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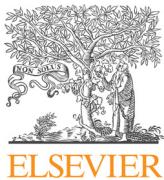
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Spatial distribution of soil nematodes relates to soil organic matter and life strategy



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ABSTRACT

Soils are among the most biodiverse and densely inhabited environments on our planet. However, there is little understanding of spatial distribution patterns of belowground biota, and this hampers progress in understanding species interactions in belowground communities. We investigated the spatial distribution of nematodes, which are highly abundant and diverse metazoans in most soil ecosystems. To gain insight into nematode patchiness, we mapped distribution patterns in twelve apparently homogeneous agricultural fields (100 m × 100 m each) with equal representation of three soil textures (marine clay, river clay and sandy soil). Quantitative PCRs were used to measure the abundances of 48 distinct nematode taxa in ~1200 plots. Multivariate analysis showed that within this selection of sites, soil texture more strongly affected soil nematode communities than land management. Geostatistical analysis of nematode distributions revealed both taxon-specific and field-specific patchiness. The average geostatistical range (indicating patch diameter) of 48 nematode taxa in these fields was 36 m, and related to soil organic matter. Soil organic matter content affected the spatial variance (indicating within-field variation of densities) in a life-strategy dependent manner. The r-strategists (fast-growing bacterivores and fungivores) showed a positive correlation between organic matter content and spatial variance, whereas most K-strategists (slow-growing omnivores and carnivores) showed a negative correlation. Hence, the combination of two parameters, soil organic matter content and a general life-strategy characterisation, can be used to explain the spatial distribution of nematodes at field scale.

1. Introduction

Belowground communities are extremely biodiverse, and drive the flow of carbon and nutrients in terrestrial ecosystems (Bardgett and Van der Putten, 2014; Wall et al., 2015). In spite of the contribution of soil biota to major ecosystem processes such as carbon fixation, nutrient cycling, pathogen incidence and disease suppressiveness, little is known about their spatial distribution (Ettema and Wardle, 2002). Here, we examine the spatial distribution of nematodes, which are a major component of soil communities represented in all trophic levels of the soil food web.

Physical and chemical soil characteristics are important determinants of soil microbial communities. Soil texture co-defines aspects such as aeration, water holding capacity and the topology of root systems that affect the spatial distribution of species in soil communities (Ruamps et al., 2011). Fine-textured soils typically contain more

microbes and smaller nematode taxa than coarse textured soils (Naveed et al., 2016; Sechi et al., 2018). Evidently, species in soil communities are influenced by the application of additional nutritional inputs. Short-lived flushes of easily accessible carbon and nitrogen applied in conventional agriculture have been shown to result in bacterial-dominated communities, whereas a more dominant role of fungi in the soil food web is observed when more recalcitrant food sources are introduced to the system (Maharning et al., 2009; de Vries et al., 2012; Morriën et al., 2017). These studies illustrate how soil type and land management may steer the composition and distribution of soil food web constituents.

Even in apparently homogeneous agricultural fields, where gradients in physical or chemical soil characteristics are expected to be less steep than in natural systems, the spatial distribution of soil biota at field scale is still patchy (Robertson and Freckman, 1995; Ettema and Wardle, 2002). Microbial patchiness was first pinpointed in an arable field by Franklin and Mills (2003) who used AFLP markers to map

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bacterial communities. Patch diameters of several meters (5–50 m) typified various fractions of the bacterial community in grasslands (Ritz et al., 2004; Philippot et al., 2009a, 2009b; Regan et al., 2017). With regard to their ecological characteristics, members of individual bacterial phyla present in soil were shown to form remarkably coherent groups (Fierer et al., 2007; Philippot et al., 2010). This implies that even information about the bacterial distribution patterns at phylum level is ecologically informative. Spatial distribution data on bacterial taxa, functional genes and enzymatic activities from apparently homogeneous soil ecosystems all show distance decay relationships at a scale of several meters (Philippot et al., 2009b). To better understand the functioning of the soil food web, it is essential to gain insight in the spatial distribution at field scale level from other major organismal groups as well. However, such data from soil biota other than bacteria are scarce, and often limited to a very few representatives of a given organismal group (e.g. Ettema et al., 1998). Green and Bohannan (2006) hypothesized that there might be no fundamental differences in spatial scaling between the micro and macro-organism in soil. So far it has been impossible to test this hypothesis.

As compared to soil bacteria of which 60% has a diameter smaller than 1.2 μm (Portillo et al., 2013), soil nematodes are considerably larger. The length of terrestrial nematodes ranges from 150 to 1500 μm , with a width of 10–55 μm (Vonk et al., 2013). Nematodes are therefore labelled as microfauna. Bacteria and fungi are the main nutritional resource of bacterivorous and fungivorous nematodes, which are in turn the prey of predatory nematodes. Hence, mapping the distribution of a wide range of nematode taxa will allow us to test whether there are fundamental differences in distribution patterns between microbes, their consumers and the top-consumers of the soil food web.

Unlike bacteria and fungi, nematodes do not directly contribute to primary decomposition of organic material. Bacterivorous, fungivorous, herbivorous, omnivorous and carnivorous nematodes can be discerned, and as such they are represented in all higher trophic levels of the soil food web. Life strategies of nematode families have been ranked on a 1–5 colonizer persister (cp) scale (Bongers, 1990). Nematode in cp category 1 are opportunistic and grow fast (r-strategists *sensu lato*), whereas taxa with cp-5 are characterized by a long generation time, low fecundity and a high sensitivity to disturbances (K-strategists *sensu lato*). For nematodes, feeding preference and life strategies are loosely correlated: bacterivores are mainly found in cp categories 1–3, fungivores in cp-2-3, and omnivores and predators cp-4-5. Based on this, we hypothesize that patch sizes at field level of bacterivorous members of cp classes 1–3 might be different – probably larger – than those of omnivores or plant parasites in cp-3-5.

Robertson and Freckman (1995) were among the first that published spatial distribution maps of nematodes from various trophic groups, in this case an apparently homogeneous 48-ha corn field. The range for bacterivores, fungivores and omnivores/predators was determined at 35, 77 and 41 m respectively with relatively high sample variances, and plant parasites did not show any spatial dependency at this scale. The fact that trophic groups are composed of multiple, phylogenetically unrelated lineages (e.g. Holterman et al., 2006) may have contributed to this level of uncertainty. In a detailed study by Ettema et al. (1998), the distributions of eight different bacterivorous taxa were mapped in a 0.7-ha restored riparian wetland. For six taxa, ranges were all in the tens of meters scale: 28 m for a cp-1 representative (Rhabditinae), 66 m for *Acrobeloides* (Cephalobidae; cp-2), and 24 m for *Rhabdolaimus* (Rhabdolaimidae; cp-3). These studies revealed divergent spatial distribution patterns for individual taxa and feeding types in single fields. Due to practical limitations – spatial distribution studies at field scale are extremely labour intensive – broader surveys that cover multiple fields and focus on nematode taxa that differ e.g. in feeding type, life strategy and body size, are so far lacking.

