Community structure and spatial variability of soil nematodes in an alluvial soil in a semiarid region of Pernambuco state, Brazil

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HIGHLIGHTS

• This is the first report of soil nematode community in an alluvial soil of Brazilian semiarid.
• Soil attributes influence nematode community structure.
• Different soil attributes determine distinct spatial distributions of nematode trophic groups.
• A high level of human intervention in the experimental plot was revealed by the low dominance of Dorylaimidae and the high dominance of plant parasitic nematodes.

ABSTRACT: Caatinga, a biome of deciduous dry forest and shrub vegetation, predominates in the semiarid northeastern region of Brazil. In this dry biome, research on soil nematode community structure and spatial distribution is scarce but helpful to address soil management. In this work the spatial variability of nematode communities was studied in relation to soil properties. Plant-parasitic nematodes (PPN) was the dominant trophic group followed by bacterivores, omnivores, fungivores and predators. PPN positively correlated with both soil coarse sand and water content, whereas omnivores and bacterivores negatively correlated with coarse sand and clay fraction, respectively. Despite differences in density, omnivores, bacterivores and fungivores were quite similar in spatial patterns. The low dominance of Dorylaimidae (6.4%) and the high dominance of PPN (84.53%) indicates a high level of human intervention in the experimental plot.

Keywords: agroecosystem, alluvial valley, geoestatistical analysis, nematode trophic structure, caatinga.

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INTRODUCTION

Caatinga is a native vegetation of deciduous dry forest and shrub vegetation, which predominates in the semiarid region of Northeast Brazil[1,2] (Figure 1). As such, studies about its agricultural and environmental characteristic are highly encouraged. The climate is characterized by low precipitation – 250-800 mm per year with 607 mm annual mean - distributed in a three to five month-rainy season, high mean air temperature – 24 to 26 °C –, and high potential evapotranspiration – around 2,000 mm per year[3-6]. Therefore, the main characteristic of this region is water scarcity coupled to a rapid process of desertification due to inappropriate use of its natural resources[7].

Soil quality is evaluated based on soil physical, chemical and biological attributes for agricultural systems' sustainability[8]. Regarding biological attributes, nematodes have been used widely as
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Indicators of soil quality, disturbances, characteristics and habitat stability, due to their abundance and omnipresence in ecosystems[9-12].

As part of the soil fauna, nematodes are important primary consumers, participating in organic matter mineralization, nutrient – particularly C and N – and energy cycles in the soil food web[13]. Soil nematode community structure is determined by, among other factors, soil texture, organic matter content and structure, climate, biogeography, and natural and anthropogenic disturbances. Hence, soil management, including soil cover changes, may lead to alterations in resource availability that may change nematode community diversity[14].

Studies on nematode communities in semiarid regions are scarce, particularly in the caatinga biome. In a study on soil nematode communities in caatinga areas under three different stages of laminar erosion (initial, intermediate and severe), Ramos et al.[15] observed greater dominance of free-living nematodes in the area with severe erosion, while plant-parasitic nematodes were more abundant in less severely eroded areas.

Knowledge about nematode spatial distribution is critical for understanding nematode diversity and dynamics in soil food chains. Geostatistics has been used as a powerful tool for characterizing nematode spatial variability[16-23]. However, this tool has not been used in caatinga areas, particularly at semiarid alluvial valleys, in order to provide a better understanding about nematode spatial distribution patterns in soils.

Also long drought periods associated with high evapotranspiration rates limit crop development, and affect flora and soil fauna of the region. According to Maltchik & Florin[24], Brazilian semiarid streams (and their alluvial fans) are characterized by flooding and drought extremes, thus influencing sediment dynamics, texture distribution, and nutrient content.

The aim of this study was to describe the spatial structure of nematode community associated with soil properties in a region of extreme climate conditions (droughts and occasional floodings). We hypothesize that: i) plant-parasitic nematodes are the dominant trophic group in the semiarid region; ii) plant-parasites’ dominance is related to sandy soils and low densities of predators and omnivores and iii) species-specific life strategies lead to different spatial distribution patterns.

