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The nematode fauna from the top soil to the vadose zone in a forested groundwater recharge area

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Abstract

Soil nematodes are major microfaunal grazers that drive the turnover of organic matter as they foster the activity of microorganisms. The latter are an essential component for water purification processes. The present study is the first study that investigates the nematode community along an entire depth transect from top soil to the vadose zone at a forested groundwater recharge area, the 'Lange Erlen', which provides drinking water to the city of Basel (Switzerland). Vertical core drills were performed from 0–450 cm depth at two locations in the study area. The vertical transect was divided into 30 cm thick soil sections. Nematodes were extracted, counted, identified and divided into five trophic groups (i.e. plant feeders, fungal feeders, bacterial feeders, omnivores, predators). Based on the classification of functional groups the Maturity Index (*MI*), Plant Parasitic Index (*PPI*), as well as the Shannon-Weaver Index (*H'*) were assessed.

A total of 67 taxa were identified comprising 26 nematode families. The nematode population density was low with an average of 6.26 and 0.85 ind./10 g DW soil across depths at the sampling sites HST and VW, respectively. Density decreased strongly with depth, with on average 46 % of the total nematode density located in the uppermost soil layer (0–30 cm). Although soil samples were taken down to a depth of 450 cm, no nematodes were found below 240 cm, except for *Cephalobus persegnis* Bastian, 1865, which was the only species present in the lower vadose zone (220–450 cm). Plant feeders were the dominant trophic group (65 %) throughout the entire depth transect. Decomposition was mainly mediated by the bacterial carbon and energy channel as indicated by the low number of fungal feeders. The general low *MI*, *PPI* and *H'* were neither depth nor site dependent, suggesting similar environmental conditions at the two investigated locations due to frequent flooding. SIMPER analysis revealed that the dissimilarity in nematode community patterns at HST and VW increased with depth. Plant feeders contributed to the community dissimilarity in the upper soil layers, while the impact of bacterial feeders increased with depth, indicating that the main resource changes along the depth profile.

Keywords flooding | depth transect | soil microfauna | species composition | diversity | trophic structure

1. Introduction

Nematodes are the most abundant soil metazoa with up to 30 million individuals per square meter (Petersen & Luxton 1982). They occur worldwide in almost all soil types from arctic regions to the tropics, with a maximum diversity generally observed in temperate broadleaf forests (van den Hoogen 2019). However, Lawton et al. (1996) report the huge number of 431 morpho-species from a single tropical forest site. Molecular studies suggest nematodes to be the second most diverse metazoa group on earth with around a million different species (Blaxter 2003). Moreover, nematodes have evolved feeding groups at each trophic level of the soil food web (Yeates et al. 1993)

Although nematodes are common animals in groundwater (Eisendle-Flöckner & Hilberg 2015), their abundance and diversity can be highly variable due to

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the heterogeneity and constant changes of groundwater habitats (Hahn 2006). Nevertheless, the occurrence of nematodes in nearly all soils, their high density as well as great species and trophic diversity, makes nematodes a useful biomarker group for soil nutrient status, functioning and disturbance. Nematodes react quickly and specifically to environmental changes. For example, bacterial grazers are good indicators for the decomposition rate of organic matter: Due to their position in the food chain just above microorganisms, the abundance of bacterial grazers indicates the abundance of easily-decomposable organic matter (Wasilewska 1998). Further, the high trophic diversity of nematodes offers the possibility for assessing the availability of food resources and of prey communities (Yeates & Williams 2001).

For the analysis of the soil state and functioning several diagnostic concepts have been developed to supply information on the environmental conditions for soil organisms (Ferris et al. 2001).

A feasible way to estimate the magnitude of soil disturbance is the Maturity Index (*MI*). This concept uses weighted *c-p* values for nematode families, which represent different life history strategies with *r*- and *K*-strategists located at each end of a scale from *c-p* 1 to 5 (Bongers & Bongers 1998).

Artificial groundwater recharge systems are a common practice for water purification in which large areas are periodically, i.e. artificially, flooded. Thereby, surface and subsurface microbial communities are major contributors to pollutant degradation and maintenance of groundwater quality (Albers et al. 2015). Frequently, unvegetated sand filters are used, comprising of microorganisms, microfauna and small crustaceans building a biofilm matrix, are responsible for water purification (Bugge Harder et al. 2019). Microorganisms have been studied on account of the mechanism for contaminant attenuation in upper soil layers (Nishiwaki et al. 2018) as well as in deeper soil horizons down to 10 m soil depth (Odukoya et al. 2013). However, investigations of the accompanied soil fauna are scarce. Especially nematodes as major microbial grazer may have a significant impact on degradation processes. By their feeding activity nematodes enhance mineralization processes and liberate nutrients bound in microbial biomass for plant uptake (Ingham et al. 1985). In particular bacterial feeders contribute significantly to these processes by grazing on and assimilation of microbial tissue and thereby altering microbial community composition (Freckman 1988).

The present study investigates a groundwater recharge zone used to obtain drinking water for the city of Basel (Switzerland). This site is a former floodplain area of the river Wiese called ‘Lange Erlen’ that was altered by artificial landfill and afforestation in the 1970s and 1980s. Embanked forested sites are regularly flooded by water of the river Rhine to increase groundwater resources. In contrast to the common sand filter systems, no biofilm is generated. Nevertheless, water infiltration and purification capacity is still satisfying despite of the long performance of the system since 1912 (Rüetschi 2004). To date, the processes of water purification are not understood in detail. Recent studies in the ‘Lange Erlen’ reported an altered microbial community structure due to periodic flooding, predominantly in the upper vadose zone (Schütz et al. 2009, 2010). The vadose zone extends from the soil surface to the groundwater table lacking permanent water saturation (Holden & Fierer 2005). Schütz et al. (2009, 2010) further indicated that nutrient limitations were reversed due to flooding with Rhine water, allowing a specialized microbial community to effectively degrade organic compounds.

For these microbial investigations, core drillings from the soil surface down to a maximum of 450 cm depth were performed at the ‘Lange Erlen’. This offered the unique possibility to study the accompanied nematode fauna in a transect from the top soil to the aquifer. Studies that investigated the functional properties of the vertical distribution of nematodes either focused only on the first 100 cm of the depth profile (e.g. Knox et al. 2020), or considered single nematode trophic groups (Villate et al. 2008). The few studies that reported nematode findings from soil layers deeper than 200 cm, however, did not focus on the vertical distribution of nematode assemblages (e.g. Hilberg & Eisendle-Flöckner 2016).

To the best of our knowledge the present work is the first investigation of the nematode fauna in an entire depth transect from top soil to the aquifer. The objectives of this study were to assess the vertical distribution of the nematode fauna in this periodically flooded ecosystem in order to (i) identify nematode taxa along a depth gradient, from the top soil over the vadose zone to the groundwater table (ii) determine the relationship between soil properties and resources and nematode density and trophic structure, and (iii) detect the changes of the nematode community structure and diversity along the investigated depth gradient.

2. Materials and methods

2.1 Infiltration system

For artificial groundwater recharge the water of the river Rhine is pre-filtered through a rapid sand filter (80 cm quartz sand filter). Afterwards it is periodically seeped into 11 wooded flooding areas (total area 22 ha). Each flooding

area has a dimension of 1 to 2 hectare and is divided into three fields with a size of 3000 to 8500 m^2 by dams with a height of about 50 cm. Ten days of flooding is usually followed by 20 days of drying and regeneration. Due to revisions, longer interruptions occur. Depending on soil surface structure and the percolation time water fills up to variable heights with a maximum of 50 cm. The percolation occurs with a speed of 1 to 2 m day^{-1} through mull humus and fluvial silt layer of 30–90 cm, followed by a sand/gravel layer of 2–3 m before reaching the groundwater table at 3–4 m depth. Additionally, the water flows horizontally from northeast to southwest within the aquifer for 200 to 800 m. After the average retention time in the aquifer of 10–30 days, purified water is pumped out of groundwater wells and collected in the pumping station. Following a brief chemical treatment with chloride dioxide (ClO_2) the water is provided to consumers.

2.2 Study sites

The study sites are located in the north east of the city Basel, Switzerland (for map, see Schütz et al. 2008). The area 'Lange Erlen' with a size of about three square kilometres is part of the semi-natural floodplain of the river Wiese, descending from the southwest Black Forest, Germany. It is a straightened tributary of the river Rhine. A part of the 'Lange Erlen' is used since 1912 for artificial groundwater recharge and allocates today nearly half of the drinking water (15 x 10^6 m^3 ha^{-1} $year^{-1}$) of the city Basel.

