Heliyon 10 (2024) e40715

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

Soil health in Moroccan olive agroecosystems: The bioindication role of terrestrial nematode dynamics

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ARTICLE INFO

Keywords:
Biodiversity
Dynamics
Olive
Soil health
Terrestrial nematodes

ABSTRACT

Terrestrial nematodes are important soil microorganisms that modulate biological processes in soil ecosystems. Thus, these microorganisms have strong potential as soil health bioindicators. This study aimed to investigate their distribution patterns in Moroccan olive agroecosystems and to evaluate their structural and functional dynamics shaping soil disturbance status. An extensive survey was conducted across 65 representative olive fields (orchards and nurseries combined) located in 7 distinct regions during the 2023 season. For each region, several indices were calculated to assess nematode biodiversity alongside their involvement in soil food web diagnostics. The results revealed 63 nematode genera that were detected and classified into different trophic groups: 21 bacterial feeders, 7 fungal feeders, 6 omnivores, 6 predators, and 22 plant feeders. Most soil ecosystems showed low to moderate disturbance with maturing food web conditions, whereas a few showed notable soil disturbance with bacterial and conducive properties. Structural and functional dynamics revealed that both bacterial and plant feeders effectively contributed to undisturbed and disturbed soils, respectively. This study provides novel insights into the biodiversity and dynamics of terrestrial nematodes associated with Moroccan olive agroecosystems and their contribution as effective soil health bioindicators.

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https://doi.org/10.1016/j.heliyon.2024.e40715
Received 17 March 2024; Received in revised form 21 November 2024; Accepted 25 November 2024
Available online 27 November 2024
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1. Introduction

Olive (*Olea europaea* L.) is an important crop widely cultivated across the Mediterranean region, covering more than 11 million hectares worldwide [1]. Its cultivation is concentrated in Spain, Italy, Morocco, Greece, and Türkiye. Olive production in these countries is a major contributor to their economies, especially as it employs millions of people [2]. Morocco is the 5th largest olive producer (1.59 million tons) in the world, with more than 1.07 million hectares of olive orchards, accounting for approximately 45 % of the country's total agricultural land [1]. The olive tree, an evergreen species, is well suited to the Mediterranean climate and is characterized by hot and dry summers and mild/rainy winters. Olive oil production in Morocco is concentrated in the regions of Meknes, Marrakech, Fes, and Taza [2]. Morocco is also a major exporter of olive oil, with more than 70 % of its production exported to European countries such as Spain, Italy, and France [1]. In recent years, there has been a growing demand for organic and high-quality olive oil, which has prompted Moroccan farmers to adopt sustainable and eco-friendly agricultural practices to meet consumer demand and protect the environment [2].

Olive cultivation productivity is threatened by various biotic and abiotic factors [3]. Plant-parasitic nematodes (PPNs) are among the most significant biotic factors that can damage olive trees [4]. These microscopic soil-borne pathogens attack and damage the roots of olive trees, leading to stunted growth, reduced fruit production, and tree death in severe cases [5]. The most commonly encountered PPNs in olive cultivation are root-knot nematodes (RKNs, *Meloidogyne* spp.) and root-lesion nematodes (RLNs, *Pratylenchus* spp.) [4,6]. These nematodes are found in many olive-growing regions worldwide and can cause significant economic losses [7]. Addressing these challenges through sustainable practices and improved management strategies can help increase the productivity and profitability of olive cultivation and reduce reliance on imports [4].

Root-knot nematodes (RKNs), particularly *Meloidogyne javanica*, *M. incognita*, and *M. arenaria* cause significant damage translated by various symptoms (e.g., root galls) to olive trees in Morocco [8,9]. While certain RKN species may negatively affect olive varieties [4], the presence of other nematode groups can indicate a functional soil food web interfering with the caused damage. Studies identifying new RKN species such as *M. spartelensis* highlight the need for ongoing research to understand the full spectrum of nematodes in Moroccan olive groves [10]. Similarly, root-lesion nematodes (RLNs) such as *Pratylenchus neglectus*, *P. pinguicaudatus, P. crenatus*, and *P. mediterraneus* also cause prominent damage resulting in various symptoms to the olive rhizosphere [11,12]. However, a diverse nematode community encompassing more species can indicate a more balanced soil environment [5,13]. RKNs and RLNs are just one component of the soil ecosystem, and their presence doesn't necessarily signify unhealthy soil.