In the present study, we examined belowground distribution patterns of 48 nematode taxa including all major feeding types, all cp

categories and a range of body sizes. Twelve apparently homogeneous fields (each 1 ha, 100 m \times 100 m) were investigated: four fields from each of the three selected soil textures (marine clay, river clay and sandy soil). Nine arable farmlands were included next to three semi-natural grasslands (one for each soil texture type). Based on a sampling design optimized for geostatistical modelling, about 100 composite samples were collected from each of the twelve fields, and 35,000 quantitative data points on abundances of individual nematode taxa were generated. Within-field spatial variation of nematode taxa was analysed by a Bayesian geo-statistical method using Integrated Nested Laplace Approximations (INLA). The combined use of a sampling scheme optimized for geostatistical analysis, and a quantitative high throughput system for the characterization of nematode communities, allowed us to generate ‘nemascapes’; maps of the belowground distribution of nematodes at field level. With these ‘nemascapes’ we were able to verify whether there is a fundamental difference in spatial distribution between microbiota such as soil bacteria, and soil fauna here represented by nematodes. The current data also allowed us to test whether patch sizes at field level of bacterivorous members of cp classes 1–3 are different – probably larger – from those of omnivores or plant parasites in cp-3-5.

2. Material and methods

2.1. Sampling design

Across the Netherlands, twelve fields were sampled: nine arable farmlands and three semi-natural grasslands on three soil types (marine clay, river clay and sand; Table 1 and Fig. 1). 1476 composite soil samples were collected during the winter-period between December 2012 and April 2013. Each location ($n = 12$) had a single management regime for at least 15 years. No nematicides had been applied in the fields during this period. Taking into consideration prior knowledge about land-use history, disturbances, productivity and soil texture, a visually homogeneous area (1 ha, 100 \times 100 m) was demarcated within each location. Such a 1 ha square is referred to as a “field”. A sampling design was developed for geo-statistical analysis at field scale and contained in six fields $16 \times 6 = 96$ plots and in six other fields $96 + 20 = 116$ plots. To facilitate soil sampling, each field was divided into 16 sub-fields (25 \times 25 m). In or near the centre of each sub-field (Fig. 1), six plots (here defined as a circular surface of 0.25 m^2) were placed along a transect. A Golomb-ruler was used to position the plots along the transects, and the direction of the transects was regularly alternated in such a way that a more-or-less even distribution of distances between plots was obtained ranging from 0.5 to about 100 m (Fig. 1). In six out of 12 fields, four additional plots were sampled in fivefold, in the centre (for details see Fig. 1 and Quist et al., 2017). This sampling design resulted in a total of $6 \times 96 + 6 \times 116 = 1272$ plots for nematode community analysis. Based on previous results of Quist et al. (2017) composite samples were collected from these plots that consisted of 12 soil cores (\varnothing 1.5 cm, depth: 20 cm).

Abiotic soil characteristics (pH, organic matter, total nitrogen, total phosphorous, and clay content) were determined by Blgg AgroXpertus (Wageningen), a NEN-EN-ISO 17025 certified service laboratory, using standardized procedures. For this, one composite soil sample of 60 cores (\varnothing 1.5 cm, depth: 20 cm, using a standardized “W”-shaped sampling design) was collected from each of the fields. For organic matter (OM) content measurement, one composite sample of 12 cores (\varnothing 1.5 cm, depth: 20 cm) was collected from each transect, resulting in 16 composite samples per field and 192 composite samples for OM over the whole experiment. Immediately after sampling, all composite samples were mixed thoroughly and stored at 4 °C until further processing.

Table 1

Major soil characteristics of the 1-ha fields under investigation. Soil samples were collected from arable fields (just before the onset of the growing season), and from semi-natural grasslands with high plant diversity. Soil types are indicated by 'm' (marine clay), 'r' (river clay), and 's' (sand) (See also Fig. S1). For each of the locations, five major abiotic soil characteristics were determined: pH (pH-CaCl₂ \pm sd), total nitrogen (N; mg N/kg dry soil), total phosphorus (P; mg P₂O₅/kg dry soil), organic matter (OM \pm SD; %) and clay content (Clay; % soil particles $< 2 \mu\text{m}$). *: Grasses were grown for two consecutive years. ** See Fig. S2 for spatial maps of pH and OM in location De Mossel.

Field	Coordinates	pH	N	P	OM	Clay	Crops in rotation/dominant plant species
Schoondijke (Zeeland; m1)	51° 19' N 3° 31' E	7.5	980	1540	2.6 \pm 0.2	17	Potato, onion, sugar beet, wheat
Draaibrug (Zeeland; m2)	51° 18' N 3° 27' E	7.5	1080	1650	2.9 \pm 0.4	20	Potato, onion, sugar beet, wheat
Lelystad (Flevoland; m3)	52° 32' N 5° 33' E	7.2	1410	1410	2.8 \pm 0.3	17	Potato, onion, sugar beet, wheat
Lauwersmeer (Friesland; m4)	53° 20' N 6° 09' E	7.2	2360	1440	5.0 \pm 0.7	17	<i>Holcus lanatus</i> , <i>Agrostis stolonifera</i> , <i>Ranunculus repens</i> , <i>Trifolium pratense</i>
Wageningen (Gelderland; r1)	51° 57' N 5° 38' E	6.5	1780	2260	5.6 \pm 0.3	32	Potato, barley, sugar beet, grass*
Cortenoever (Gelderland; r2)	52° 06' N 6° 12' E	7.0	1230	1460	2.6 \pm 0.5	7	Corn
Houten (Utrecht; r3)	52° 02' N 5° 09' E	6.7	1760	1910	3.5 \pm 0.5	25	Corn
Millingerwaard (Gelderland; r4)	51° 52' N 6° 00' E	7.0	2050	1930	3.8 \pm 0.9	19	<i>Brassica nigra</i> , <i>Solidago gigantea</i> , <i>Calamagrostis epigejos</i> , <i>Erigeron annuus</i>
Wageningen (Gelderland; s1)	51° 59' N 5° 39' E	5.7	720	1310	2.8 \pm 0.5	2	Potato, barley, sugar beet, wheat, corn, grass*
America (Limburg; s2)	51° 25' N 5° 58' E	5.4	1090	1200	3.6 \pm 0.5	2	Salsify, potato, iceberg lettuce, Chinese cabbage
Sint Kruis (Zeeland; s3)	51° 16' N 3° 30' E	5.3	1490	1440	3.8 \pm 0.5	2	Potato, grass*, barley, wheat, beans
De Mossel** (Gelderland; s4)	52° 03' N 5° 45' E	5.2 \pm 0.2	950	1200	3.2 \pm 0.4	2	<i>Agrostis capillaris</i> , <i>Jacobaea vulgaris</i> , <i>Achillea millefolium</i> , <i>H. lanatus</i> , <i>Plantago lanceolata</i>

2.2. Nematode and DNA extraction, and qPCR-based analysis

Within two weeks after sampling, nematodes were extracted from a 100 g sub-sample of the composite sample using an elutriator (Oostenbrink, 1960). Nematode suspensions were concentrated, and DNA was extracted by a lysis buffer with an internal standard as described by Vervoort et al. (2012). Thereafter, DNA extracts were

purified using a glass fibre column-based procedure (Ivanova et al., 2006). To assess nematode diversity per field, a mixture was made by mixing 3 μl from all the DNA extracts from a given field, and analysed first. All purified DNA extracts were stored at -20°C awaiting further qPCR analyses.