The semi-natural forest sites of the 'Lange Erlen' are characterized as *Galio-Carpinetum* (i.e oak-hornbeam) forests (Burnand & Hasspacher 1999). The regularly flooded sites have been modified by activities such as landfill as well as afforestation with poplars (*Populus canadensis*), ash (*Fraxinus excelsior*), alder (*Alnus nigra*) and willows (*Salix* spp.) (Schütz et al. 2009). The upper soil layer is classified as fluvi-eutric cambisol, and the aquifer is composed of 80 % Rhine gravel (the lower part consists mostly of limestone) and 20 % Wiese gravel (upper part, mostly silicates and limestone) (Schütz et al. 2008).

The first sampling site, 'Hintere Stellimatten' (HST), was established in 1977 after afforestation. By reason of too high infiltration rates (11 m^3 m^{-2} d^{-1}) and in consequence of insufficient retention time an artificial landfill (loess loam) and soil compaction by bulldozing was performed in 1981. The site is mainly overgrown with an alder swamp forest containing *P. canadensis*, *A. nigra* and *Salix* spp. while the herb layer is dominated by *Rubus caesius* and *Urtica dioica*. On unvegetated regions some small spots of *Poa trivialis*, *Potentilla reptans*, *Agropyron repens* and *G. urbanum* occurred.

The second sampling site, 'Verbindungsweg' (VW), was established as flooding area after artificial landfill (loess loam) and afforestation in 1970. The forest is composed of old poplars, ash-leaved maple (*Acer negundo*) and oak trees. The understory consists of *Lysimachia nummularia*, *Urtica dioica*, *Phalaris arundinacea*, *Rubus caesus/fruticosus*, *Duchesnea indica*, *Iris preudacorus*, *Seneco aquaticus* and *Cardamine pratensis*. In the shady northern part of the site poplars are most dominant and the soil is bare of vegetation.

2.3 Sampling

Soil sampling at the sites HST and VW took place in November 2005. To do so, the groundwater level had to be lowered by stopping the flooding interval four weeks before sampling. For analyses, the depth profile was sectioned randomly in three zones: The surface soil layer reached from 0 to 100 cm soil depth, whereat the section from 0 to 30 cm soil depth is referred to as 'uppermost soil layer' in this study. The unsaturated layer below, i.e. the vadose zone, comprises solid, aqueous and gaseous compartments with rapidly changing soil conditions from saturation to desiccation (Kieft & Brockmann 2001). The vadose zone was separated into upper vadose zone (100–220 cm soil depth) and lower vadose zone (220–450 cm soil depth). The groundwater table was reached below a soil depth of 450 cm.

For the depth transect three vertical core drillings (diameter 25 cm) were taken on each site from the soil surface to the groundwater level in 450 cm depth by a construction company (Glanzmann, Basel, Switzerland). Cores were taken in sections of 50 cm. Afterwards the cores were transferred into soil core boxes, representing the entire depth transect. Subsequently, soil samples were taken every 30 cm along the soil profile resulting in 14 soil layers that represent the entire depth transect (0–30 cm, 30–60 cm, 60–90 cm, 90–120 cm, 120–150 cm, 150–180 cm, 180–210 cm, 210–240 cm, 240–270 cm, 270–300 cm, 300–330 cm, 330–360 cm, 360–390 cm, 390–450 cm). The soil samples of each layer were taken with a shovel from the inner part of the cores.

For the soil analysis (including PLFA analysis), 100 g fresh weight (FW) soil were taken per sample, transported to the laboratory and frozen (-20°C) until analysis. Before conducting all analyses, i.e. determination of soil parameters and PLFA analysis, the soil samples were thawed at 8°C for 24 h. Visible organic material (fine roots and leaves) were removed and the soil was sieved (5 mm mesh size). Overall, 42 soil samples were taken at each site along the entire depth transect. For the investigation of the nematode fauna, another 100 g

FW soil were taken per sample and stored for 3–5 days at 7–8°C until nematode extraction. All soil samples were weighed before and after extraction and nematode numbers were given as individuals per 10 g dry weight (DW) soil. On average, 50 g FW soil was extracted by a modified Baermann method according to Ruess (1995). This comprises 24 h extraction at room temperature (18–20°C), followed by a heating regime temperature program for 6 h started with 20°C and raised at 5°C/h to 45°C. Overall, 84 nematode samples were extracted, three replicates from each of the 14 soil layers of the entire depth transect (0–450 cm) at HST and VW.

The nematodes were preserved by addition of 4% cold formaldehyde solution and stored in vials until examination in a fridge at a temperature of 8°C. Despite careful handling one sample of each site got lost by leakage of damaged vials. Nevertheless, the missing samples did not affect statistical analyses and interpretation.

2.4 Soil analysis

2.4.1 Chemical and physical soil parameters

The chemical and physical characteristics of the soil were analyzed to detect variations of pH, carbon (C), nitrogen (N), dissolved organic carbon (DOC), nitrate (NO_3^-), sulfate (SO_4^{2-}) and moisture content. The soil pH was measured in 0.01 M calcium chloride ($CaCl_2$) solution (1 : 4 w/v) after stirring and incubating at room temperature for 1 h. Total soil contents of C and N were analyzed from oven-dried (65°C, 3 days) and pulverized (swing mill, Retsch MM 200) aliquots of the bulk soil with an element analyzer (CHN 1000, Leco, USA). Results are given in percentage of the soil DW. The determination of the soil moisture content was performed by drying the soil samples at 105°C for 24 h and calculating the mass difference before and after drying.

DOC, NO_3^- and SO_4^{2-} were extracted from 5 g FW soil for 0–200 cm depth and from 10 g FW soil for 200–450 cm. A solution with soil and 0.01 M $CaCl_2$ (1 : 4 w/v) was prepared, shaken for 1 h (200r.p.m.) and centrifuged for 15 min (450 *g*). Supernatants of each soil solution were filtered through sterile membrane filters (0.45 µm; Millex, HA, USA) and stored in the fridge (1 h) until analysis. DOC analysis was carried out after acidification and air-purging (N55, O45, Carbagas, Gümligen, Switzerland) with a TOC analyzer (TOC-5000 A, Shimadzu) in quintuplicate. NO_3^- and SO_4^{2-} were measured via an ion chromatograph (IC-690, Metrohm, Herisau, Switzerland). The results are expressed as mg g^{-1} DW soil.

2.4.2 PLFA analysis

Lipid extraction and methylation were conducted after Frostegård et al. (1993a, b). PLFAs were extracted from 3 g FW soil in 0–30 cm, from 6 g in 30–90 cm and from 10 g in 90–450 cm. Identification and quantification of PLFAs were performed using a GC interfaced to an electron ionization mass spectrometer (GC/EI-MS). Analyses were carried out using a 3400/Saturn 4D iontrap GC/MS system (Varian, Darmstadt, Germany). For detailed protocol of PLFA analysis see Schütz et al. (2009). The total PLFA density is expressed as nmol g^{-1} DW soil.

2.5 Nematode fauna

Total nematode numbers extracted from each sample were counted under a dissecting microscope (Axiolab, Zeiss, Oberkochen, Germany) using 100 x magnification. Further, 10% of each sample but not less than 100 individuals were determined to species or genus level. The identification of the nematodes was performed using the Axiolab microscope coupled with a three mega pixel digital camera (ScopeTek, DCM 310) and picture imaging software (ScopeTek, ScopePhoto 3.0.12) to assess body ratios according to de Man's formula (de Man 1880). Nematodes were identified using the keys of Meyl (1960), Bongers (1994) and Andrassy (1984, 2005, 2007) and assigned to feeding types according to Yeates et al. (1993). The subgroups sedentary parasites, migratory endoparasites, semi-endoparasites, ectoparasites, root epidermal cell and root hair feeders were all summarised as plant feeders.

Following Bongers (1990) nematode taxa were assigned as colonizers or persisters by their specific *c-p* values ranging from 1–5. This scale represents different life history strategies where *c-p* 1 consists of *r*-strategists with high fecundity, small eggs, and short generation time. On the other hand, *c-p* 5 represents *K*-strategists with low fecundity, large body size, and long generation time. The latter are sensitive to changing environmental conditions and disturbance. Both classifications of feeding type and *c-p* value enable the assignment to functional guilds and the calculation of indices for rating the ecological state of a soil system in relation to disturbance and functioning (Bongers & Bongers 1998).

The Maturity Index (*MI*) was calculated by exclusions of plant feeders and dauerlarvae of Rhabditidae as proposed by Bongers & Bongers (1998). Dauerlarvae of Rhabditidae were detected, but since these are inactive stages, their presence does not indicate current nutrient rich conditions. The trophic group of plant feeders were

considered by calculation of the Plant Parasitic Index (*PPI*), following Bongers (1990):

$$MI \text{ or } PPI = \sum \upsilon(i) \cdot p(i)$$

where υ = *c-p* value of taxon i, p = proportion of taxon i in a sample, with the *MI* comprising free-living and the *PPI* plant parasitic taxa.