Recently, there has been an increasing focus on the relationships between diversity, soil-related functions, and the concept of soil health. This concept is defined as the ability of the soil to maintain steady plant health by achieving organic production sustainability and environmental quality within an ecosystem [14]. A key indicator of soil health is the structure of the nematode community, which can provide information on soil processes, food webs, and the stability of soil biodiversity and agroecosystems [15]. Nematodes are valuable bioindication agents for studying environmental changes [16,17]. Moreover, nematodes play a crucial role in enhancing the physical properties of soil and maintaining ecosystem health attributes through their contribution to soil food web channels [18]. Consequently, numerous studies have shown that nematode entities can be used to assess soil health, making it essential to understand the mechanisms and dynamics underlying nematode diversity patterns in order to establish adequate large-scale soil and plant health programs for sustainable agriculture [19,20].

Several studies have focused on assessing the effects of different disturbances on soil biological processes and activities using ecological indices, with a particular focus on nematode communities [21]. Thus, effective analysis targeting these communities serves to characterize soil functions and services in a range of agroecosystems subject to various disturbance events [19]. Neher et al. [22] noted that the structural attributes of terrestrial nematodes are the best bioindicators for soil health. Furthermore, the presence of plant parasitic and predatory nematodes can indicate the impact of human activities on the soil and its physicochemical characteristics [18, 23]. However, few studies have been conducted on the contribution of terrestrial nematodes to soil disturbance status in olive agroecosystems. Thus, scientific research in this area has focused more on PPNs, with little attention given to other free-living nematodes (FLNs) as potential bioindicators for olive soil health assessment in Morocco. Therefore, this study aimed to (i) investigate terrestrial nematode groups associated with Moroccan olive agroecosystems, (ii) assess nematode ecological community alongside soil functioning patterns, and (iii) establish an in-depth analysis of the structural and functional dynamics defining the biodiversity patterns of nematode trophic groups (TGs) in shaping olive soil health patterns. The surveyed olive areas are hypothesized to have various disturbance responses translated by prominent nematode biodiversity trends and extensive structural and functional dynamics. This study provides genuine insights into the active assessment of agricultural soils using terrestrial nematodes as reference microorganisms.

2. Material and methods

2.1. Background of study areas and sampling

An extensive study was conducted to investigate the biodiversity of nematode communities in different olive agroecosystems across seven regions in Morocco during the 2023 season. The fields surveyed were chosen based on the annual olive productivity, soil properties, and geographical distribution (Table S1). The study included 65 representative fields, including olive nurseries and orchards, from 13 localities (provinces) (Fig. 1). Soil samples were collected using a systematic zigzag pattern, with 15 subsamples randomly taken from a layer of 25 cm topsoil across 2–3 ha areas of olive orchards. These subsamples were combined to form a

composite sample weighing 2 kg. To preserve nematode populations and prevent moisture loss, the samples were stored in polyethylene bags at 4 °C [24]. Soils across all surveyed localities were given a full classification according to the World Reference Base (WRB) for Soil Resources [25]. Four soil groups (Arenosol, Cambisol, Luvisol, and Vertisol) occurred in olive agroecosystems (Table 1). Each of these groups has distinct characteristics defined at different levels including overall soil texture, organic matter (OM), and mineral content.