The field-specific DNA mixture was used as template in qPCR using 59 nematode taxon-specific primer sets. Between 25 and 34 taxa were

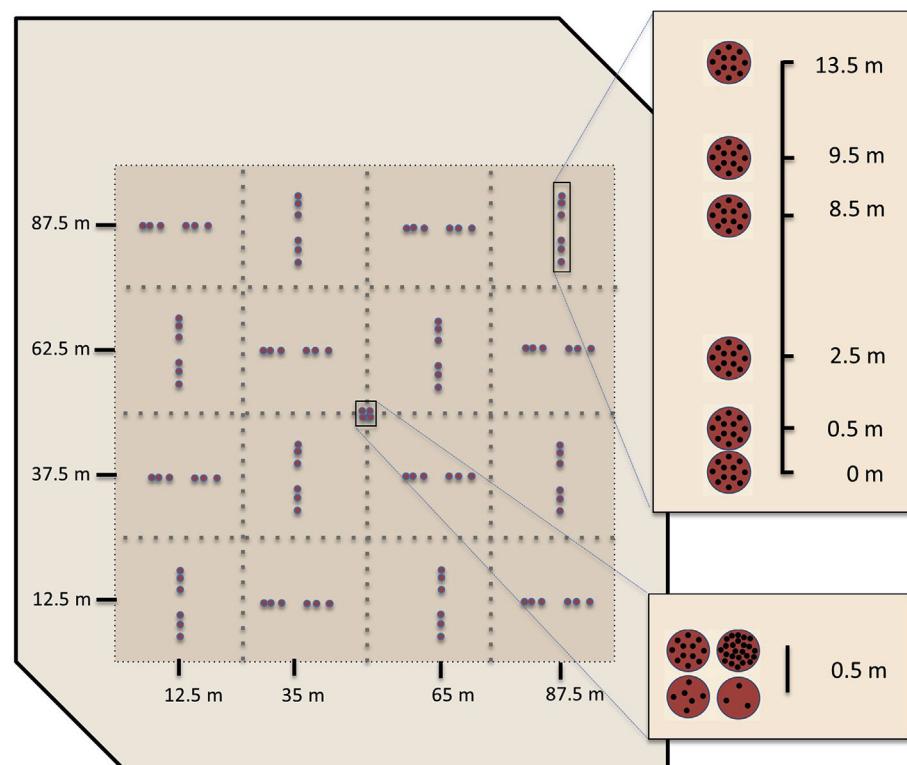


Fig. 1. Sampling design optimized for geostatistical analysis. In or near the centre of each 25 \times 25 m subfield a transect was positioned with six circular plots of 0.25 m². Composite samples were collected by mixing 12 soil cores (\varnothing 1.5 cm, depth: 20 cm). In six fields four additional plots were positioned in the centre of the field, five replicates were sampled from each of these plots.

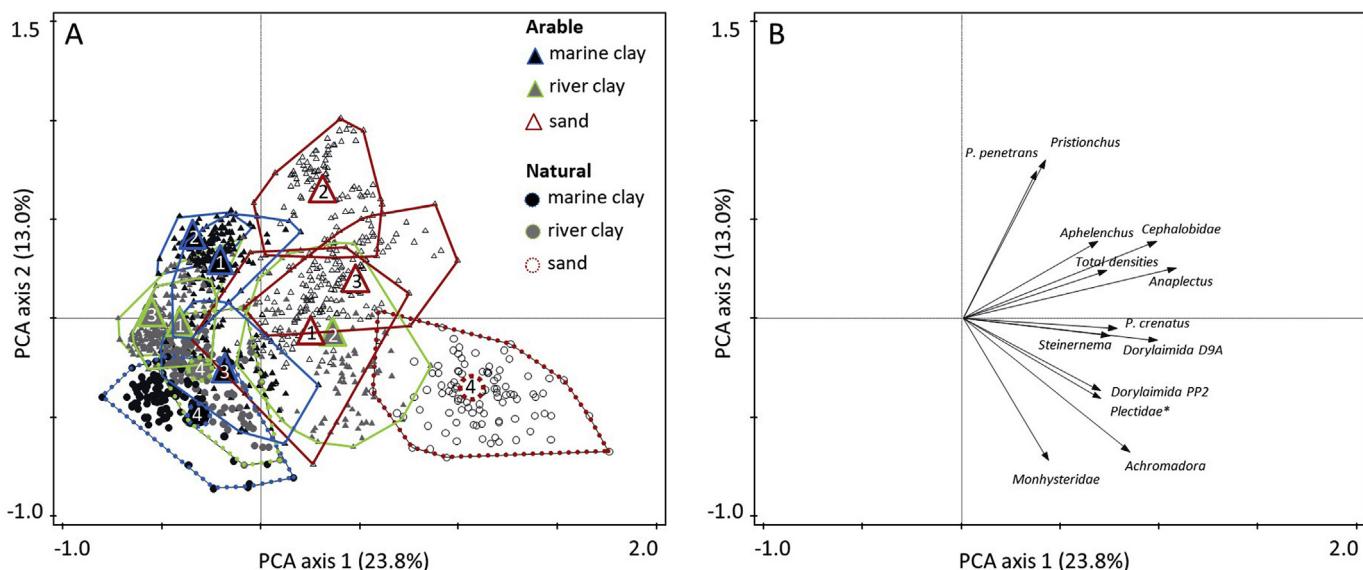


Fig. 2. Ordination plots showing the first and second axis of a principal component analysis (PCA) of the nematode community composition. The percentage of variation explained by each of the axes is shown between brackets. A) Envelopes are drawn around the nematode communities in samples from the same field. The colour of the envelopes refers to soil type: brick, sandy; green, river clay; blue, marine clay. Unbroken lines define envelopes of arable fields, dashed-lines were used for semi-natural grasslands. River clay field 2 ('Cortenoever') had an exceptionally low clay content (7%, while other clay fields had 17–32%). Field numbers (1–4) corresponds to numbers used in Table 1. B) Characterization of nematode community composition in the 12 fields by specific nematode taxa. Thirteen of the nematode taxa that contributed the most to the separation of communities between the fields are shown. The direction and length of the arrows shows the relation of nematode taxa with soil type and land use, as well as the strength of this relation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

detected per field (Table S1). Depending of the nematode diversity assessment, between 24 and 33 nematode taxon-specific primer sets were selected to assess the nematode community in each plot of a given field. Further, primer sets were used to assess total nematode densities and measure an internal control. The internal control was used to monitor loss of DNA during sampling handling. Quantitative PCR reactions were performed, and C_t values were converted to nematode densities by making use of the known linear relationships between C_t values and $^{10}\log$ (number of target nematodes). The maxima of the negative, first mathematic derivative of the melting curves were checked to confirm the correct nature of the amplicons (Vervoort et al., 2012).

2.3. Data analysis

To examine whether system (arable or natural) and soil type (river clay, marine clay or sandy soil) had an effect on nematode community composition, we used principal component (PCA) and redundancy (RDA) analyses (in CANOCO version 5.03, Smilauer and Leps (2014); Fig. 2). The choice of linear methods was justified by the short length of gradients (less than 3.0 SD units). Significances in multivariate analyses were tested using a Monte Carlo permutation test with 999 restricted permutations. The samples collected within one field were permuted at the field level to take into account that these samples are pseudo-replicates. For our analyses, the additional 20 samples collected in the centre of the fields were not included. Three missing samples were replaced by the average values of the fields to which they belonged. The nematode data were $^{10}\log$ -transformed prior to the multivariate analyses. Nematode abundances were analysed further using a model-based two-step procedure:

- 1) For every taxon – field combination, containing the given in at least five plots, the spatial pattern of abundances was quantified with a set of derived parameters, using a (Bayesian) generalized linear geostatistical model analysis. As a by-product, distribution maps of nematode abundances were produced.