The biological diversity was measured by computing the Shannon Index of diversity (*H'*) (Shannon & Weaver 1949):

$$H' = -\sum p(i) \cdot \ln p(i)$$

where p = the proportion of species i in the total nematode community.

2.6 Statistics

Statistical analyses were performed using R (version 4.0.2, 'Taking Off Again'). Firstly, the Shapiro-Wilk normality test and Levene test were applied, followed by the Mann-Whitney-U test and Kruskall-Wallis rank sum test. If significant differences were detected Dunn`s test with Bonferroni correction (significance level at $P < 0.05$) was performed as post hoc test. The Spearman's rank order correlation coefficient was calculated to assign the association between nematode population density and soil parameters. This non-parametric correlation was applied as data did not meet normal distribution. Multivariate statistics were performed with PRIMER 7 (version 7.0.13). The density of nematode populations was subjected to analysis of similarity (ANOSIM), followed by similarity percentages procedure (SIMPER) to determine the differences between sites and depths. The Bray-Curtis similarity index was applied to the data.

For the index calculation and application of multivariate statistics only the depths from 0 to 120 cm were taken into account, since there were no obvious differences between nematode communities at HST and VW in deeper soil layers.

3. Results

3.1 Soil texture and parameters

The soil texture of the sites differed predominantly in the upper soil layers (Tab. 1). Landfill loess loam expanded from the surface to a depth of 100 cm at HST but was only present up to a depth of about 40 cm at VW. Beneath sand and gravel occurred down to 400 cm depth at both sites. Interspersed silt and clay lenses were present in the layers between 160 and 280 cm at HST and between 280 and 340 cm at VW. Partial FeMn depositions were detected in deeper soil layers, indicating periodical water logging and anoxic conditions.

At HST, total PLFA density, NO_3^- and water content (% DW soil) decreased significantly with depth ($P < 0.05$) (Tab. 2). The soil C and N content (% DW soil) as well as the C/N ratio declined with depth from 2.2 % to 0.4 %, 0.1 % to 0.04 % and 16.2 to 8.1, respectively. The DOC and SO_4^{2-} content declined to a depth of 180 cm but increased again in lower soil layers. The pH values ranged from 6.0 to 7.4 across depths.

At VW, DOC, NO_3^- and soil C and N content (% DW soil) decreased significantly with depth ($P < 0.05$). The total PLFA content decreased from 54.85 ± 23.78 nmol g^{-1} DW soil in 0–30 cm to 2.44 ± 0.94 nmol g^{-1} DW soil in 210–240 cm soil depth. The water content (% DW soil) decreased from 17 % to 9 %. Contrasting this, the pH value increased with depth from 7.0 to 7.5. The C/N ratio ranged from 7.3 to 9.0 across depths.

3.2 Nematode species

In total, 67 nematode taxa were identified with 36 taxa occurring solely at HST, 11 at VW and 20 taxa occurring at both sites (Tab. 3). 33 taxa were restricted to a single soil layer. The most common species were *Rotylenchus quartus*, *Filenchus* spp. and *Gracilacus* spp. at HST and *Filenchus teres* at VW with individuals of each species found in 5 different soil depths. *Cephalobus persegnis* was the species with the widest range, i.e. with a distribution from 30 cm down to 240 cm depth. *Gracilacus* spp. and *Pratylenchus pseudopratensis* were the species with

Table 1. Soil textures in the soil depths 0–40, 40–100, 100–160, 160–220, 220–280, 280–340 and 340–400 cm at the sites Hintere Stellimatten (HST) and Verbindungsweg (VW).

Depth [cm]	HST	VW
0–40	landfill loess loam	landfill loess loam
40–100	landfill loess loam	silt, gravel, sand, clay
100–160	gravel, sand, silt, clay	gravel, sand
160–220	gravel, sand, silt	gravel, sand
220–280	gravel, sand, silt	gravel, sand, silt
280–340	gravel, sand, silt	gravel, sand, silt
340–400	gravel, sand	gravel, sand, silt, clay

Table 2. Soil parameters (mg g^{-1} DW soil ± SD) and total PLFA (phospholipid fatty acid) density (nmol g^{-1} DW soil ± SD) in the soil depths 0–30, 30–60, 60–90, 90–120, 120–150, 150–180, 180–210, and 210–240 cm at the sites Hintere Stellimatten (HST) and Verbindungsweg (VW). % C, % H and % N represent the proportion of the respective element on the dry weight in percent. Means within a column with no or the same letter are not significantly different (Dunn's test, $P < 0.05$).

Site	Depth [cm]	DOC	NO_3^-	SO_4^{2-}	pH	% C	% H	% N	PLFAs	% Water content
HST	0–30	1.70 ± 0.25	2.09 ± 1.12a	2.03 ± 0.73	7.39 ± 0.21	2.24 ± 0.09	0.62 ± 0.01	0.14 ± 0.02	53.77 ± 49.01**a**	19.34 ± 1.78**a**
	30–60	2.21 ± 0.68	1.85 ± 0.55a	1.55 ± 0.47	6.88 ± 0.54	1.42 ± 0.40	0.63 ± 0.08	0.14 ±0 .03	23.14 ± 5.20	18.46 ± 0.44
	60–90	1.81 ± 0.48	0.88 ± 0.13	1.13 ± 0.11	7.05 ± 0.16	1.18 ± 0.13	0.59 ± 0.05	0.11 ± 0.03	13.03 ± 2.10	14.44 ± 1.89
	90–120	1.69 ± 0.33	0.69 ± 0.11	1.14 ± 0.12	7.39 ± 0.22	0.84 ± 0.07	0.47 ± 0.05	0.08 ± 0.01	16.32 ± 5.72	13.88 ± 0.58
	120–150	1.18 ± 0.22	0.23 ± 0.16	1.24 ± 0.43	7.37 ± 0.08	0.38 ± 0.01	0.37 ± 0.01	0.04 ± 0	10.34 ± 4.27	7.55 ± 1.49
	150–180	0.73 ± 0.09	0.16 ± 0.07	1.05 ± 0.19	7.41 ± 0.05	0.38 ± 0.02	0.34 ± 0.01	0.04 ± 0	4.42 ± 1.13	5.86 ± 0.29**b**
	180–210	0.85 ± 0.32	0.31 ± 0.23	1.08 ± 0.11	7.21 ± 0.34	0.43 ± 0.19	0.37 ± 0.03	0.05 ± 0.02	3.82 ± 3.35	9.68 ± 3.21
	210–240	0.93 ± 0.01	0.09 ± 0.01**b**	1.69 ± 0.88	7.25 ± 0.40	0.56 ± 0.36	0.41 ± 0.12	0.07 ± 0.04	1.57 ± 1.67**b**	7.10 ± 1.56
VW	0–30	2.74 ± 1.62**a**	1.77 ± 0.72**a**	2.13 ± 0.28	6.98 ± 0.08	2.14 ± 1.16**a**	0.83 ± 0.14	0.23 ± 0.11**a**	54.85 ± 23.78	17.37 ± 1.31
	30–60	1.49 ± 0.23	0.83 ± 0.19	1.05 ± 0.03	7.24 ± 0.23	0.64 ± 0.37	0.36 ± 0.31	0.05 ± 0.01	7.02 ± 1.65	11.91 ± 2.46
	60–90	1.15 ± 0.41	0.68 ± 0.26	1.39 ± 0.50	7.50 ± 0.20	0.47 ± 0.10	0.42 ± 0.06	0.05 ± 0.01	7.03 ± 2.29	8.66 ± 0.34
	90–120	0.82 ± 0.55	0.35 ± 0.27	1.16 ± 0.44	7.41 ± 0.09	0.36 ± 0.09	0.35 ± 0.04	0.05 ± 0.01	3.04 ± 1.64	7.22 ±0.92
	120–150	0.68 ± 0.01	0.22 ± 0.02	0.85 ± 0.11	7.43 ± 0.22	0.34 ± 0.22	0.35 ± 0.02	0.05 ± 0.01	4.74 ± 1.57	7.86 ± 0.99
	150–180	0.67 ± 0.14	0.23 ± 0.06	0.93 ± 0.36	7.47 ± 0.12	0.29 ± 0.12	0.30 ± 0.02	0.04 ± 0.01	4.09 ± 1.62	7.23 ± 0.90
	180–210	0.47 ± 0.03	0.17 ± 0.01	0.87 ± 0.09	7.46 ± 0.07	0.24 ± 0.07	0.29 ± 0	0.03 ± 0	2.50 ± 2.29	7.67 ± 1.60
	210–240	0.40 ± 0.04**b**	0.16 ± 0.01b	1.06 ± 0.12	7.34 ± 0.35	0.25 ± 0.55**b**	0.27 ± 0.02	0.03 ± 0**b**	2.44 ± 0.94	8.50 ± 1.08

Table 3. Nematode taxa present in a soil gradient from 0 to 240 cm depth for Hintere Stellimatten (HST) and Verbindungsweg (VW). Classification and nomenclature after Meyl (1960), Bongers (1994) and Andrassy (1984, 2005, 2007). ● present at HST and VW, ○ present only at HST, ◊ present only at VW. Major habitat with respective reference indicated as 'a' – aquatic and 't' – terrestrial, with brackets assigning occasional occurrence.