**MATERIAL AND METHODS**

**Study area**

The experimental site was located in the Nossa Senhora do Rosário farm (0.7 hectare, with geographic coordinates 8° 21’ 28”S and 36° 41’ 47” W) in the sub-basin of Ipanema river, in the Pesqueira municipality, Pernambuco state. The soil is sandy-loam and classified as Fluvisols[25], presenting approximately 70%, 13% and 17% of sand, clay and silt content, respectively. According to Köppen Climate Classification, local climate is BSh (hot semi-arid)[20]. The study area, located in a guava (*Psidium guajava* L.) orchard, was irrigated once a day by drip irrigation. The irrigation water, from shallow wells, presented electrical conductivity (EC) average values of 0.69, 0.62 and 0.60 dS m⁻¹ for October, November and December 2012, respectively.

![Natural landscape of caatinga biome and alluvial valley in Pesqueira-Pernambuco, Brazil.](image-url)
**Soil sampling**

Samples were collected in November, 2012 following a 64-point grid (Figure 2). The samples were collected under the canopy of the guava trees, where trenches were opened for sampling at 0.2-0.4 m depth for soil physical and nematode analysis. Approximately 0.5 kg of soil was collected per point. Each of the 64 samples were processed separately.

**Soil properties analysis**

Soil temperature was determined at 0.2 m depth with Raytemp™3 infrared thermometer. Soil water content was determined by gravimetric method, in which the samples were weighed and placed in an oven at 105 °C and the dry weights measured after reaching constant mass. The grain size fractions of sand, silt and clay were established by the hydrometer method using a mechanical stirrer as physical dispersant and 25 mL of sodium hexametaphosphate was added as chemical dispersant. Soil water pH and electrical conductivity were carried out for all 64 soil samples according to Claessen[26].

**Nematodes analysis**

From each sample 300 cm³ of soil were processed using 60 and 400 mesh sieves for nematode extraction by the centrifugal flotation method using sucrose solution (1.18 sp.gr) at 1500 g for 4 min[27]. The suspensions obtained were placed in vials and refrigerated for not more than three days until counting and identification.

Soil nematode density was estimated in 1 mL aliquots in Peters’ slides, under an optical microscope at 20X magnification in two replicates, and results expressed as number of specimens per 300 cm³ of soil. All soil nematodes were identified to genus or family level at an optical microscope at 40× and 100× magnification. For identification to genus level, temporary slide was prepared by killing nematodes in hot water (85-95 °C) and adding equal volume of boiling 6% formaldehyde to the suspension.

Nematodes were classified according to feeding habits in five trophic groups (plant-parasitic, bacterivores, fungivores, predators and omnivores), based on the morphology of the stoma and esophagus region, according to Yeates[9]. Plant-parasitic nematodes identification was performed at genus level according to May et al.[28] and free-living nematodes to the family level according to Tarjan et al.[29].

**Statistical and geoestatistical methods**

Data were submitted to Pearson’s coefficient analysis using the Statistical Analytical System (SAS) software, and descriptive analysis was performed to evaluate data dispersion and central tendency measures. Data was log-transformed log (x + 1) and the coefficient of variation was classified according to...
to Warrick & Nielsen\textsuperscript{[30]} as low (CV ≤ 12%), mean (12 < CV ≤ 60%) and high (CV > 60%). In addition, data were analyzed for normal distribution through Kolmogorov-Smirnov adherence normality test at 5% significance level.

The spatial dependence analysis was performed by the classic semivariogram with the semivariance estimation\textsuperscript{[31]}, as observed on Equation 1, with the Geoestatistical Environmental Assessment Software tool\textsuperscript{[32]}.

\[
\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N} \left[ Z(x_i + h) - Z(x_i) \right]^2
\]  

(1)

Where \(\hat{\gamma}(h)\) corresponds to the estimated value of experimental data semivariance, \(Z(x_i + h)\) and \(Z(x_i)\) are observed values of a regionalized variable, \(N(h)\) is the number of pairs of measured values, separated by a lag distance \(h\).