- 2) The derived geostatistical parameters were related to nematode and field characteristics using a (frequentist) linear mixed model analysis.

In the first step to quantify the spatial patterns of the abundance of each nematode taxon per field, we applied a Bayesian geostatistical analysis method using SPDE (Stochastic Partial Differential Equations) and INLA (Integrated Nested Laplace Approximations) as available in the R Package R-INLA (Lindgren and Rue, 2015). Because many nematode taxa showed relatively large number of absences at plot level, we used a joint analysis of abundances and presence/absence scores as described by Krainski (2015). We employed a generalized linear geostatistical model with binomial distribution (and logit link function) for the presence/absence data and with gamma distribution (and log link function) for the positive abundances, while specifying a joint Gaussian random field for both, with an extra Gaussian random field for the presence/absence part. In the geostatistical analysis, the Matérn covariance function was used to quantify the spatial distribution (Minasny and McBratney, 2005). For the prior distributions of the parameters in INLA, default settings were used.

In this first step, posterior distributions of geostatistical parameters were determined that together describe the spatial variation. We focused on the following five parameters: mean density (on log-scale), detection probability (DP, on logit-scale), the dispersion of the gamma distribution (on log-scale), and 'range' and 'spatial variance' of the joint Gaussian random field (both on log-scale) being two Matérn covariance function related parameters. 'Range' quantifies how quickly spatial correlations (of the log abundances) decay with distance, whereas 'spatial variance' is a measure for the variation (of the log abundances) explained by the spatial process. The dispersion parameter of the gamma distribution quantifies the non-spatial variation of the abundances, and as such resembles the nugget from Gaussian geostatistical models. It is a relative factor, expressing to what extent the remaining variance is larger (> 1) or smaller (< 1) than the square of the mean nematode densities. Based on the geostatistical models, distribution maps were plotted to assess nematode densities in areas between the

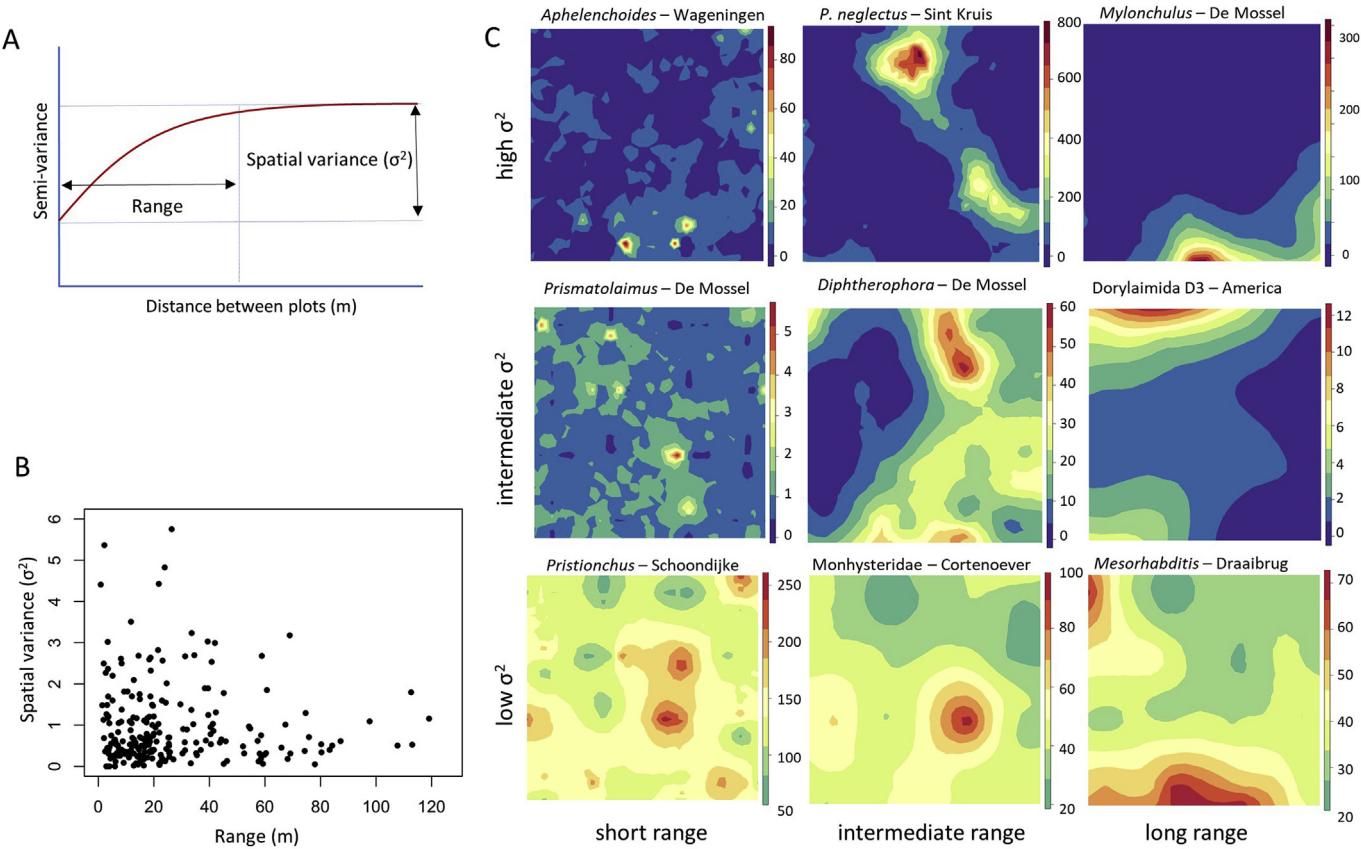


Fig. 3. Patchiness of nematodes at field-scale. 3A. Visualisation of two geostatistical parameters: the spatial variability of abundances (spatial variance: σ^2) and the range (meters). 3B. Analysis of 48 nematode taxa in 12 fields reveal a wide variety in patchiness. A small portion (5%) of the geostatistical models for nematode taxon-specific distributions resulted in a σ^2 above 6, and/or a range longer than 125 m, these points were excluded from this Fig. 3C. Nine 1-ha taxon-specific kriging-maps illustrating low ($\sigma^2 < 0.5$), intermediate ($1.5 < \sigma^2 < 2.5$) and high spatial variability ($3.5 < \sigma^2 < 5$) of nematode abundances (colour bar: # individuals per 100 g soil), in combination with short (4–8 m), intermediate (25–35 m) and long (more than 75 m) ranges. It is noted that scales differ among individual nematode taxa. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sampling points (Figs. 3C and 4).

In the second step, the five geostatistical parameters were analysed. For each geostatistical parameter, the mean of the posterior distribution obtained in step 1 was related both to field characteristics and nematode characteristics. In these analyses, we applied mixed linear models for trait-environment relationships using a tiered forward model selection as described in Jamil et al. (2012). With this method repeated measurements per field (multiple nematode taxa) and per nematode taxon (multiple fields) were accommodated. The null model contained crossed random effects for fields (environments) and taxa. Next, it was determined whether the null model could be improved (1) by inclusion of random field trait trends by taxon (i.e. whether taxa showed variability in their response to field characteristics), (2) by inclusion of fixed field trait trends (i.e. allowing that over-all field trait effects differed from zero), and (3) by inclusion of fixed nematode trait trends, and their interaction with selected field traits. Field traits included system (arable or natural), organic matter content, the standard deviation of organic matter content, pH, nitrogen and phosphorus concentration, and clay content. Nematode traits comprised trophic level, cp value, and nematode body-weight ($^{10}\log$ -transformed). The inverse of the variances of the posterior distributions obtained in step 1 was used as weight in the mixed models. We used R with packages lmer, lmerTest and pbkrtest. Results were visualized using plots, showing trends and predictions of random slopes for taxa.