Family	Taxon	Depth [cm]								Habitat	Reference
		0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240		
Achromadoridae	*Achromadora* Cobb, 1913, spp.				◊					a,t	Andrassy (2005)
Alaimidae	*Alaimus* de Man, 1880, spp.	○	◊	○		○				a,t	Bongers (1994)
	Paramphidelus Andrassy, 1977, spp.	○		◊						a,t	Bongers (1994)
Anguinidae	*Ditylenchus* Filipjev, 1936, spp.	◊								t	Andrassy (2007)
Aphelenchidae	*Aphelenchus avenae* Bastian, 1865	○	◊	○		○				t	Andrassy (2007)
	Aphelenchus Bastian, 1865, spp.	○	◊							t	Andrassy (2007)
Aphelenchoididae	*Aphelenchoides* Fischer, 1894, spp.						○			a,t	Andrassy (2007)
	Aprutides Scognamiglio, Talame & S'Jacob, 1970, spp.	○								t	Andrassy (2007)
Cephalobidae	*Acrobeles* Linstow, 1877, spp.				○					t	Andrassy (2005)
	Cephalobus persegnis Bastian, 1865	●		●	○		○		◊	t	Andrassy (2005)
	Cephalobus Bastian, 1865, spp.	○			○					t	Andrassy (2005)
	Eucephalobus cf *striatus* (Bastian, 1865) Thorne, 1937		◊							t	Andrassy (2005)
	Eucephalobus mucronatus (Kozlowska & Roguska-Wasilewska, 1963) Andrassy, 1967	○			○					t	Andrassy (2005)
	Eucephalobus Steiner, 1936, spp.		◊			○				t	Andrassy (2005)
	Heterocephalobus cf *bisimilis* (Thorne, 1925) Andrassy, 1967	◊								(a),t	Eyualem-Abebe et al. (2006)
	Heterocephalobus cf *longicaudatus* (Buetschli, 1873) Andrassy, 1967	○	◊							(a),t	Eyualem-Abebe et al. (2006)
	Heterocephalobus filiformis (de Man, 1880) Andrassy, 1967			○						t	de Man (1880)

Table 3 continued

Family	Taxon	Depth [cm]								Habitat	Reference
		0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240		
	Heterocephalobus Brzeski, 1960, spp.	○								t	Andrassy (2005)
Criconematidae	*Criconema mutabile* (Taylor, 1936) Raski & Luc, 1985				○					(a),t	Bongers (1994)
	Criconema Hofmaenner & Menzel, 1914, spp.			○						t	Andrassy (2007)
Desmodoridae	*Prodesmodora* Micoletzky, 1923, spp.			○						a,(t)	Andrassy (2005)
Diphtherophoridae	*Diphtherophora* cf *obesa* Thorne, 1939			○						t	Bongers (1994)
	Diphtherophora de Man, 1880, spp.				○					t	Bongers (1994)
Dolichodoridae	*Merlinius* Siddiqi, 1970, spp.	○								t	Andrassy (2007)
	Paratrophurus Arias, 1970, spp.	○								t	Andrassy (2007)
	Trophurus Loof, 1957, spp.	○	◊							t	Bongers (1994)
	Tylenchorhynchus Cobb, 1913, spp.	○			○					(a),t	Andrassy (2007)
Hemicycliophoridae	*Hemicycliophora* de Man, 1921, spp.		◊	◊						a,t	Andrassy (2007)
Hoplolaimidae	*Rotylenchus fallorobustus* Sher, 1965	○	○		○					t	Andrassy (2007)
	Rotylenchus quartus (Andrassy, 1958) Sher, 1961	○	●	○	○		○			t	Andrassy (2007)
	Rotylenchus Filipjev, 1936, spp.	○		◊						t	Andrassy (2007)
Leptonchidae	*Tylencholaimus* de Man, 1876, spp.			○						(a),t	Bongers (1994)
Monhysteriae	*Eumonhystera filiformis* (Bastian, 1865) Andrassy, 1981				○					a,t	Andrassy (2005)
	Eumonhystera longicaudatula (Gerlach & Riemann, 1973), Andrassy, 1981					◊				a	Andrassy (2005)
	Eumonhystera Andrassy, 1981, spp.				◊	○				a,t	Andrassy (2005)

Table 3 continued

Family	Taxon	Depth [cm]								Habitat	Reference
		0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240		
Mononchidae	*Mylonchulus subtenius* Cobb, 1917			○						t	Bongers (1994)
Panagrolaimidae	*Panagrolaimus* Fuchs, 1930, spp.	○								(a),t	Andrassy (2005)
Paratylenchidae	*Gracilacus* Raski, 1962, spp.	○	○	○	○	○				t	Andrassy (2007)
	Paratylenchus bukowinensis Micoletzky, 1922			○						t	Bongers (1994)
	Paratylenchus projectus Jenkins, 1956		○	○		○		○		t	Andrassy (2007)
	Paratylenchus tenuicaudatus Wu, 1961					○				t	Wu (1961)
	Paratylenchus Micoletzky, 1922, spp.	◊		○	○	○	○			t	Andrassy (2007)
Plectidae	*Plectus geophilus* de Man, 1880		◊							t	Andrassy (2005)
	Plectus rhizophilus de Man, 1880	○		◊						(a),t	Andrassy (2005)
	Plectus Bastian, 1865, spp.		◊							a,t	Andrassy (2005)
Pratylenchidae	*Pratylenchus pseudopratensis* Seinhorst, 1968	◊	◊	◊						t	Bongers (1994)
	Pratylenchus Filipjev, 1936, spp.		●		○					(a),t	Bongers (1994)
Qudsianematidae	*Dorydorella* Andrassy, 1986, spp.			○						(a),t	Bongers (1994)
	Eudorylaimus centrocerus de Man, 1880		◊							a,t	Bongers (1994)
Rhabditidae	*Rhabditis* Dujardin, 1845, spp.	●	○			○				a,t	Andrassy (2005)
Thornenematidae	*Prodorylaimus filiarum* Andrassy, 1964	●	○	◊		○				a,t	Eyualem-Abebe et al. (2006)
	Prodorylaimus Andrassy, 1959, spp.	○	○							a,t	Eyualem-Abebe et al. (2006)
	Prodorylaimus uliginosus Loof, 1985			○						a,t	Eyualem-Abebe et al. (2006)

Table 3 continued

Family	Taxon	Depth [cm] 0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240	Habitat	Reference
Trichodoridae	*Trichodorus* Cobb, 1913, spp.			○		○				(a),t	Eyualem-Abebe et al. (2006)
Tripylidae	*Tripyla* Bastian, 1865, spp.			○						a,t	Bongers (1994)
Tylenchidae	*Filenchus compositus* Eroshenko, 1971				○					t	Geraert (2008)
	Filenchus criniformicaudatus (Kazachenko, 1975) Siddiqi, 1986	○					○			(a),t	Geraert (2008)
	Filenchus quartus (Szczygiel, 1969) Siddiqi, 1986	○	◊							t	Bongers (1994)
	Filenchus Andrassy, 1954, spp.	○	◊	○	○	○	○			a,t	Andrassy (2007)
	Filenchus teres (Eroshenko, 1971) Siddiqi, 1986	●	●	◊	◊		◊			t	Geraert (2008)
	Lelenchus cf *leptosoma* (de Man, 1880) Andrassy, 1954		◊							(a),t	Andrassy (2007)
	Malenchus Andrassy, 1968, spp.	○		○	○					(a),t	Andrassy (2007)
	Psilenchus de Man, 1921, spp.	○								(a),t	Andrassy (2007)
	Tylenchus maius Andrassy, 1979				○					t	Geraert (2008)
	Tylenchus Bastian, 1865, spp.	○	◊	○	○	○				a,t	Andrassy (2007)
Tylodoridae	*Cephalenchus leptus* Siddiqi, 1963	○		○	○		○			t	Andrassy (2007)
	Cephalenchus (Goodey, 1962), spp.	○			○					t	Andrassy (2007)
Number of identified individuals (total)	**HST**	**150**	**74**	**46**	**48**	**19**	**11**	**2**			
	VW	**18**	**31**	**12**	**3**	**1**	**1**		**2**		
Number of species (total)	**HST**	**32**	**9**	**22**	**20**	**13**	**7**	**1**			
	VW	**8**	**19**	**8**	**3**	**1**	**1**		**1**		

the highest density across depths with 25.8 ± 3.0 and 0.8 ± 0.6 ind./10 g DW at HST and VW, respectively. *Filenchus* was the most diverse genus at HST (5 species), while *Filenchus* and *Plectus* (3 species, respectively) were most diverse at VW. The highest species diversity at HST occurred in a depth from 0–30 cm and declined constantly from a depth of 60–90 cm. At VW, the highest species diversity was found in a depth from 30–60 cm and decreased rapidly at greater depths. The decline in species number with depth at both sites was significant (Kruskall, HST: $P = 0.025$; VW: $P = 0.044$). However, this trend was not statistical meaningful after the post hoc test. Below a soil depth of 240 cm no nematodes were found.