The data was fitted to experimental semivariograms and tested for spherical (Equations 2a, 2b), exponential (Equation 3) and Gaussian (Equation 4) models\textsuperscript{[33]}. The following parameters were defined: nugget effect (\(C_0\)), sill (\(C_0 + C_1\)) and range (\(A\)).

\[
\hat{\gamma}(h) = C_0 + C_1 \left[ 1.5 \cdot \frac{h}{A} - 0.5 \left( \frac{h}{A} \right)^3 \right] \text{ for } h < A
\]  

(2a)

\[
\hat{\gamma}(h) = C_0 + C_1 \text{ for } h \geq A
\]  

(2b)

\[
\hat{\gamma}(h) = C_0 + C_1 \left[ 1 - \exp\left( -\frac{h}{A} \right) \right]
\]  

(3)

\[
\hat{\gamma}(h) = C_0 + C_1 \left[ 1 - \exp\left( -\frac{h}{A} \right)^2 \right]
\]  

(4)

The degree of spatial dependence (DSD) was evaluated according to Cambardella et al.\textsuperscript{[34]}, observing the proportion of the nugget effect (\(C_0\)) in relation to the sill (\(C_0 + C_1\)), thus presenting strong (DSD < 25%), moderate (25 > DSD ≤ 75%) or weak (DSD > 75%) dependence.

The adjusted models were ranked according to the coefficient of determination (R\(^2\)) and then they were submitted to cross-validation using the Jack-Knifing test\textsuperscript{[35]}, observing the mean values approximately zero and standard deviation close to unity. The contour maps, which represent spatial distribution, were created using the Surfer 7.0 software.

RESULTS AND DISCUSSION

Soil nematode community structure

Twenty taxa were recorded in the area, classified into sixteen genera and four families. Six plant-parasitic genera were identified, while two taxa were identified only to family level (Criconematidae and Tylenchidae). Ten free-living nematode families were recorded: three bacterivores, two fungivores, one predator and four omnivores (Table 1).

Plant-parasitic nematodes were the most abundant trophic group (84%), followed by bacterivores (7.26%), omnivores (4.88%), fungivores (3.19%) and predators (0.13%). These proportions are similar to those observed in other studies\[14, 16, 17\]. Among the plant-parasitic nematodes, \textit{Hemicycliophora} was the most abundant genus (52.5%), followed by \textit{Helicotylenchus} (12.8%) and \textit{Meloidogyne} (11.18%).

It is known that soil nematode communities’ diversity in polyculture systems is greater than in monocultures, due to the diversity of plant species that increase food sources and food chain complexity. Moreover, in monoculture systems usually only one plant-parasitic genus dominates, due to its species-specific habitat requirements, and also due to food source limitation, soils and climate conditions or others factors which influence plant-parasitic nematodes’ survival. This could explain why \textit{Hemicycliophora} was more abundant.

Free-living nematodes presented a dominance of 15.47%, of which omnivores corresponded to 0.64% and were represented by the Dorylaimidae family. Intense human intervention on ecosystems as well as environmental disturbance resulted in a lower dominance of omnivores (< 25%) because of their high trophic level in the soil food web, compromising food regulation in the soil\[36\].
As omnivores feed on different food sources, including microorganisms and other nematode trophic groups, their low dominance may result in an increase of plant-parasitic abundance. On the other hand, low number of predators also contributes to high plant-parasitic dominance. Predators and omnivores act as natural enemies of plant-parasitic nematodes, decreasing their population.

According to Freckman & Caswell, agricultural soils usually present low densities of Mononchida. Eisenhauer et al. suggest that plant species’ diversity could increase predators population density due to an increase of soil food chain complexity.