Based on the final mixed models pseudo- R^2 values for geostatistical parameters were calculated, using and modifying methods introduced by Nakagawa and Schielzeth (2013) and Johnson (2014). In this way, we quantified which percentage of the total variance could be explained

by fixed and random effects (both nematode and field related), and 2) which percentage of total variance could be explained by fixed effects and random effects of nematode traits and field related traits separately.

3. Results

3.1. Impact of soil texture and land management on nematode community composition

Nematode community composition as well as abundance of individual taxa in the fields under investigation were examined by principle component analysis (PCA). The first two principal component axes of nematode communities explained 37% of the variation in nematode community composition (Fig. 2). Nematode communities differed between natural and arable fields, but these differences depended on soil type (RDA: system type \times soil type interaction: $F = 135$, $P = 0.02$; 37% adjusted explained variation). For sandy soils, nematode community composition of the semi-natural field ('De Mossel') was clearly distinct from the three arable fields in an unconstrained analysis (Fig. 2A). However, there was no difference in nematode community composition between natural and arable fields on soils with a high clay content, irrespective whether these were marine or river clay soils (Fig. 2A). About 80% of the nematode taxa showed a higher abundance in sandy than clay soils (see the direction of the arrows in Fig. 2B). Above all, Cephalobidae, *Anaplectus*, *Dorylaimida* D9A (mainly *Nygolaimus* and *Clavicaudoides*) and *Achromadora* contributed most to the separation of nematode communities among fields. In sandy soils, some taxa had

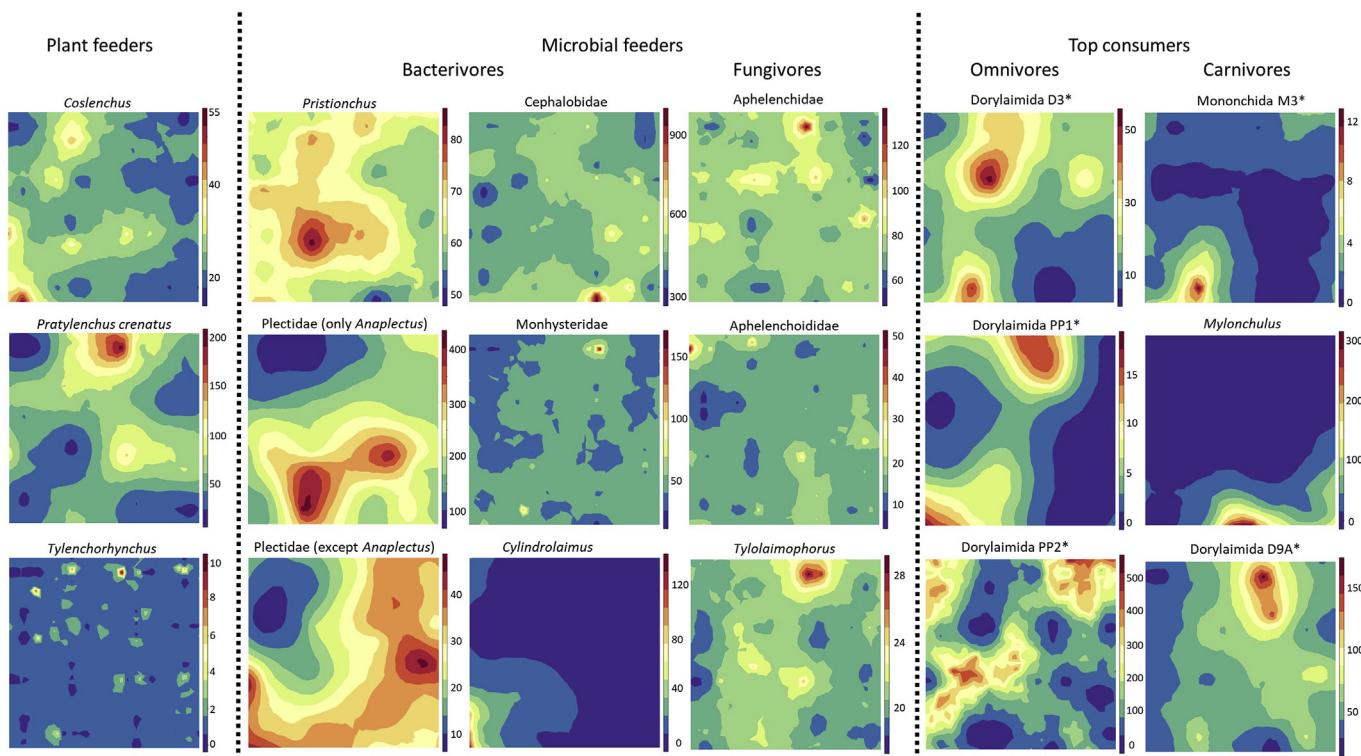


Fig. 4. Field-scale kriging maps of plant feeders, microbial feeders (bacterivores and fungivores) and top consumers (omnivores and predators) in one single field 'De Mossel'. Colour bar: # individuals per 100 g soil. It is noted that scales differ among individual nematode taxa. * For definition of groupings within the orders Dorylaimida (PP1, PP2, D3 and D9A) and Mononchida (M3) see Holterman et al. (2008). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

different abundance in arable fields than in semi-natural grasslands. *Pratylenchus penetrans*, *Mesorhabditis* and *Pristionchus* were more abundant in arable fields, whereas *Monhysteridae*, *Plectidae*, *Achromadora* and *Dorylaimida* PP2 (*Pungentus*) reached higher densities in semi-natural grasslands (Fig. 2B). The plant-parasitic genera *Ditylenchus* and *Basiria* were most abundant in clay soils (Table S2A).

3.2. Distribution patterns of nematodes at the field scale

Overall, the range and the spatial variance of 48 nematode taxa in 12 fields reveal a continuum of spatial patterns (Fig. 3A and B). In total over 300 1-ha taxon-specific distribution maps were generated. Nine maps are shown to illustrate low, intermediate and high spatial variability of nematode abundances, in combination with short, intermediate and long ranges (Fig. 3C). The degree of patchiness from nematode taxa varied between the fields and among nematode taxa (Table S3).

Comparison of the maps of multiple nematode taxa within single fields, revealed taxon-specific abundances and levels of patchiness (Fig. 4). Distribution patterns were also different between members of the same trophic group; for example, we found great dissimilarity in distributions between polyphagous plant parasites *Coslenchus*, *Pratylenchus crenatus* and *Tylenchorhynchus* in a semi-natural grassland field. Likewise, we found no indications for systematic co-occurrence or avoidance among the fungivores. The high levels of *Aphelenchidae* and *Tylolaimophorus* in the top parts of the relevant kriging maps of Fig. 4 was incidental; it was not observed in other fields where *Aphelenchidae* and *Tylolaimophorus* were co-occurring.