35 species are typical inhabitants of terrestrial habitats, while 31 species are known to occur in terrestrial as well as aquatic habitats. The species *Eumonhystera longicaudatula* occurs exclusively limnic.

3.3 Nematode density

The nematode population density ranged from 30.4 ± 39.1 ind./10 g DW (0–30 cm) to 0.2 ± 0.3 ind./10 g DW (210–240 cm) at HST and from 3.1 ± 1.8 ind./10 g DW (30–60 cm) to 0.1 ± 0.1 ind./10 g DW (210–240 cm) at VW (Fig. 1). The nematode density strongly declined with depth at both sites (Kruskall, HST: $P = 0.025$; VW: $P = 0.011$). However, this trend was not significant after the post hoc test.

In total 26 nematode families were observed in the soil across depths at the two investigated sites with more families occurring at HST than at VW (except in 30–60 cm depth) (Tab. 4). Paratylenchidae had the highest density (19.56 ± 33.62 ind./10 g DW, HST, 0–30 cm) and Alaimidae and Tripylidae the lowest (0.04 ± 0.07 ind./10 g DW, HST, 60–90 cm). Generally, family number and density were not affected by depth or site.

3.4 Community structure and diversity

The major trophic groups of nematodes across depths (0–120 cm) and sites were plant feeders with an average relative abundance of 65 %, followed by bacterial feeders (26 %), omnivores (7 %) and fungal feeders (2 %). Predators were scarce with a proportion of less than 1 % and occurred only at HST (60–90 cm depth). Generally, the occurrence of trophic groups was not affected by depth or site.

The overall abundance of nematodes was related to soil parameters and resources across all depths and both sites (Tab. 5). In detail, each trophic group was positively correlated to DOC and nitrate ($P < 0.05$) at VW. Plant feeders were positively linked to C ($P < 0.05$), H ($P < 0.05$) and N ($P < 0.05$) at HST and VW, respectively. Plant and bacterial feeders showed a positive correlation to PLFAs, which was more pronounced at HST ($P < 0.001$ and $P < 0.01$, respectively) than at VW ($P < 0.05$ and $P < 0.05$, respectively). A negative correlation occurred between each trophic group at VW and predators at HST and pH, albeit not significantly.

Several indices were calculated to assign the impact of soil depth (0–120 cm) on nematode community structure with a focus on disturbance and diversity (Tab. 6). Generally, none of the indices were affected by depth or site. The low Maturity Index (*MI*) at HST (1.72 ± 2.44 to 2.95 ± 1.83) and at VW (1.21 ± 1.72 to 2.83 ± 1.44) revealed a high disturbance at both investigated sites. In

Figure 1. Population density of nematodes (ind./10 g DW soil ± SD) at Hintere Stellimatten (HST) and Verbindungsweg (VW). The decline in density was significant at both sites (Kruskall-Wallis rank sum test), but showed no significant differences after Dunn's post hoc test.

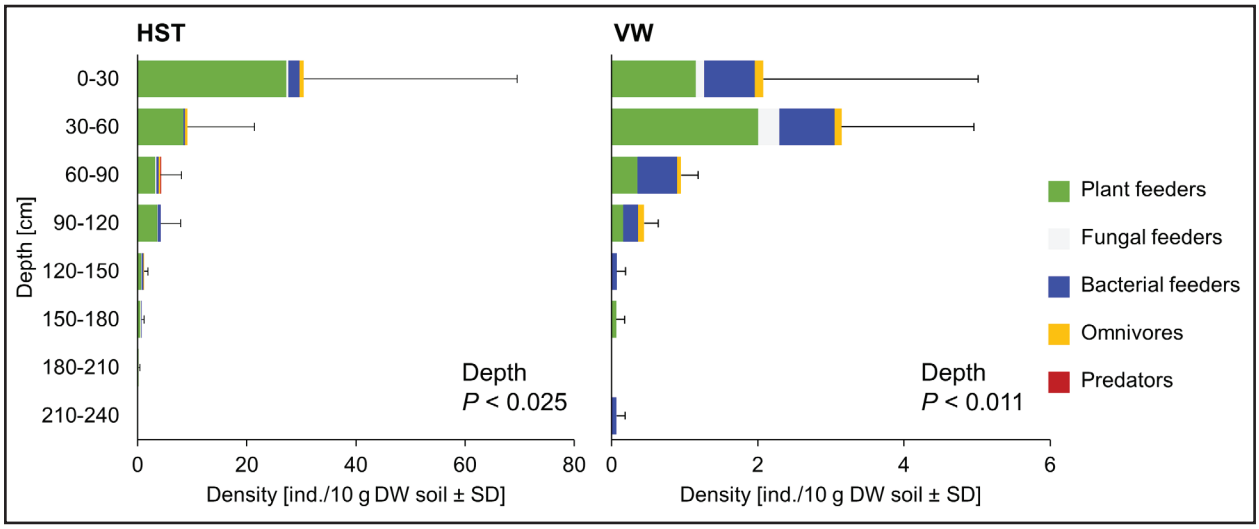

Table 4. Density of nematode families (ind./10 g DW soil ± SD) present in a soil gradient from 0 to 120 cm depth for Hintere Stellimatten (HST) and Verbindungsweg (VW). Nematode families are arranged by trophic group and *c - p* values after Bongers (1990) are given.

Trophic group	*c - p*	Nematode family	HST				VW			
			0–30	30–60	60–90	90–120	0–30	30–60	60–90	90–120
Plant feeders	3	Criconematidae			0.10 ± 0.17	0.22 ± 0.37				
	3	Dolichodoridae	3.02 ± 5.22			0.11 ± 0.1 9		0.22 ± 0.20		
	3	Hemicycliophoridae						0.25 ± 0.43	0.05 ± 0.09	
	3	Hoplolaimidae	2.02 ± 3.24	0.37 ± 0.52	0.19 ± 0.34	0.40 ± 0.52		0.19 ± 0.33	0.05 ± 0.09	
	2	Paratylenchidae	19.56 ± 33.62	7.79 ± 11.02	2.03 ± 2.28	1.83 ± 2.89	0.12 ± 0.16			
	3	Pratylenchidae		0.25 ± 0.16		0.11 ± 0.19	0.69 ± 0.98	0.28 ± 0.29	0.16 ± 0.16	
	4	Trichodoridae			0.19 ± 0.34					
	2	Tylenchidae	2.49 ± 4.31	0.11 ± 0.16	0.61 ± 0.85	0.62 ± 0.87	0.35 ± 0.49	1.06 ± 0.60	0.09 ± 0.16	0.16 ± 0.27
	2	Tylodoridae	0.18 ± 0.32		0.10 ± 0.17	0.29 ± 0.33				
Fungal feeders	2	Anguinidae					0.12 ± 0.16			
	2	Aphelenchidae	0.28 ± 0.48		0.10 ± 0.17			0.29 ± 0.50		
	2	Aphelenchoididae	0.09 ± 0.16							
	3	Diphtherophoridae			0.10 ± 0.17	0.08 ± 0.14				
Bacterial feeders	4	Alaimidae	0.37 ± 0.64		0.04 ± 0.07			0.10 ± 0.17	0.05 ± 0.09	
	2	Cephalobidae	1.02 ± 1.52		0.19 ± 0.34	0.43 ± 0.27	0.46 ± 0.65	0.32 ± 0.29	0.09 ± 0.16	
	3	Desmodoridae			0.17 ± 0.30					
	1	Monhysteridae				0.16 ± 0.28				0.21 ± 0.36
	1	Panagrolaimidae	0.09 ± 0.16							
	2	Plectidae	0.09 ± 0.16					0.34 ± 0.38	0.39 ± 0.16	
	1	Rhabditidae	0.47 ± 0.57	0.25 ± 0.35			0.23 ± 0.33			
Omnivores	3	Achromadoridae								0.08 ± 0.14
	4	Leptonchidae			0.10 ± 0.17					
	4	Qudsianematidae			0.10 ± 0.17			0.10 ± 0.17		
	5	Thornenematidae	0.73 ± 0.84	0.49 ± 0.70	0.10 ± 0.17		0.12 ± 0.16		0.05 ± 0.09	
Predators	4	Mononchidae			0.10 ± 0.17					
	3	Tripylidae			0.04 ± 0.07					
Number of families (total)			**13**	**6**	**16**	**10**	**7**	**10**	**8**	**3**