2.2. Nematode processing and identification

Nematode extraction was performed using the modified Baermann method [26] on soil (100 cm^3). After a 72-h incubation period, the nematodes were collected and assessed using a stereomicroscope (Olympus LS, Japan). To immobilize and preserve the samples, hot formaldehyde solution (4 %) was added to a water droplet in a glass cavity vessel. The terrestrial nematodes were then transferred to a mixture of formaldehyde and pure glycerin (99:1, % v/v) (solution I) and placed in a desiccator partially filled with 96 % ethanol (1/10th, v). After 24 h, the watch glass was removed from the desiccator and incubated (37 °C). A mixture of glycerin (95:5,%) and ethanol (solution II) was added in three separate instances, with each addition occurring at 3-h intervals. Finally, ethanol and glycerin (50:50, %) constituting solution III (2 ml) were added and the watch glass was incubated overnight at 37 °C [27]. Nematodes were diagnosed at the genus level using specific keys focused on morphological characteristics [28–35].

2.3. Soil mineral and organic content analyses

Soil mineral and organic contents were analyzed using established methodologies [36]. Soil texture characteristics were determined by examining the proportions of clay (Cla), sand (San), and loam (Loa) [37]. Electrical conductivity (EC) and pH were measured using a specific soil-to-water ratio technique [38]. Atomic absorption spectrometry was used to quantify magnesium (Mg), manganese (Mn), potassium (K), and exchangeable acidity [39]. The soil mineral percentages were determined using the Allison method [40]. The nitrogen (N) and carbon (C) concentrations were determined separately using the Kjeldahl and Walkley–Black techniques [41], and the C:N ratio was computed to evaluate the quality of OM. The humic and total portions (HOM and TOM) were analyzed using a combination of wet oxidation methods, such as the Walkley-Black procedure for TOM, and spectrophotometric techniques for quantifying HOM fractions following extraction with alkaline solutions [41,42]. Other soil components, such as calcium (Ca), copper (Cu), iron (Fe), phosphorus (P), sodium (Na), and zinc (Zn), were quantified using colorimetry and a spectrophotometer (Shimadzu UV–1205,