3.3. Evaluation of factors underlying nematode patchiness within the fields

The average spatial variance found in this study was 1.3, with a median at 0.6 (Figs. 3B and 5; Table S2C). Among soil properties, the best predictor of the spatial variance was the organic matter content.

For nematode taxa within cp groups 1–2 (mainly bacterivores and fungivores), a positive correlation was shown between organic matter content and spatial variance. However, for nematode taxa belonging to cp-4–5 (mainly omnivores and carnivores) a negative relationship between organic matter and the spatial variance was observed. For cp 3, the relation between the range and organic matter content was slightly positive but less pronounced (Fig. 5). Spatial variance was also more variable among r-strategists, than typical K-strategists. We found that widespread taxa, such as *Cephalobidae*, *Monhysteridae*, *Filenchus* group III and *Plectidae* (except *Anaplectus*), had a relatively low spatial variance (Fig. 5).

The average patch diameter of all nematode taxa under investigation was 36 m, with a median of 19 m (Figs. 3B and 6; Table S2B). Among soil properties, the patch size of nematode patterns was best predicted by the organic matter content. Patch sizes of widespread taxa, including the bacterivorous taxa *Monhysteridae*, *Mesorhabditis*, *Plectidae*, and the fungivorous genus *Aphelenchoides*, were positively related with organic matter content. For other widespread taxa, such as *Cephalobidae* and *Pristionchus*, the patch size was similar in all fields. The patch sizes of widespread fungivorous *Aphelenchus* was clearly smaller in fields containing more organic matter.

A negative relation was found between organic matter content and total nematode densities, as well as between organic matter and densities of dominant taxa at most of the study sites such as *Cephalobidae* and *Pristionchus* (respectively bacterivorous, and bacterivorous/predacious; Fig. S3).

3.4. Quantification of deterministic or stochastic drivers of spatial pattern formation

Variation in mean densities and the detection probability were largely attributed to nematode traits and field characteristics (pseudo $R^2 = 29.9\%$ and 94.9% , respectively; Table 2). Distribution patterns

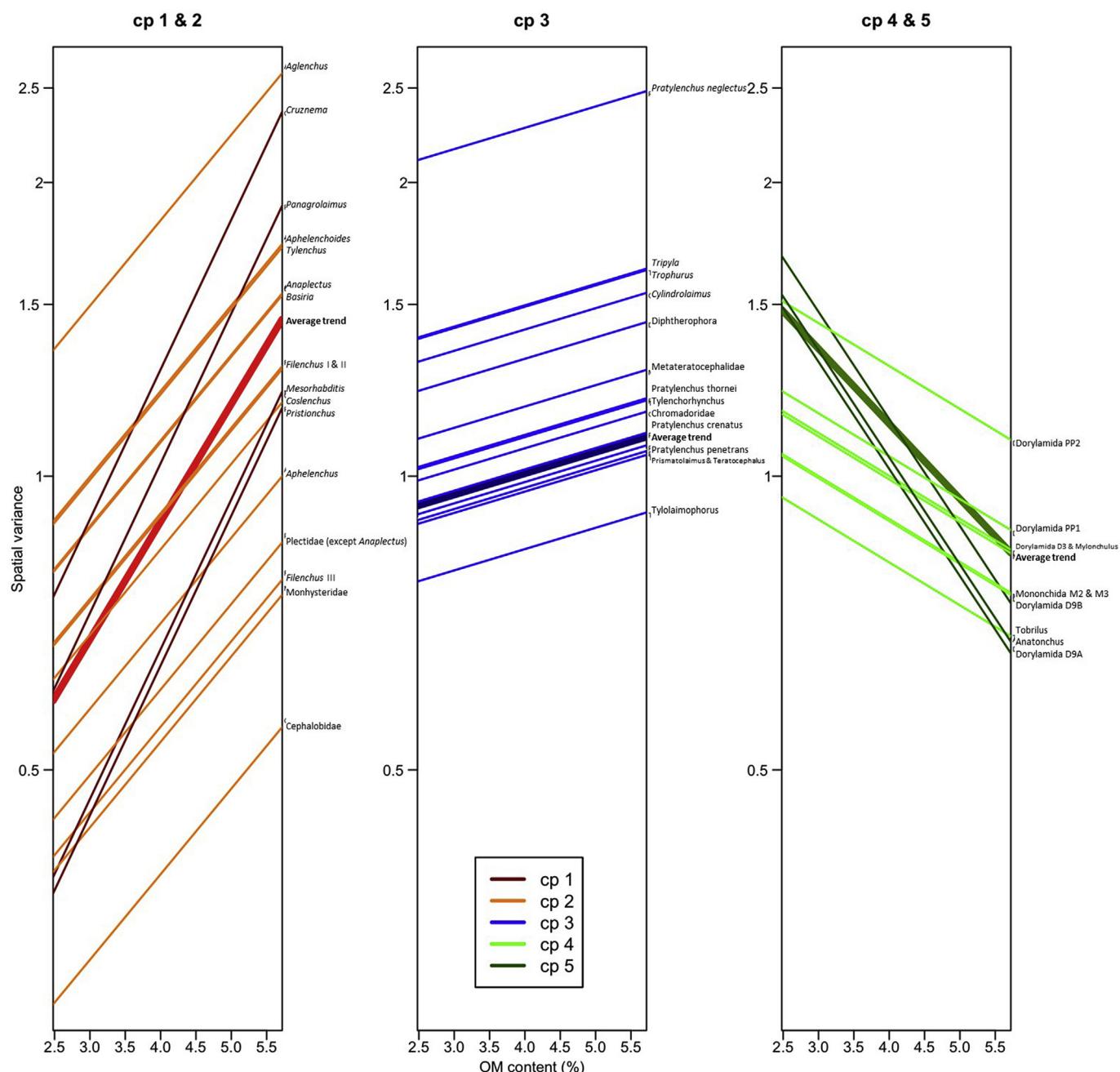


Fig. 5. Relationship between the median spatial variance (σ^2), a measure for intra-field variation of nematode abundances, and the mean organic matter content (OM %) in individual fields ($n = 12$) for nematode taxa with various life strategies (categorized as 1–5 on a colonizer-persister (cp) scale) (Bongers, 1990)). Thick lines indicate average trends for cp-1-2 (red), cp-3 (blue) and cp-4-5 (green). For details on the final model we refer to Table S3. Trends and predictions of random slopes for nematode taxa are based on mixed linear models for trait-environment relationships using a tiered forward model selection (for further details see Data analysis section in Material and Methods). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

could be explained by the factors measured in this research to a much smaller degree as compared to nematode densities and detection probability. For the range, the pseudo R^2 was 8.9% and for the spatial variance 8.5%. The technical error was quantified by the dispersion parameter of the gamma distribution. This parameter resulting from analysis by r-INLA is comparable to the ‘nugget’ parameter in frequentist geostatistical models (see e.g. Ettema and Wardle, 2002). The dispersion parameter of the gamma-distribution had a pseudo R^2 of only 2.3% (Table 2).