Table 5. Spearman correlation coefficient (ρ) for nematode trophic groups (ind./g DW soil) and soil parameters and total PLFA (phospholipid fatty acid) density across all soil depths (0–240cm) for Hintere Stellimatten (HST) and Verbindungsweg (VW). % C, % H and % N represent the proportion of the respective element on the dry weight in percent.

Site	Trophic group	DOC		NO_3^-		SO_4^{2-}		pH		% C		% H		% N		PLFAs	
		ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*
HST	Plant feeders	0.7	**0.0003**	0.74	**0.0001**	0.21	0.358	0.06	0.779	0.62	**0.008**	0.55	**0.021**	0.51	0.038	0.8	**0.007**
	Fungal feeders	0.15	0.505	0.19	0.401	0	0.992	0.19	0.393	0.19	0.470	-0.02	0.940	0.05	0.855	0.21	0.359
	Bacterial feeders	0.54	**0.010**	0.59	**0.004**	0.22	0.331	0.28	0.204	0.41	0.102	0.32	0.208	0.26	0.308	0.64	**0.001**
	Omnivores	0.41	0.058	0.33	0.134	0.42	0.053	0.21	0.344	0.3	0.240	0.31	0.228	0.18	0.481	0.4	0.069
	Predators	0.24	0.292	0.22	0.321	-0.12	0.602	-0.28	0.213	0.15	0.557	0.15	0.557	0.1	0.696	0.05	0.830
	Total population density	0.74	**0.0001**	0.76	**0.022**	0.21	0.342	0.02	0.923	0.65	**0.003**	0.6	**0.009**	0.54	**0.022**	0.81	**0.003**
VW	Plant feeders	0.53	**0.010**	0.61	**0.002**	0.26	0.239	-0.26	0.228	0.52	**0.027**	0.51	**0.030**	0.52	**0.029**	0.45	**0.031**
	Fungal feeders	0.46	**0.026**	0.41	**0.049**	0.22	0.308	-0.15	0.502	0.35	0.153	0.35	0.153	0.35	0.154	0.32	0.138
	Bacterial feeders	0.41	**0.048**	0.5	**0.016**	0.33	0.125	-0.02	0.942	0.42	0.083	0.41	0.089	0.36	0.139	0.42	**0.043**
	Omnivores	0.52	**0.010**	0.5	**0.016**	0.41	**0.050**	-0.27	0.206	0.37	0.134	0.39	0.107	0.42	0.079	0.08	0.704
	Predators																
	Total population density	0.74	0.058	0.7	**0.0002**	0.52	**0.011**	-0.15	0.488	0.79	**0.0001**	0.74	**0.001**	0.73	**0.001**	0.65	**0.001**

Table 6. Maturity Index (*MI*), Plant Parasite Index (*PPI*) and Shannon diversity Index (*H'*) ± SD for nematode communities present in a soil gradient from 0 to 120 cm depth for Hintere Stellimatten (HST) and Verbindungsweg (VW).

Index	Habitat	Depth [cm]			
		0–30	30–60	60–90	90–120
MI	HST	2.95 ± 1.83	1.72 ± 2.44	2.14 ± 1.85	1.94 ± 0.10
	VW	1.21 ± 1.72	1.50 ± 1.32	2.83 ± 1.44	1.33 ± 1.53
PPI	HST	2.23 ± 0.25	2.25 ± 0.35	2.11 ± 0.18	2.33 ± 0.17
	VW	1.18 ± 1.67	2.47 ± 0.29	1.78 ± 1.58	0.67 ± 1.15
H‘	HST	1.70 ± 1.02	0.91 ± 0.31	1.54 ± 0.78	1.83 ± 0.65
	VW	0.93 ± 1.31	1.71 ± 0.57	0.87 ± 0.80	0

Table 7. Similarity percentage (SIMPER) analysis of the individual nematode family contribution (%) to the dissimilarity of nematode community patterns in 0–30, 30–60, 60–90 and 90–120 cm soil depth at Hintere Stellimatten (HST) and Verbindungsweg (VW).

Groups (sites & depths)	Average group dissimilarity	Families	Average abundance		Average family dissimilarity	Contribution of families to group dissimilarity (%)
HST0-30 & HST30-60	80.21		HST0-30	HST30-60		
		Paratylenchidae	0.86	0.62	24.60	30.66
		Tylenchidae	0.29	0.07	9.02	11.24
		Hoplolaimidae	0.31	0.14	8.20	10.23
		Cephalobidae	0.23	0.00	8.01	9.99
		Dolichodoridae	0.32	0.00	5.69	7.09
HST0-30 & HST60-90	79.42		HST0-30	HST60-90		
		Paratylenchidae	0.86	0.41	17.45	21.97
		Tylenchidae	0.29	0.19	10.30	12.97
		Hoplolaimidae	0.31	0.08	7.25	9.14
		Cephalobidae	0.23	0.08	6.60	8.31
		Rhabditidae	0.17	0.00	5.60	7.05
HST0-30 & HST90-120	73.48		HST0-30	HST90-120		
		Paratylenchidae	0.86	0.30	18.46	25.12
		Tylenchidae	0.29	0.13	8.11	11.03
		Dolichodoridae	0.32	0.06	6.44	8.76
		Hoplolaimidae	0.31	0.15	6.30	8.57
		Rhabditidae	0.17	0.00	5.72	7.78
HST30-60 & HST60-90	76.76		HST30-60	HST60-90		
		Paratylenchidae	0.62	0.41	25.62	33.37
		Tylenchidae	0.07	0.19	8.54	11.12
		Pratylenchidae	0.07	0.00	5.49	7.16
		Thornenematidae	0.16	0.06	5.13	6.68
		Hoplolaimidae	0.14	0.08	4.63	6.03

Table 7 continued

Groups (sites & depths)	Average group dissimilarity	Families	Average abundance		Average family dissimilarity	Contribution of families to group dissimilarity (%)
HST30-60 & HST90-120	82.75		HST30-60	HST90-120		
		Paratylenchidae	0.62	0.30	22.56	27.26
		Cephalobidae	0.00	0.20	9.96	12.04
		Tylodoridae	0.00	0.19	9.56	11.55
		Tylenchidae	0.07	0.13	8.51	10.29
		Hoplolaimidae	0.14	0.15	8.00	9.67
VW0-30 & VW30-60	63.80		VW0-30	VW30-60		
		Pratylenchidae	0.37	0.14	8.92	13.99
		Rhabditidae	0.21	0.00	7.90	12.38
		Cephalobidae	0.30	0.14	6.64	10.41
		Anguinidae	0.15	0.00	5.58	8.75
		Paratylenchidae	0.15	0.00	5.58	8.75
VW0-30 & VW60-90	76.36		VW0-30	VW60-90		
		Pratylenchidae	0.37	0.10	13.22	17.31
		Cephalobidae	0.30	0.06	11.78	15.42
		Rhabditidae	0.21	0.00	10.25	13.42
		Tylenchidae	0.26	0.06	9.83	12.88
		Anguinidae	0.15	0.00	7.25	9.49
VW0-30 & VW90-120	88.12		VW0-30	VW90-120		
		Pratylenchidae	0.37	0.00	20.19	22.91
		Cephalobidae	0.30	0.00	16.49	18.71
		Rhabditidae	0.21	0.00	11.66	13.23
		Tylenchidae	0.26	0.11	8.34	9.46
		Anguinidae	0.15	0.00	8.24	9.35
VW30-60 & VW60-90	71.05		VW30-60	VW60-90		
		Tylenchidae	0.31	0.06	17.35	24.43
		Plectidae	0.15	0.11	10.65	14.99
		Cephalobidae	0.14	0.06	7.08	9.97
		Pratylenchidae	0.14	0.10	6.56	9.24
		Hemicycliophoridae	0.09	0.04	6.54	9.21
VW60-90 & VW90-120	91.65		VW60-90	VW90-120		
		Plectidae	0.11	0.00	19.83	21.64
		Monhysteridae	0.00	0.12	17.36	18.94
		Tylenchidae	0.06	0.11	15.64	17.06
		Pratylenchidae	0.10	0.00	12.27	13.39
HST0-30 & VW0-30	69.65		HST0-30	VW0-30		
		Paratylenchidae	0.86	0.15	13.62	19.55