The presence of the families Qudsianematidae (genera *Eudorylaimus* and *Labronema*) and Thornenematidae (genera *Laimydorus* and *Prodorylaimus*) in the samples indicates that the soil environment is stable. These nematodes are characterized by large bodies, lowest fecundity and longest life cycle among soil nematodes; therefore, they are negatively affected by disturbed, polluted, or intensely-managed environments.

| Trophic Group | Family | A | Mean ± SD | D (%) |
|---------------|--------|---|-----------|-------|
| Bacterivores  | Acrobeles (Cephalobidae) | 6024 | 94.1 ± 117.7 | 7.3 |
|               | Prismatalaimus (Prismatolaimidae) | 322 | 5.0 ± 18.8 | 0.4 |
|               | Rhabditidae (Rhabditidae) | 293 | 4.6 ± 20.4 | 0.4 |
|               | **Fungivores** | **2650** | **41.4 ± 67.7** | **3.2** |
|               | Apheles | 301 | 4.7 ± 14.2 | 0.4 |
|               | *Aphelenchoides* (Aphelenchoididae) | 2349 | 36.7 ± 60.6 | 2.8 |
|               | **Predators** | **112** | **1.8 ± 7.2** | **0.1** |
|               | Mononchida (Mononchida) | 112 | 1.8 ± 7.2 | 0.1 |
|               | **Omnivores** | **4047** | **63.2 ± 67.4** | **4.9** |
|               | *Dorylaimus* (Dorylaimidae) | 434 | 6.8 ± 28.3 | 0.5 |
|               | *Eudorylaimus* (Qudsianematidae) | 26 | 0.4 ± 3.3 | 0.0 |
|               | *Labronema* (Qudsianematidae) | 2002 | 31.3 ± 58.4 | 2.4 |
|               | Laimyda (Thornenematidae) | 105 | 1.6 ± 8.8 | 0.1 |
|               | *Mesodorylaimus* (Dorylaimidae) | 99 | 1.6 ± 7.1 | 0.1 |
|               | *Prodyrlaimus* (Thornenematidae) | 104 | 1.6 ± 7.6 | 0.1 |
|               | *Thornia* (Nordiidae) | 1277 | 20.0 ± 25.0 | 1.5 |
|               | **Free-Living** | **12833** | **226.6 ± 197.7** | **15.5** |
|               | **Plant-parasitic** | **70103** | **1095.4 ± 1079.2** | **84.5** |
|               | *Criconematidae* (Criconematidae) | 632 | 9.9 ± 28.1 | 0.8 |
|               | *Helicotylenchus* (Hoplolaimidae) | 10643 | 166.3 ± 259.0 | 12.8 |
|               | *Hemicycliophora* (Hemicycliophoridae) | 43576 | 680.9 ± 1007.1 | 52.5 |
|               | *Meloidogyne* (Heteroderidae) | 9276 | 1449.0 ± 280.0 | 11.2 |
|               | *Pratylenchus* (Pratylenchidae) | 3398 | 531.6 ± 65.1 | 4.1 |
|               | *Rotylenchulus* (Rotylenchulidae) | 2352 | 36.8 ± 87.2 | 2.8 |
|               | *Tylenchidae* (Tylenchidae) | 116 | 1.8 ± 11.2 | 0.1 |
|               | *Trichodoras* (Trichodoridae) | 110 | 1.7 ± 10.0 | 0.1 |
|               | **Total of nematodes** | **82936** | **1321.9 ± 1276.9** | **100.0** |

(A: Abundance or sum of nematodes in 64 samples per 300 cm³ of soil. Mean ± SD: mean and standard deviation of nematodes per 300 cm³ of soil. D (%) dominance of each trophic group and taxa expressed as a percentage.)
Correlations between nematode community and soil properties

Water, air content and temperature were the main abiotic factors influencing local nematode distribution. The water content was positively correlated with the ectoparasitic nematodes, especially *Hemicycliophora*.

Soil temperature was negatively correlated with Aphelenchidae (genus *Aphelenchoides*), fungivores, plant-parasitic and ectoparasitic nematodes (Table 2). Bakonyi et al.[43] emphasized that soil temperature effects can be modified by local climate, soil type and plant community. Yeates[9] stated that climate changes can alter nutrient distribution, which in turn modify trophic groups structure and therefore food chain dynamics[44].