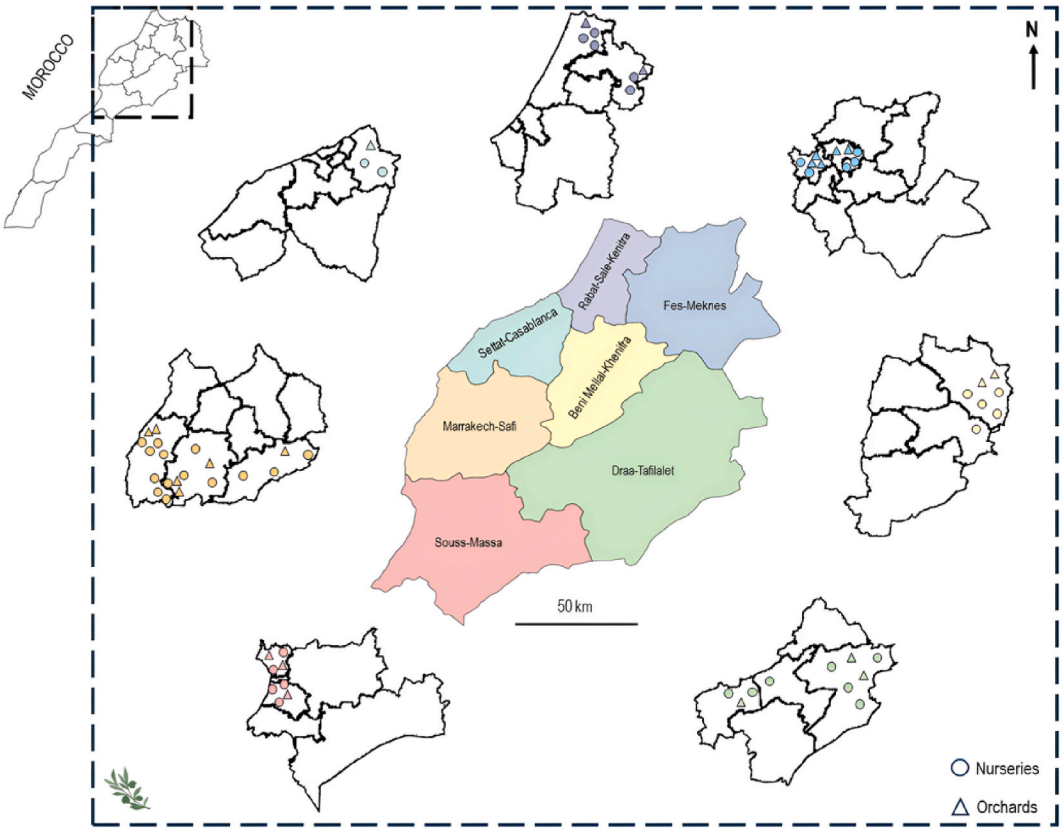


Fig. 1. Survey map of terrestrial nematodes in Moroccan olive nurseries and orchards.

Table 1
Sampling characteristics of the surveyed olive-growing regions and localities in Morocco.

Region	Localities (Provinces)	Soil Classification	GPS Coordinates (Latitude, Longitude)	Site N° (N/O)	SPS
Beni Mellal-Khenifra (BK)	Tadla	Chromic Cambisol (Loamic, Humic, Drainic)	33.6887649, −7.392079	5/2	8
Draa-Tafilalet (DT)	Tafilalet	Eutric Arenosol (Humic, Nechic, Aric)	31.2456745, −4.266280	4/2	6
	Ouarzazate	Chromic Luvisol (Clayic, Hypereutric, Neocambic)	30.920193, −6.9109230	3/1	6
Fes-Meknes (FM)	Fes	Stagnic Cambisol (Arenic, Humic, Drainic)	34.0346534, −5.016192	3/2	12
	Meknes	Chromic Cambisol (Loamic, Humic, Drainic)	33.8984131, −5.532158	2/3	15
Marrakech-Safi (MS)	Chichaoua	Chromic Vertisol (Grumic, Hypereutric, Aric)	31.5469033, −8.759546	4/2	6
	Essaouira	Gypsiric Cambisol (Loamic, Ochric, Novic)	31.5118281, −9.762090	4/2	6
	Haouz	Chromic Vertisol (Grumic, Hypereutric, Aric)	31.460070, −7.6236078	3/1	10
	Marrakech	Chromic Vertisol (Grumic, Hypereutric, Aric)	31.625825, −7.9891608	3/1	20
Rabat-Salé-Kenitra (RSK)	Gharb	Terric Luvisol (Loamic, Epidystric, Pyric)	34.264570, −6.5701690	3/1	5
	Sidi Kacem	Skeletic Cambisol (Loamic, Humic, Magnesic)	34.226412, −5.7114340	2/1	3
Settat-Casablanca (SC)	Benslimane	Brunic Arenosol (Humic, Nechic, Aric)	33.6168709, −7.123036	2/1	5
Souss-Massa (SM)	Agadir	Irragric Luvisol (Clayic, Siltic, Aric)	30.4205162, −9.583853	5/3	22

Soil classification according to the World Reference Base (WRB) for Soil Resources.
Site N°: Number of sites.
N/O: Nurseries/Orchards.
SPS: Samples per site.

Columbia, MD, USA).

2.4. Nematode biodiversity

Several indices were calculated to assess the biodiversity of the nematode communities in each surveyed olive area. These diversity indices encompass various metrics, such as the Shannon–Weaver index (H') [43], which indicates overall nematode diversity, and the maturity index (MI), which is computed as the product summation of the c–p values (representing the r and k properties) of each nematode genus i and its frequency (f_i) in a given sample. In addition, the plant-parasitic index (PPI) was determined using a similar approach, with only p-p values being considered [44]. The channel (CI), enrichment (EI), structure (SI), and basal (BI) indices were calculated to provide insights into the structural attributes of the food web [18,19,45,46].