Table 7 continued

Groups (sites & depths)	Average group dissimilarity	Families	Average abundance		Average family dissimilarity	Contribution of families to group dissimilarity (%)
		Pratylenchidae	0.00	0.37	9.93	14.26
		Tylenchidae	0.29	0.26	9.31	13.37
		Hoplolaimidae	0.31	0.00	6.62	9.50
		Dolichodoridae	0.32	0.00	5.16	7.41
HST30-60 & VW30-60	78.44		HST30-60	VW30-60		
		Paratylenchidae	0.86	0.00	19.59	24.98
		Tylenchidae	0.07	0.31	11.48	14.63
		Plectidae	0.00	0.15	6.50	8.29
		Cephalobidae	0.00	0.14	5.92	7.55
		Dolichodoridae	0.00	0.12	5.15	6.56
HST60-90 & VW60-90	89.59		HST60-90	VW60-90		
		Paratylenchidae	0.41	0.00	21.35	23.83
		Tylenchidae	0.19	0.06	13.07	14.59
		Plectidae	0.00	0.11	8.08	9.02
		Pratylenchidae	0.00	0.10	5.90	6.58
		Desmodoridae	0.08	0.00	5.61	6.27
HST90-120 & VW90-120	92.55		HST90-120	VW90-120		
		Cephalobidae	0.20	0.00	14.89	16.09
		Paratylenchidae	0.30	0.00	14.77	15.96
		Tylodoridae	0.19	0.00	14.37	15.53
		Tylenchidae	0.13	0.11	12.45	13.45
		Hoplolaimidae	0.15	0.00	12.35	13.34

line with this is the low Plant Parasite Index (*PPI*) ranging from 2.11 ± 0.18 to 2.33 ± 0.17 at HST and from 0.67 to 2.47 ± 0.29 at VW. The diversity at both investigated sites was low as indicated by a Shannon diversity Index (*H'*) ranging from 0.91 ± 0.31 to 1.83 ± 0.65 at HST and from 0 to 1.71 ± 0.57 at VW.

3.5 Community distribution

Multivariate analysis of nematode population density with one-way ANOSIM (habitat x depth) revealed a separation by site but not depth (Global R = 0.057, significance level of sample statistic = 32.2 %).

The SIMPER analysis (Tab. 7) revealed that the average group dissimilarity between communities was higher between HST and VW (83 %) than within communities at HST (79 %) and VW (78 %). In detail, the highest average group dissimilarity occurred between HST and VW in a depth of 90–120 cm (93 %) with the family Cephalobidae contributing most to the group dissimilarity with 16 %. The lowest group dissimilarity existed between the depths of 0–30 cm and 30–60 cm at VW (64 %). In general, Paratylenchidae and Tylenchidae were the families that contributed most to the group dissimilarity with an average of 23 % and 14 %, respectively.

4. Discussion

Although nematode findings have been reported down to 1.4 km (Borgonie et al. 2015), the aspect of depth distribution of nematodes has been studied very rarely so far. Thus, the present work gives first insights about the nematode fauna in an entire depth transect from topsoil to the aquifer. The sampling campaign at the forested flooding site 'Lange Erlen' of an artificial groundwater recharge system was carried out together with the authors Schütz et al. Therefore, the results concerning microbial

biomass, activity and PLFA patterns cited in the following refer to the same bore cores as the nematode data and are discussed in detail in Schütz et al. (2008, 2009, 2010).

4.1 Nematode taxa along a depth gradient

The investigation of the vertical distribution of nematode species along the depth gradient from the soil surface to a depth of 450 cm at the 'Lange Erlen' revealed a heterogenous distribution pattern of species. Around half of all taxa occurred in only one soil layer which implies the existence of several distinct microhabitats derived from changes in soil physical properties and resource availability. For example, *Heterocephalobus* cf *bisimilis* and *Heterocephalobus* spp. were restricted to the 0–30 cm soil layer. Analogously, *Heterocephalobus* was only found in the top soil layer in a *Pinus radiata* stand (Yeates et al. 2000). All taxa of the Dolichodoridae, except *Tylenchorhynchus,* were restricted to the upper soil layers, i.e. *Merlinius* spp. and *Paratrophurus* spp. to 0–30 cm and *Trophurus* spp. to 0–60 cm soil depth. Although both are ectoparasites and exploit the same resources, the taxa of the Paratylenchidae, especially *Gracilacus* spp. and *Paratylenchus* spp., did not just have a higher vertical distribution but also a higher abundance than the Dolichodoridae. This matches findings from natural birch forests where the abundance of paratylenchids exceeds that of dolichodorids (Renčo et al. 2012). The dominance of Paratylenchidae over Dolichodoridae is likely caused by their higher colonization potential and tolerance to disturbances (Bongers & Bongers 1998). *Cephalobus persegnis* was the only species present in the lower vadose zone (220–450 cm). The occurrence of the genus *Cephalobus* at higher depth corresponds to a study of Liang et al. (2005) investigating the bacterial grazing nematode community under different land uses in a gradient from surface layer down to 150 cm. As *Cephalobus persegnis* is the most common species of the genus living in various terrestrial habitats (Andrassy 2005) it is not surprising to find exactly this species at greater depth at the 'Lange Erlen'.

Of all the species found, 52 % are terricolous while 46 % occur also in water habitats. The high proportion of nematodes found in the investigated soil adapted to aquatic environments fits to the periodical flooding at the 'Lange Erlen'. Even the predominantly limnic *Prodesmodora* spp. and the exclusively limnic species *Eumonhystera longicaudatula* were found at the artificial water recharge area. Although the flooding water was not examined for nematodes, it is likely that these species were transported into the 'Lange Erlen' habitat by flooding with river Rhine water. Even though the soil sampling was carried out four weeks after the last flooding, the ability of *Prodesmodora* spp. to exist in terrestrial circumstances (Andrassy 2005), presumably allowed it to survive the draining period. Further, *Eumonhystera longicaudatula* can be found in the sediment of lakes (Andrassy 2005), where environmental conditions may be similar to those in the soil at the 'Lange Erlen' floodplain and thus enable survival.

Nevertheless, the most abundant and common species found at the 'Lange Erlen' are exclusively terrestrial. In detail, the root feeders *Gracilacus* ssp. and *Pratylenchus pseudopratensis* were the species with the highest abundance across depths with a total of 149 and 11 individuals in HST and VW, respectively. However, in comparable deciduous forests not affected by inundation the abundances of these two genera were already much higher at a depth of 0–20 cm with 510 and 294 individuals for *Gracilacus* and *Pratylenchus*, respectively (Renčo et al. 2012), indicating that flooding affects nematode numbers. The most common species were the plant feeders *Rotylenchus quartus*, *Gracilacus* spp. and *Filenchus teres* with individuals of each species found in 5 out of 8 different soil depths. Correspondingly, a study investigating the depth distribution of nematodes from the top soil (0–10 cm) over the rooted zone (40–50 cm) to the root-free zone (60–70 cm) in an arable soil reported *Filenchus* findings from all three examined soil layers (Ewald et al. 2020). However, *Rotylenchus* occurred only once in the 40–50 cm layer while *Gracilacus* was completely absent. This low distribution matches a report from an oak forest where both genera were found in less than half of the samples (Lazarova et al. 2004). The high vertical occurrence at the 'Lange Erlen' is, therefore, likely caused by the translocation of individuals by flooding with river water.

4.2 Relationship between soil properties and nematode density

The population density of nematodes at the examined regularly flooded forest sites strongly decreased with depth from the surface soil layer (0–100 cm) to the lower vadose zone (220–450 cm) at HST and VW with on average 46 % of the total nematode density located in the uppermost soil layer (0–30 cm). In comparison, the upper and lower vadose zone combined (100–450 cm) comprised on average 2 % of the total nematode density. This decline is most likely attributed to a decrease in major resources and changing soil properties (Yeates & Bongers 1999). Nematode density particularly correlated with the decline of DOC, NO_3^-, SO_4^{2-}, H, C and N, suggesting that

mineralization processes take place predominantly in the first 30 cm of the soil profile. Correspondingly, microbial biomass and PLFA content were highest in the top soil as reported by Schütz et al. (2010). Microbial activity i.e. mineralization rates and nutrient supply are highest in the rhizosphere (Kuzyakov & Xu 2013). Subsequently, a decline in root density with depth indirectly causes a decline in nematode density as a result of a decreasing number of microorganisms. Mirroring this, nematode numbers strongly decreased below the assumed rooting depth of the herbaceous vegetation cover (approximately at 90 cm soil depth) at the 'Lange Erlen'. The finding of only two nematode individuals in the lower vadose zone (below 220 cm soil depth) further underlines the decline in nutrients and microbial food sources along the depth gradient.