Omnivores positively correlated with pH (Table 2), as opposed to the negative correlations found by Matos et al.[45]. Indirectly, pH may either decrease or increase antagonistic microorganisms densities[46]. Melakeberhan[47] reported that plant-parasitic nematodes can stand great fluctuations in soil pH, but Wang et al.[40] observed that root-knot nematodes as *Meloidogyne javanica* (Treub) Chitwood, *M. incognita* (Kofoid & White) Chitwood and *M. hapla* Chitwood prefer pH ranging from 4.5 to 5.4. In the present work, plant-parasitic nematodes did not correlate with pH probably because it was higher than those cited (pH = 6.52, Table 2).

Sand fraction was negatively correlated with *Labronema* and the plant-parasitic nematode *Helicotylenchus*, and positively correlated with *Hemicycliophora* (Table 2). In contrast, silt fraction was positively correlated with *Helicotylenchus*. Clay fraction, however, correlated positively with free-living nematodes, *Labronema* and the omnivore trophic group, but negatively with Rhabditidae and bacterivores. Olabiyi et al.[49] stated that in sandy soils the population of plant-parasitic nematodes is higher than in clay soils because there is more pore space, facilitating aeration and locomotion, in addition to fewer microorganisms that compete with or prey these nematodes. Several studies reported that some genera of plant-parasitic nematodes present higher density in soils with high content of sand[50, 51], while other nematodes present higher density in soils richer in clay or silt[51-53].

A negative correlation was observed between sand and coarse sand fractions and *Labronema* abundance, indicating that omnivorous nematodes thrive in fine-textured soils. Moreover, we did not observe correlations between predators and soil texture. It is hypothesized that sandy soils together with nematode life-history characteristics, lower plant species diversity in monoculture, food source scarcity, and other factors may influence omnivores-predators behavior.

Omnivores correlated negatively to electrical conductivity (EC) as also reported by Pen-Mouratov et al.[54], who found negative correlations between EC and free-living nematodes.

### Table 2. Significant correlation coefficients between soil physical properties and genera and trophic groups in a nematode community in an alluvial soil in Pernambuco semiarid region, Brazil.

| Soil properties | Temperature | GSWC[8] | pH | Sand fraction | Clay fractions | Silt fraction | Coarse sand | Fine sand | EC[9] |
|----------------|-------------|--------|----|---------------|----------------|---------------|-------------|-----------|-------|
| *Labronema*    | -0.26*      | 0.39** | -0.35** | 0.46** | -0.40** |
| *Omnivores*    | 0.25*       | 0.33* | -0.31** | 0.43** | -0.37** |
| *Rhabditidae*  |             |       | -0.28* |        |          |
| *Bacterivores* |             |       | -0.30* |        |          |
| *Aphelenchoides* | -0.28*     |        |       |          |          |
| *Fungivores*   | -0.30*      |        |       |          |          |
| *Helicotylenchus* |           | -0.29* | 0.38** |        | 0.30* |
| *Hemicycliophora* |           | -0.27* | 0.29* | 0.27* | 0.33** |
| *Ectoparasites* | -0.32*      | 0.28* | 0.29** |        | 0.29** |
| *Plant parasites* | -0.36**    | 0.29* |        |          | 0.26** |

[8]GSWC: Gravimetric soil water content. [9]EC: Electrical conductivity. *Significant at 5% according to Pearson’s coefficient analysis. **Significant at 1% according to Pearson’s coefficient analysis.
Descriptive statistics for soil nematodes, trophic groups and soil attributes

The Kolmogorov-Smirnov test revealed the normal distribution of soil nematodes, trophic groups and soil attributes. According to Warrick & Nielsen classification, the coefficients of variation (CV) for soil nematodes and trophic groups were high (Table 3), while for soil attributes they ranged from low to moderate (Table 4). The extremely elevated CV values obtained in the present work indicate that soil nematode populations were heterogenous in the study area, as discussed by Frogbrook et al., analyzing spatial variability structures in cereal fields.