4. Discussion

Over the last two decades, a wide range of studies exploiting the resolution offered by high throughput molecular techniques has provided us with a basic knowledge on the astonishing biodiversity of soil life. However, insight in another key element in ecology, a fundamental understanding about distribution patterns, is largely missing. In this study, we generate detailed field-scale distribution maps of 48 nematode taxa with representatives of all 5 cp-categories and all major trophic ecologies. Comparison of maps of a given nematode taxon between fields, as well as the comparison of the maps of multiple nematode taxa within individual fields, revealed field-dependent levels of

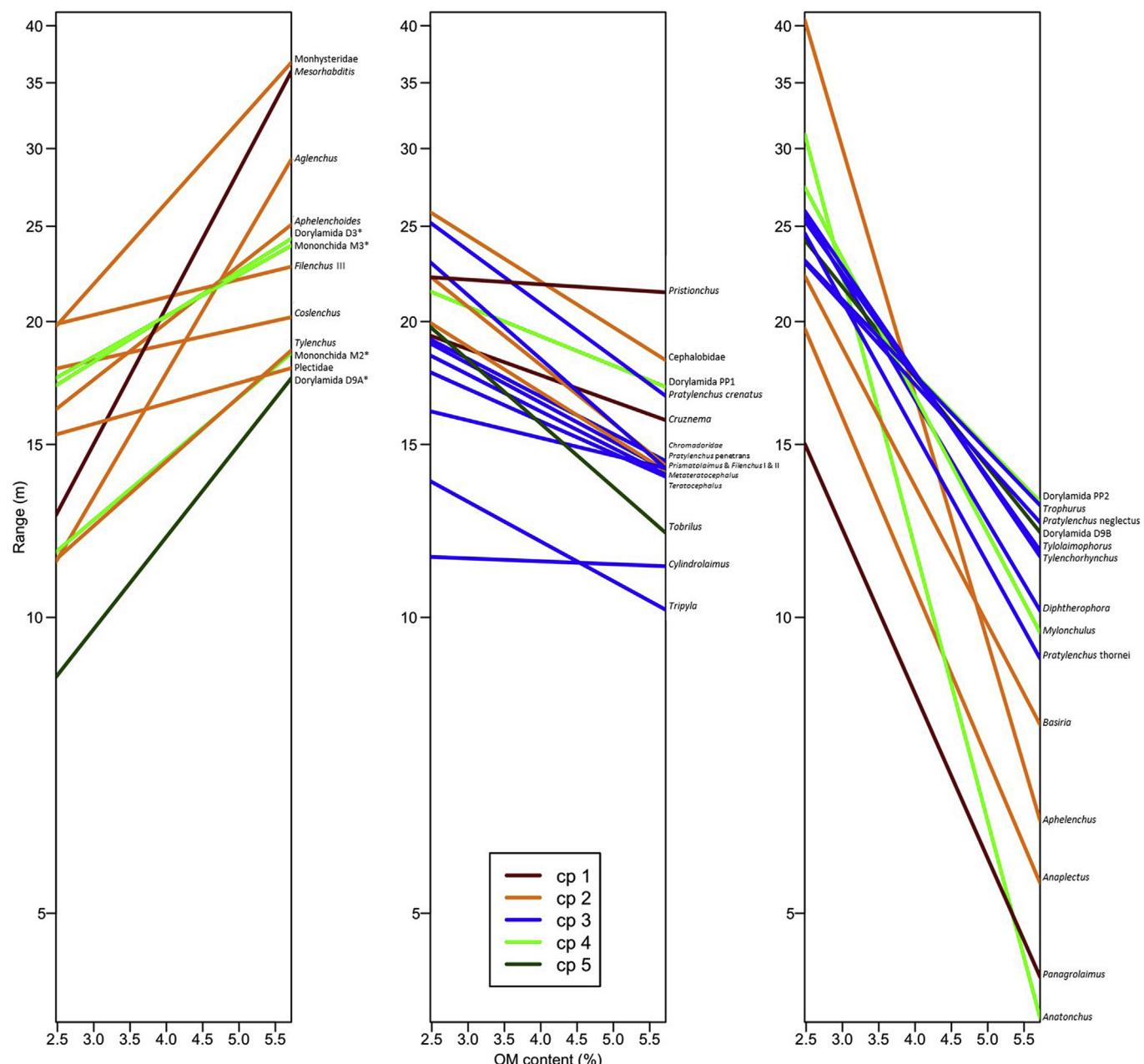


Fig. 6. Relationship between the median range (meters) – a proxy for patch size – and the mean organic matter content in different fields ($n = 12$) for nematode taxa from a different life-strategies on a colonizer-persister-scale (cp 1–5) (Bongers, 1990); see colours. Trends and predictions of random slopes for nematode taxa are based on mixed linear models for trait-environment relationships using a tiered forward model selection (for details see data analysis). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

patchiness per taxon, and taxon-specific levels of patchiness per field. We identified organic matter content as the abiotic factor best explaining nematode patchiness. The effect organic matter on spatial patterning was shown to be life strategy dependent.

4.1. Impact of soil type on nematode communities

Soil particles and porosity affect the movement and feeding of nematodes in soil. In the present study, overall nematode density and the

Table 2

Final mixed models including nematode density data from all twelve fields were used to determine the pseudo R^2 values for multiple geostatistical parameters. The percentages of the total variance explained by both field- and nematode-related factors, as well as by nematode and field properties alone were determined.

Pseudo R^2	Mean density	Detection probability	Range	Spatial variance	Dispersion of gamma-distribution
including all fixed and random effects	29.9%	94.9%	8.9%	8.5%	2.3%
including nematode properties only	27.3%	88.0%	7.5%	7.7%	1.5%
including field properties only	2.5%	6.9%	1.4%	0.8%	0.8%
unexplained variation	70.1%	5.1%	91.1%	91.5%	97.7%

community composition were field-specific, and more strongly affected by soil type than land management. Nematodes were significantly more abundant in sand than in clay soils, and this relates to a large extent to the size of the soil pore space. Nematode can only migrate in soil through pores with a diameter $> 30 \mu\text{m}$ (Jones, 1975). The total pore volumes in Dutch clayey and sandy soils are distinct and take respectively around 62% and 45% of the total soil volume. Pore size distributions are highly soil texture dependent. Nematode biomass correlated well with the percentage of soil pores in the 30–90 μm category, whereas in a previous study on other fields, bacterial biomass was positively correlated with the pore size fraction 0.2–1.2 μm (Hassink et al., 1993). In Dutch sandy soils approximately 4.5% of the pore volume is in the first category, whereas this was $< 0.7\%$ in case of clay soils. In clay soil a higher fraction of the pores was within the fraction 0.2–1.2 μm (10.5% versus 3.6%; Hassink et al., 1993). This implies that in clay a smaller fraction of the bacterial community can be grazed upon by nematodes than in sandy soil. Hence, differences in pore size distribution is a likely explanation for the observed contrast in overall nematode abundance between sandy and clay soils.

We found that nematodes with large body sizes, such as *Anaplectus* and *Dorylaimida* 9A (*Nygolaimus*), and *Dorylaimida* PP2 (*Pungentus*), were abundant in sand, and nearly absent in clay fields. Plant-parasitic nematode genera such as *Ditylenchus* and *Basilia* are relatively small (average fresh weights respectively 0.58 and 0.17 μg) and almost exclusively found in clay soils. These results are in line with results of Sechi et al. (2018), who found that bacterivores, fungivores and plant parasites are longer in sandy than in clayey soils (Sechi et al., 2018). So, body size is an important parameter to explain the observed differences in community composition between sandy and clayey soils.

Two taxa that showed higher densities in semi-natural grasslands, *Monhysteridae* and *Achromadora*, have a preference for wet soil conditions (Abebe et al., 2006). Contrary to arable fields, these areas are not subject to active water management (i.e. drainage), and, hence, the increased presence of these two taxa corresponds with the ecology of these taxa.