2.5. Structural nematode dynamics

Nematode structural dynamics were assessed based on the spatial contribution (response) of each TG in undisturbed and disturbed soils. For this purpose, SIMPER (similarity percentages) and ANOSIM (analysis of similarities) approaches were used [20,47]. To predict nematode TG successions in terms of soil disturbance level, a random forest algorithm (machine learning method), known for its ability to handle complex relationships between input features and the target variable, was employed [48]. The algorithm constructs multiple decision trees and combines their predictions to obtain accurate classification. This study used a dataset comprising soil characteristics and disturbance indicators (based on nematode community analyses) as input features, with nematode TG serving as the target variable. The dataset was preprocessed by handling missing values and encoding the categorical variables. The data were then divided into training and testing sets using an 80:20 split ratio. A random forest classifier (RandomForestClassifier) was trained on the training set to construct multiple decision trees via bagging [49]. Hyperparameters, including the tree number, maximum depth of each tree, and number of features considered at each split, were tuned using cross-validation methods. The performance of the trained model was evaluated using accuracy as an evaluation metric. Finally, the trained random forest model was used to predict nematode TG successions (as percentages) for new and unseen data points. The generated values represent the weighted species richness percentage (WSRP) (i.e., a measure used to assess biodiversity by giving different weights to species based on certain criteria, such as abundance and frequency) calculated for each TG entity [20]. All data preprocessing, model training, hyperparameter tuning, and evaluation steps were implemented using scikit-learn libraries in Python (*sklearn.ensemble*, *sklearn.model_selection*, and *sklearn.metrics*) [50]. The random forest model was trained and evaluated on high-end hardware using Python (version 3.11) and scikit-learn (version 1.2.2).

2.6. Functional nematode dynamics

The support vector machine (SVM) algorithm was employed to predict the functional contribution (response) of nematode functional guilds (FG) under various soil disturbance conditions [51]. The dataset included input features such as nematode abundance and soil indices, along with the corresponding functional contributions of nematode FG (target variable) in disturbed, and undisturbed soils. To enhance the performance and interpretability of the model, feature selection was conducted using techniques, such as correlation analysis and feature importance assessment. The dataset was then split into training and testing sets to ensure a balanced representation of the disturbed, and undisturbed soils in both sets. For simplicity, the SVM model, specifically the SVR (regression)

variant, was separately trained (for each FG group) using the training data and a linear kernel [52]. The performance of the model was evaluated using appropriate metrics, such as accuracy or mean squared error, by employing cross-validation techniques. Predictions of functional contributions were generated for new, unseen soil samples, and the results were visualized using a lollipop plot, where the observed contributions were plotted against the predicted contributions for each FG. The SVM algorithm, combined with feature selection and model evaluation techniques, enabled the accurate prediction of nematode functional contributions under different soil conditions. All data preprocessing, model training, parameter scaling, and evaluation steps were implemented using the scikit-learn library in Python (*sklearn.svm* and *sklearn.preprocessing*) [50]. The SVM model was trained and evaluated on high-end hardware using Python software (version 3.11) and scikit-learn (version 1.2.2).

2.7. Statistical processing

To explore the distribution patterns of nematode communities in the surveyed olive agroecosystems, redundancy (RDA) and multidimensional scaling (MDS) analyses were performed to reveal the utmost nematode presence and spatial distribution trend, respectively. The nematode and soil entities (input variables) associated with these analyses were subjected to ANOVA following