Spatial dependence analysis of nematofauna and soil attributes

Semivariograms were fitted to trophic groups: omnivores, bacterivores, fungivores, free-living, endoparasitic, and plant-parasitic nematode genus *Meloidogyne*; soil properties: clay, silt, sand, soil temperature, gravimetric soil water content (GSWC) and EC; but *Pratylenchus*, ectoparasitic nematodes, plant-parasitic and pH presented “pure nugget effect” (Table 5, Figures 3, 4). Pure nugget effect indicates

Table 3. Descriptive statistics for soil nematodes, trophic groups and coefficient of variation after logarithmic transformation log (x+1) in an alluvial soil in Pernambuco semiarid region, Brazil.

| Soil nematode group | Mean | Median | Min | Max | Amplitude | Variance | SD | Kurtosis coefficient | Skewness coefficient | Max error | KS | MTD | CV(%)(3) | TD | CV(%) |
|---------------------|------|--------|-----|-----|-----------|----------|-----|----------------------|---------------------|-----------|----|-----|--------|-----|--------|
| Omnivores           | 63.2 | 45     | 0.0 | 378 | 378       | 4544.4   | 67.4| 6.8                  | 2.1                 | 0.159     | 0.205 | 207.7| 53.7   |
| Bacterivores        | 94.1 | 54.5   | 0.0 | 559 | 559       | 13861.3  | 117.7| 5.5                  | 2.3                 | 0.200     | 0.205 | 125.1| 45.5   |
| Fungivores          | 41.4 | 40.5   | 0.0 | 406 | 406       | 7963.1   | 67.7| 5.4                  | 2.3                 | 0.205     | 0.205 | 130.0| 55.4   |
| Free-living         | 226.6| 150.0  | 13.0| 800 | 787       | 39098.6  | 197.7| 1.2                  | 1.4                 | 0.086     | 0.205 | 87.3 | 18.9   |
| Endoparasites       | 198.0| 126.0  | 0.0 | 1944| 1944      | 89437.0  | 299.1| 19.8                 | 4.1                 | 0.141     | 0.205 | 151.0| 34.0   |
| Ectoparasites       | 883.9| 488.0  | 0.0 | 4515| 4515      | 1068047.0| 1033.5| 2.9                  | 1.7                 | 0.181     | 0.205 | 116.9| 31.8   |
| Plant parasites     | 1095.4| 663    | 27.0| 4575| 4548      | 1164599.0| 1079.2| 1.5                  | 1.4                 | 0.176     | 0.205 | 98.5 | 18.2   |
| *Meloidogyne*       | 144.9| 69.0   | 0.0 | 1932| 1932      | 78386.0  | 280.0| 27.7                 | 4.8                 | 0.194     | 0.205 | 193.2| 56.5   |
| *Pratylenchus*      | 53.1 | 36.5   | 0.0 | 410 | 410       | 4241.6   | 65.1 | 14.3                 | 3.2                 | 0.196     | 0.205 | 122.7| 47.2   |

(1)SD: Standard deviation. (2)KS: Kolmogorov-Smirnov normality adherence test significant at 1%. (3)NTD: Non-transformed data. (4)TD: Transformed data.

Table 4. Descriptive statistics for properties of an alluvial soil in Pernambuco semi-arid region, Brazil.