Hence, the composition of nematode communities related to soil texture and land use is in line with the wide body of literature that has been published mainly on the basis of microscopic community analyses.

4.2. The effect of the size of soil inhabitants for their patchiness

Geostatistical analysis of field-scale variation of nematode abundances resulted in taxon-specific distribution maps with an average patch size of 36 m. Patchiness usually occurs at multiple, nested scales (Ettema and Wardle, 2002; Ritz et al., 2004), and by taking composite samples from 0.25 m^2 plots we excluded microscale patchiness from our analysis (for nematode distribution at microscale see Quist et al., 2017). Only a few studies have been published on non-plant parasitic nematode distributions at field level. These studies focussed on single fields and on nematodes at either functional group level, or a small set of nematode taxa (Robertson and Freckman, 1995; Ettema et al., 1998, 2000). Keeping the intrinsic limitations of these set ups in mind (single field studies and low number of cores per subsample), it is noted that the ranges found in these previous studies (e.g. 11–88 m in Ettema et al., 1998) are in the same range as the ones found in the current research.

When average range is used as a main parameter for patchiness, the level of spatial aggregation of nematodes in visually homogeneous fields is not essentially different from those found for soil bacteria. Concentrating on soil bacteria at phylum level, Philippot et al. (2009a) measured autocorrelations in patch diameters (range) between 24 and 46 m. In another paper focussing on the distribution of denitrification genes at field scale showed patch diameters of 6–16 m (Philippot et al., 2009b). Although spatial distribution studies for bacteria are scarce, current data suggest that representatives of soil bacteria and soil nematodes, show no fundamental difference in spatial scaling at field

level.

4.3. Nematode patchiness is related to organic matter content and life-strategy

Comparison of kriging maps of a single nematode taxon between fields, as well as the comparison of the distribution of multiple nematode taxa within individual fields revealed field-dependent levels of patchiness per taxon, as well as taxon-specific levels of patchiness per field. Recognizing the inherent high level of unexplained variation in patterns of nematode distribution at field level, mixed linear model-based analyses allowed the identification of organic matter content as a major abiotic factor affecting nematode densities. This effect is reflected in both the spatial variance (the parameter indicating how strong abundances change over space) and the range (a proxy for patch size). When spatial variance was linked to organic matter content, individual nematode taxa responded in a manner that depended on their basic ecological characteristics (cp-value; Bongers, 1990). Increasing organic matter contents was correlated to higher spatial variance for typical colonizers (cp1-2), whereas persisters (cp4-5) tended to show lower levels of spatial variance.

When we consider maps of the belowground distribution of nematodes at field level, here coined as 'nemascapes', we observed a steepening of the hills with increasing organic matter contents of nematode families belonging to cp1-2. Member of cp-groups 1–2 are without exception feeding on primary decomposers, bacteria and fungi (Bongers, 1990). An increase in organic matter content, a highly diverse pool of energy-rich, carbon-based compounds, might differentially stimulate the primary decomposer community. An essential characteristic of nematodes belonging to cp groups 1–2 is their short life cycle (Bongers, 1990). We suggest that the higher spatial variance for opportunistic nematodes can be explained by their ability to quickly benefit from the increased availability of their main food source, bacteria and fungi. Although little is known about food preferences of bacterivorous and fungivorous nematode taxa, various experiments introducing shifts in primary decomposer community suggest for taxon-specific food preferences, and this holds both for bacterivores and fungivores (Vervoort et al., 2012; Quist et al., 2014). In other words, we hypothesize limited functional equivalence among opportunistic members of the same feeding type. Hence, while increased organic matter content was associated with higher levels of spatial variance, the 'nemascapes' of individual taxa from cp groups 1–2 members showed little overlap.

A local increase of organic matter content only indirectly affects food availability for nematode families belonging to cp-4-5 as these cp groups primarily harbour omnivorous and predacious nematodes. Higher levels of organic matter result in a physiologically more buffered environment, and especially slow growing nematodes belonging to cp-4-5 organisms that are sensitive to environmental disturbances (Bongers, 1990) will benefit from this condition. This might explain the shallower slopes of the 'nemascapes' among cp-4-5 members associated with higher organic matter contents. Hence, the predicting value of organic matter content with regard to nematode distribution at field level is taxon dependent as it relates to their trophic ecology as well as their generalized life strategy.

4.4. Reasons for unexplained spatial variation in nematode communities

Environmental conditions such as organic matter content and nematodes traits such as life-strategy only explained about 9% of the spatial variation in nematode abundances within fields. The unexplained component could be ascribed to (a combination of) stochastic processes and functional equivalence between nematodes. Nematode dispersal over distances beyond microscale is essentially a stochastic process as it occurs passively via wind, water and animal vectors. Another stochastic factor that will drive changes in nematode communities is ecological drift. Local nematode densities are co-determined

by probabilistic events such as birth, death and reproduction (Hubbell, 2001; Vellend, 2010). Hence, passive dispersal and ecological drift are two essentially stochastic factors that contribute to the formation of mosaic 'nemascapes' in areas that apparently lack environmental gradients. It has been suggested that related nematode species within a given feeding type may compete for the same ecological niche share (Ettema, 1998). This so-called functional equivalence in nematode communities could lead to species sorting through competitive interactions (Zhou and Ning, 2017), and may be a driver of nematode patchiness. However, very little is known about food preferences of bacterivores and fungivores under field conditions, and therefore the role of functional equivalence, as one of factors driving nematode patchiness, is hard to assess.

Only a few studies have been published on the relative importance of stochastic and deterministic processes in the distribution of soil biota at field scale. Bahram et al. (2016) investigated the patchiness of small soil eukaryotes in three mixed temperate forest sites. At each site, a 64×64 m plot with a homogeneous vegetation was selected, and the spatial patterning of microbial eukaryotes was determined. The authors showed that the shared effect of environmental selection and spatial processes explained less than 10% of variance. In this respect, the results of the present study on the distribution of nematode at field scale are in line with the soil eukaryote distribution patterns in temperate forests as presented by Bahram et al. (2016). The results of the present study and Bahram et al. (2016) point at a dominant role for passive dispersal and drift in the spatial distribution of nematodes and eukaryotes in soil. Both studies provide empirical support for the assumption that stochastic and deterministic processes combined cause patchiness of soil organisms at field scale.

5. Conclusions

In fields selected for minimal within-field variation in land-use history and abiotic conditions, nematode taxa showed high levels of patchiness largely irrespective of their trophic position in the soil food web. 'Nemascapes' for a range of herbivorous, bacterivorous, fungivorous, omnivorous and predacious nematodes at field scale revealed significant relationships between nematode life history traits (cp-value and trophic preference) and soil organic matter content. Opportunistic bacterivores and fungivores showed an increased spatial variance with higher organic matter contents, whereas an opposite effect was observed for omnivorous and predacious nematodes belonging to cp categories 4–5. Here we show that within individual fields, no relationship was observed in distribution patterns among distinct nematode taxa from the same trophic group, which point at distinct food preferences for individual nematode taxa within each of the trophic groups. By elucidating spatial distribution of nematode taxa from all trophic levels of the soil food web, the current results might contribute to a more detailed understanding about the impact of spatial variation of soil organisms on species interactions and the ecological functioning of soil food webs within fields.

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Appendix A. Supplementary data

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