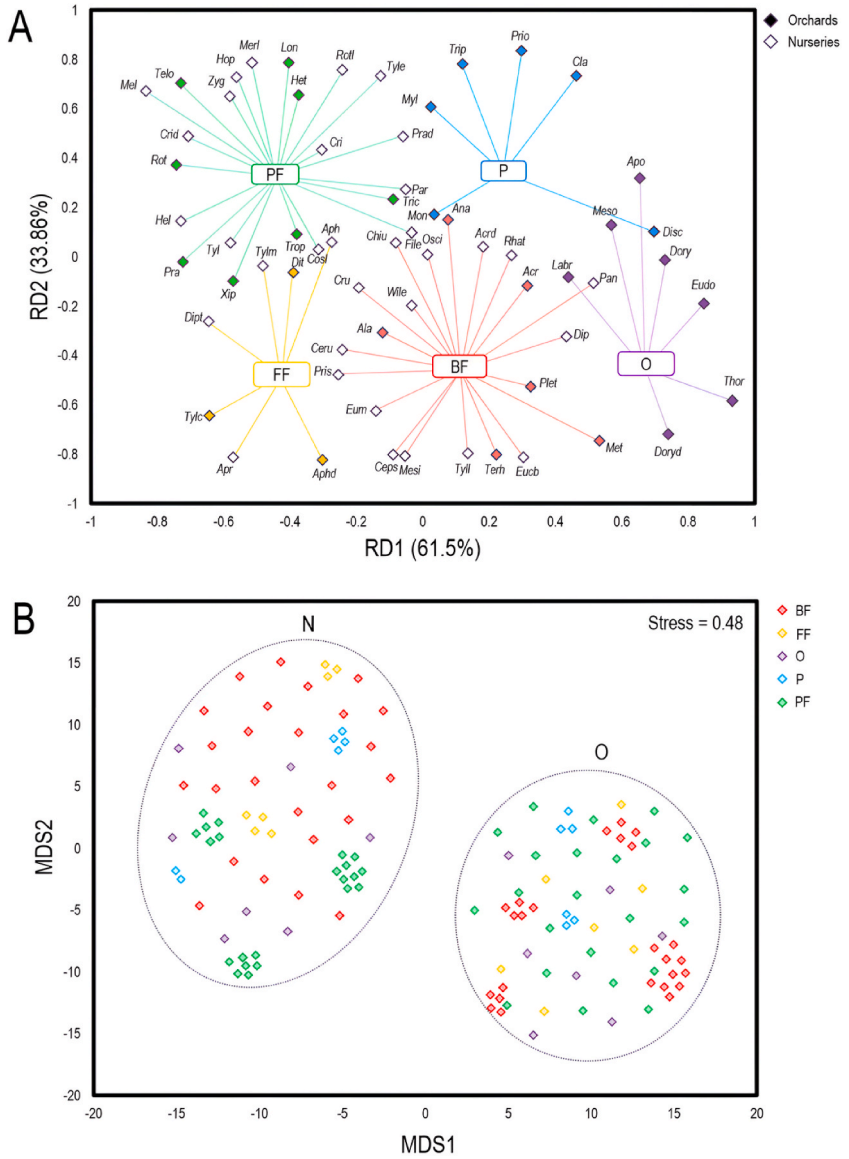


Fig. 2. Distribution patterns of terrestrial nematodes associated with Moroccan olive agroecosystems. (A) Redundancy analysis highlighting the utmost presence of nematode genera in nurseries and orchards based on their TGs. (B) Multidimensional scaling analysis depicting the general spatial distribution of nematodes TGs. N: Nursery; O: Orchard. Nematode abbreviations are listed in Table S2.

normalization [53] of the data using the XLSTAT (version 2023.1, Lumivero, USA) software. Significant differences were determined using the least significant difference approach (LSD) at $P < 0.001$. Soil health analyses represented by food web (FWA) and metabolic footprint (MFA) analyses were performed using the NINJA software [54] and Log-transformed values were considered to meet a normal distribution. Significant differences between functional footprints were processed using the Welch Two Sample *t*-test at $P < 0.001$ following a confidence interval (CIn). Co-inertia (COI) analysis was conducted to determine possible correlations between nematode taxa and soil physicochemical characteristics using the *ade4* package in R [55]. Relationships between nematode TGs and diversity indices were also revealed using the Pearson method, whereas correlations with soil mineral and organic contents were based on the Mantel test [56]. Square-root transformation was considered for both nematode and soil entities to meet normality assumptions before the implementation of the correlation analyses. All multivariate analyses were conducted using Python (version 3.11), integrated into the PyCharm IDE platform (version 2023.1). For structural and functional dynamics, Venn and lollipop plots were generated using Matplotlib-Venn and Matplotlib–lollipop modules, respectively [57,58]. RDA and MDS were performed using ordination (*skbio.stats.ordination/skbio.stats.ordination.pcoa*) and MDS (*sklearn.manifold.MDS*) libraries, respectively.