| Soil property | Mean | Median | Min | Max | Amplitude | Variance | SD | Kurtosis coefficient | Skewness coefficient | Max error | KS | MTD | CV(%) |
|---------------|------|--------|-----|-----|-----------|----------|-----|----------------------|---------------------|-----------|----|-----|--------|
| Clay fraction | 133.3| 121.0  | 53.2| 250.4| 197.2     | 1766.2   | 42.0| 1.3                  | 1.1                 | 0.142     | 0.205 |
| Silt fraction | 177.5| 170.0  | 83.6| 378.6| 295.0     | 2768.8   | 52.6| 4.2                  | 1.3                 | 0.134     | 0.205 |
| Sand fraction | 689.1| 701.4  | 393.2| 853.2| 460.0     | 7457.3   | 86.4| 12.5                 | 0.5                 | -1.1      | 0.164 | 0.205 |
| pH            | 6.5  | 6.6    | 5.4 | 7.5  | 2.1       | 0.3      | 0.5 | 7.6                  | -0.9                | -0.4      | 0.083 | 0.205 |
| Temperature   | 27.3 | 26.1   | 21.8| 36.6 | 14.8      | 11.6     | 3.4 | 12.5                 | 0.8                 | 1.2       | 0.181 | 0.205 |
| GSWC<sup>(2)</sup> | 7.6  | 6.8    | 1.0 | 17.4 | 16.3      | 13.9     | 3.7 | 49.1                 | 0.2                 | 0.7       | 0.136 | 0.210 |
| EC<sup>(2)</sup> | 2.5  | 2.5    | 0.3 | 5.7  | 5.4       | 2.0      | 1.4 | 57.3                 | -0.8                | 0.1       | 0.085 | 0.205 |

<sup>(1)</sup>GSWC: Gravimetric soil water content. <sup>(2)</sup>Electrical conductivity. <sup>(3)</sup>SD: Standard Deviation. <sup>(4)</sup>CV: Coefficient of variation in %. <sup>(5)</sup>KS: Kolmogorov-Smirnov normality adherence test significant at 1%.
Table 5. Semivariogram parameters, degree of spatial structure, and cross-validation of soil nematodes and physical properties in an alluvial soil in Pernambuco semiarid region, Brazil.

| Fitted model | C₀⁽⁰⁾ | C₀⁺C₁⁽⁴⁾ | A⁽⁵⁾ | R²⁽⁶⁾ | C₀/C₀⁺C₁⁽⁷⁾ | Spatial structure | Jack-Knifing Parameters | Mean | SD⁽⁸⁾ |
|--------------|-------|-----------|------|-------|-------------|-------------------|-----------------------|------|-------|
| **Nematodes** |       |           |      |       |             |                   |                       |      |       |
| Omnivores    | Gaussian | 3156.1 | 3003.6 | 79.2 | 0.96 | 105.1 | Weak | -0.02 | 1.09 |
| Bacterivores | Gaussian | 10094.9 | 9689.8 | 70.8 | 0.88 | 104.2 | Weak | 0.03 | 1.04 |
| Fungivores   | Spherical | 5546.4 | 2478.9 | 41.3 | 0.82 | 223.7 | Weak | 0.02 | 1.06 |
| Free-living  | Gaussian | 26155.1 | 45207.8 | 101.9 | 0.96 | 57.9 | Moderate | 0.03 | 1.01 |
| Endoparasites | Gaussian | 53514.9 | 120436.0 | 56.8 | 0.95 | 44.4 | Moderate | -0.01 | 1.13 |
| Ectoparasites | Pure nugget effect |           |      |      |             |                   |                       |      |       |
| Plant parasites | Pure nugget effect |           |      |      |             |                   |                       |      |       |
| Meloidogyne | Exponential | 02862.4 | 170064.0 | 54.0 | 0.97 | 1.7 | Strong | -0.02 | 0.94 |
| Pratylenchus | Pure nugget effect |           |      |      |             |                   |                       |      |       |
| **Soil properties** |       |           |      |       |             |                   |                       |      |       |
| Clay fraction | Spherical | 436.4 | 1450.6 | 45.9 | 0.95 | 30.1 | Moderate | 0.00 | 0.91 |
| Silt fraction | Spherical | 1953.8 | 821.2 | 64.1 | 0.81 | 237.9 | Weak | 0.05 | 1.02 |
| Sand fraction | Spherical | 3272.5 | 4730.2 | 50.3 | 0.93 | 69.2 | Moderate | -0.02 | 0.94 |
| pH | Pure nugget effect |           |      |      |             |                   |                       |      |       |
| Temperature | Spherical | 6.7 | 6.7 | 88.2 | 0.99 | 99.7 | Weak | -0.05 | 0.99 |
| GSWC⁽¹⁾ | Spherical | 10.0 | 5.1 | 68.7 | 0.68 | 195.8 | Weak | 0.01 | 1.09 |
| EC⁽²⁾ | Spherical | 1.5 | 0.7 | 80.5 | 0.47 | 2.2 | Strong | 0.02 | 1.00 |