On the other hand, nematode density did not correlate with pH, as it hardly fluctuated with depth. This is most likely due to regular flooding with Rhine water at a relatively constant pH value of 8.2 (Schütz et al. 2009).

Nematode densities varied considerably with site, with an average of 9 times higher density at HST than VW. But since the values of the soil parameters of the two sites are similar in the uppermost soil layer (0–30 cm), they can be excluded as the cause of the different nematode densities at HST and VW. The only site-specific difference is soil particle size, i.e. a higher amount of artificial landfill exists at HST compared to VW. Presumably, the higher content of silt microaggregates of the landfill layer at HST (down to 100 cm) positively affected the nematode community, as nematodes prefer coarse-textured soils (Ronn et al. 1995).

Additionally, nematode densities in the uppermost soil layer (0–30 cm) at the 'Lange Erlen' were much lower than in comparable riparian forest sites (e.g. Pavao-Zuckerman & Coleman 2007). However, similar numbers are reported from paddy fields (e.g. Hu et al. 2018). The general low nematode densities of flooded habitats compared to non-flooded sites (Háněl 2002) is caused by the waterlogging of soils. The oxygen limitation in such soils depresses nematode activity and abundance (Liu et al. 2008). Correspondingly, the occurrence of anaerobic conditions at the watered sites at the 'Lange Erlen' was indicated by high PLFA iso/anteiso ratios (Schütz et al. 2009).

4.3 Nematode trophic structure along a depth gradient

In contrast to nematode density, the pattern of trophic groups showed no distinct depth profile. At the 'Lange Erlen', frequent flooding events likely caused the vertical transfer of soil microorganisms and nutrients, resulting in soil layers with similar nutritional resources. Underlining this, Schütz et al. (2009) found comparable PLFA profiles, i.e. microbial community patterns at each depth.

The most dominant nematodes in each soil layer (except in 60–90 cm depth at VW) were plant feeders (65 % across depths). This matches reports that plant feeders are the main trophic group in riparian forests (Margenot & Hodson 2016). The top soil was predominated by plant feeders of the ectoparasitic Paratylenchidae (HST) and endoparasitic Pratylenchidae (VW). Below a depth of 90 cm, the composition of plant-associated nematodes differed between sites: At HST, obligate plant feeders, mainly Paratylenchidae dominated. On the other hand, at VW plant feeders belonged exclusively to the genus *Filenchus*, facultative root-/fungal feeders (Yeates et al. 1993) with the ability to switch to a fungal-based diet when herbaceous plant roots become sparse. However, no fungal feeders have been detected in this soil layer at VW.

Bacterial feeders occurred with a proportion of 26 % across depths at the 'Lange Erlen'. The majority of bacterial feeders were Cephalobidae and Plectidae, general opportunists (*c-p* 2) that survive under food-poor conditions and are very tolerant to disturbances (Bongers & Bongers 1998). These traits make Cephalobidae the predominating nematode family under field conditions worldwide (Yeates 2003). On the other hand, the enrichment opportunists (*c-p* 1) *Rhabditis* spp. and *Eumonhystera* spp. occurred only occasional and in low densities pointing to a generally low nutrient availability at the studied sites as these taxa are known for an explosive population growth under food-rich conditions (Bongers & Bongers 1998).

Fungal feeders were almost completely absent with a proportion of 2 % across depths. Similar findings were reported from paddy fields (Liu et al. 2008). The lack of fungal feeders indicates a minor importance of the fungal energy channel for the faunal food web at 'Lange Erlen'. Supporting this, an analysis of soil PLFAs at HST and VW revealed a low ratio of fungi to bacteria ranging from 0.04 to 0.14 across sites and depths (Schütz et al. 2009). Presumably, the frequent flooding and anaerobic conditions suppressed mycorrhizal colonization and diversity (Parádi & Baar 2006).

Omnivores and predatory nematodes were only a minor proportion (7 % across depths) of the nematode assemblage, indicating that the soil faunal community supports only few large omnivorous and predacious nematodes. However, their representatives are mostly large individuals. Hence, according to their biomass, they might play a larger role within the soil food web

than is indicated by their low abundance. Underlining this, omnivores and predators contributed much to ecosystem function in riparian woodland sites as estimated by their high biomass and metabolic footprint (Hodson et al. 2014).

4.4 Community structure and diversity along a depth gradient

The dissimilarity in nematode community patterns at HST and VW increased with depth, as indicated by SIMPER analysis. Presumably, this is caused by the soil texture at HST and VW, which starts to differ at 40 cm soil depth. Moreover, SIMPER analysis unveiled that plant feeders contributed most to the community dissimilarity in the upper soil layer, while the impact of bacterial feeders increased with depth. Likely, the differing plant species in the herb layer at HST and VW shaped distinct assemblages of plant feeders in the top soil. Correspondingly, Wasof et al. (2019) reported that vegetation composition influences nematode assemblages. On the other hand, in deeper soil layers (below 90 cm soil depth), which lack herbaceous plant roots, bacterial resources became more important in shaping the nematode communities at the 'Lange Erlen'.

The state of the ecosystem in relation to disturbance was assessed by the calculation of the indices *MI* and *PPI*. Both indices were low with values of 2.0 and 1.9 for *MI* and *PPI* across depths and sites, respectively. Higher values were reported for paddy fields and deciduous forests (Háněl 2008, Wang et al. 2019). Thus, it can be assumed that the 'Lange Erlen' area is a relatively disturbed habitat. The cyclical disturbance of waterlogging causes changes in temperature as well as aerobic and anaerobic conditions unfavorable for certain nematode taxa. Accordingly, long-living *K*-strategists that are characteristic for habitats with a long durational stability (Bongers 1990), e.g. *Prodorylaimus* and *Eudorylaimus* occurred only sporadically, as they experience several flooding and regeneration events at the 'Lange Erlen'. On the other hand, short-living *r*-strategists that are tolerant to a wide range of environmental factors (Bongers & Bongers 1998) and probably experienced only one flooding cycle, dominated the nematode fauna at 'Lange Erlen'. Further, *MI* and *PPI* showed no clear depth related pattern, indicating varying degrees of disturbance along the depth profile. Contrasting this, a PLFA analysis at HST and VW revealed that the stress indicating *trans/cis* ratio was constant with depth (Schütz et al. 2009), indicating similar levels of disturbance in different soil layers.

The diversity of the nematode community, expressed as the index *H'*, was low with values between 0.9 and 1.8 across sites and depth. Low nematode diversity as consequence of disturbance has been reported for a wide range of habitats (Hodda et al. 2009). Like *MI* and *PPI*, *H'* showed no depth dependency, but rather fluctuating values along the depth profile. Likely, spatial heterogeneity, e.g. due to differing pore sizes or changes in soil physical properties, created microhabitats with distinct nematode metacommunities and diversities (Scharroba et al. 2016).

5. Conclusion

The present study is the first investigation of the nematode fauna in an entire depth transect from top soil to the vadose zone providing new insights on the functional properties of the vertical distribution of nematodes. Analyzing the species composition of the nematode community revealed a heterogenous distribution pattern of species along the depth gradient, implying the existence of distinct microhabitats. Nematode population density strongly decreased along the depth profile, which was associated to a decline in DOC, NO_3^-, SO_4^{2-}, H, C and N. This suggests that mineralization processes take place predominantly in the uppermost soil layer (0–30 cm) at 'Lange Erlen'. Opposing nematode density, trophic structure was not altered by depth, pointing to similar nutritional conditions along the depth profile, presumably caused by flushes through frequent flooding. Decomposition was mainly mediated by the bacterial carbon and energy channel as indicated by the lack of fungal feeders. Long-term water recharge practice enhanced the overall disturbance and reduced diversity, resulting in a nematode community mainly composed of opportunistic taxa with a wide ecological amplitude.

All in all, the nematode survey at species level enabled investigations of the nematode community composition in a very high resolution. Additionally, the quantification and evaluation of the disturbance level at the 'Lange Erlen' caused by artificial water recharge highlights the importance of nematodes as biomarkers.

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