrera et al. 2011, Maraldo et al. 2008). The current study shows that during certain periods wetness indicator species predominantly occur in deeper layers of the soil (below 10 cm). Sampling to a depth of only 10 cm or organic layer + 5 cm mineral soil, often given as standard for forest soils (ISO 23611-3:2019, Toschki et al. 2021), might then be insufficient to find these species. Further, sampling under very wet conditions results in low species numbers, although in this case at least the wetness indicators are present. Given the short-term temporal fluctuations in numbers and species distribution, horizontally as well as vertically, in periodically wet forests, it becomes obvious that sampling date and depth as well as spatial arrangement of sampling points must be well chosen to detect the typical species composition. This was already demonstrated by Schlaghamerský (2007) in a disturbed floodplain habitat, even though soil moisture variability was much less pronounced there than in our study. Simply adhering to the recommended seasons and sampling depths specified in standard methods might not be sufficient, as can be seen from the sampling dates of this study.

## 5 Conclusions

Based on the results of this study, aero-hydromorphic humus forms are characterized by a high frequency of microannelid species indicating moisture. Species numbers in the topsoils studied were comparatively high, as moisture indicators occur in addition to species of aeromorphic humus forms. The interplay of species requirements regarding soil pH and soil moisture contributes to their preferential occurrence either in Moist Mull or in Moist Moder. As most moisture-indicating species do not tolerate strong acidity, the frequency of moisture indicators and total species richness are lower in Moist Moder than in Moist Mull. It was shown that, in moderately well drained forest soils, the dominance and even the presence of moisture-indicator species exhibits high temporal variability due to the only temporarily wet conditions. Thus, species richness at a sampling point can change considerably within months. Further, a high variability of vertical distribution of microannelids, depending on the soil moisture in the topsoil, was detected. It was concluded that the highly variable soil moisture conditions in the aero-hydromorphic humus forms result in high spatial and temporal dynamics in the activity of the species present.

No studies on microannelids with explicit reference to aero-hydromorphic humus forms have been conducted so far. Our results contribute to the characterisation of aero-hydromorphic humus forms that have only recently received more attention in the German field guide for soil mapping. In order to determine the limits of the distribution of microannelids in relation to water tension more precisely and to gain knowledge on migration behaviour and reproductive strategies in relation to soil moisture, more frequent sampling – e.g., on a monthly basis – would be desirable in future as part of research projects, such as PhD theses. This would also add to our knowledge concerning the role of microannelids in the development of aero-hydromorphic humus forms. Finally, moderately well drained forest habitats seem vulnerable to climate change, especially concerning drought, and simultaneously valuable in terms of climate change mitigation, for example by water retention. It would thus be desirable to include these habitats with their specific soil fauna in soil biodiversity monitoring programmes. In this regard, the results of our research suggest that sampling design (e.g. season, sampling depth) should be adapted to the specific conditions of periodically wet sites in order to yield meaningful results.

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## Supplementary Online Materials

**Tables S1–S3**. Basic statistics on species number, abundance and dominance. **Table S4**. pF data at the IMS for three sampling dates. **Table S5**. Abundance at IMS broken down by depth levels. **Figures S1–S3**. Photos of humus profiles. Accessible at https://doi.org/10.25674/509.

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