⁽¹⁾GSWC: Gravimetric soil water content. ⁽²⁾Electrical conductivity. ⁽³⁾C₀: Nugget effect. ⁽⁴⁾C₀⁺C₁: Sill. ⁽⁵⁾A: Range in meters. ⁽⁶⁾R²: Coefficient of determination. ⁽⁷⁾C₀/C₀⁺C₁: degrees of spatial structure. ⁽⁸⁾SD: Standard Deviation.

Figure 3. Experimental and theoretical semivariograms for soil nematodes. (a) Omnivores; (b) Bacterivores; (c) Fungivores; (d) Free-Living; (e) Endoparasitic nematodes; (f) Ectoparasitic nematodes; (g) Meloidogyne sp.; (h) Pratylenchus sp.; (i) Plant-parasitic nematodes.
Figure 4. Experimental and theoretical semivariograms for soil properties. (a) Clay fractions; (b) Silt fractions; (c) Sand fractions; (d) pH; (e) Soil temperature; (f) Gravimetric soil water content; (g) Electrical Conductivity.

Figure 5. Contour maps for nematodes and soil properties. Scales are on the right. (a) Omnivores; (b) Bacterivores; (c) Fungivores; (d) Free-living; (e) Endoparasitic nematodes; (f) *Meloidogyne* sp.; (g) Clay fractions; (h) Silt fractions; (i) Sand fractions; (j) Soil temperature; (k) Gravimetric soil water content; (l) Electrical conductivity.
randomized spatial distribution, therefore the sampling distance between points (10 m) used in this study was not enough to detect spatial dependence of the latter variables.

Three mathematical models were fitted (spherical, exponential and Gaussian) (Equations 2, 3 and 4) to nematode taxa and trophic groups (Figure 3). The parameters estimated by the models were validated through the Jack-Knifing test\(^{[31]}\), in which the mean values should be close to 0 and standard deviation close to 1. Soil attributes were fitted to spherical model (Figure 4). The soil attribute EC and Meloidogyne were the only variables that presented strong spatial dependence.

Nematode data and soil attributes presented degrees of spatial structure \((C_0/(C_0 + C_1))\) ranging from weak to strong (1.7 to 223.7 and 2.2 to 237.9, respectively), (Table 5) according to Cambardella et al.\(^{[34]}\). Meloidogyne was the only taxon presenting strong spatial dependence (Figure 5). Other authors\(^{[16, 18, 20]}\) revealed the same structure of spatial dependence in their studies. The strong dependence for Meloidogyne is associated to life history and feeding strategies. As a sedentary endoparasite, it deposits eggs in the same location, usually in masses, resulting in a highly aggregated spatial pattern\(^{[16]}\). The EC spatial dependence probably is a result of the lower cation exchange capacity of sand fractions, favoring high soluble salts concentration, so that the higher the sand proportion, the higher the EC, as observed in Figures 5i, 5j.

### CONCLUSIONS

Plant-parasitic nematodes were the most dominant trophic group (84.53%) in the alluvial soil area, in contrast to the low dominance (0.64%) of Dorylaimidae, indicating high human intervention level. The abundance of omnivores-predators is influenced by intrinsic nematode life-history characteristics, biotic and abiotic factors, such as low vegetation species diversity in monoculture, food source scarcity, clay content and electrical conductivity; while plant-parasitic nematode dominance is positively related to sand content, probably because this trophic group needs pore space to migrate towards plant roots. Different spatial patterns were observed for each trophic group. Collectively, these data improve knowledge concerning nematode life strategies and in turn, offer insights on management of infested agricultural areas.

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