3. Results

3.1. Distribution patterns of soil nematodes in Moroccan olive agroecosystems

This study aimed to explore the diversity and distribution of terrestrial nematodes in different olive agroecosystems in Morocco. In total, 63 nematode genera were identified in this survey (Table S2). The TG composition of the olive nematodes was thoroughly analyzed across surveyed regions (Fig. S1) and followed their overall density per soil sample (Fig. S2). The most abundant TGs were bacterial feeders (BF), which accounted for 45 %, followed by plant feeders (PF) (27 %), fungal feeders (FF) (13 %), predators (P) (10 %), and omnivores (O) (5 %) (Fig. S1A). The majority of FLNs were BF (≥65 %), whereas other groups were less common (Fig. S1B). The PF varied in their parasitic behavior, with sedentary endoparasites (e.g., *Meloidogyne* spp.) being the dominant group (>50 %), followed by migratory endoparasites (e.g., *Pratylenchus* spp.) (>35 %), ectoparasites (e.g., *Xiphinema* spp.) (8 %), semi endoparasites (e.g., *Rotylenchulus reniformis*) (4 %), and root hair feeders (e.g., *Filenchus* spp.) (3 %) (Fig. S1C). Moreover, these nematode taxa were classified based on the colonizer–persister (c–p) and plant–parasitic (p–p) values, constituting different life strategies. The c-p 2 subgroup (general opportunists) was the most prevalent in all areas (>50 %), followed by the c-p 1 subgroup (enrichment opportunists) (>30 %). However, the higher c-p groups c-p 4 and 5 (persisters) also had proportions of 25 % and 7 %, respectively (Fig. S1D). Regarding the p– p values, the p– p 3 level was the most abundant (>75 %), followed by the p– p 2 level (Fig. S1E).

The distribution patterns representing the utmost presence of nematode genera in olive nurseries and orchards were examined by the RDA approach (Fig. 2). The first two RDA axes (RD1 and RD2) explained 61.50 % and 33.86 % of the variance, respectively (Fig. 2A). The nematode TGs were clearly separated, with some overlap between nematode genera. In addition, this separation was also established in terms of nematode utmost presence. In that manner, nematode TGs including 14 BF (e.g., *Acrobeloides*, *Rhabditis, Panagrolaimus, Diplogasteriana, Eucephalobus, Tylocephalus, Mesorhabditis, Cephalobus, Eumonhystera,* and *Prismatolaimus*), 4 FF (e.g., *Aphelenchus*, *Aprutides*, and *Tylencholaimus*), and 14 PF (e.g., *Criconemoides*, *Meloidogyne*, *Zygotylenchus*, *Hoplolaimus, Helicotylenchus, Rotylenchulus,* and *Coslenchus*) were more present in nursery agroecosystems. The rest of the genera from these groups prevailed more in orchards. On the other hand, all of the O (e.g., *Aporcelaimus*, *Dorylaimus*, *Eudorylaimus*, and *Thornenema*) and P (e.g., *Discolaimus*, *Mylonchulus*, *Clarkus*, and *Tripyla*) groups had more presence in the orchard settings (Fig. 2A).

The general spatial distribution of identified nematodes was visualized using MDS analysis taking into account the overall densities obtained in nurseries and orchards. In terms of their TGs, nematode entities were differently distributed and had a patchily pattern overall (Fig. 2B). In nursery settings, BF and O groups had a wide spatial distribution, while FF, PF, and P groups had a narrow trend. On the other hand, PF and FF nematodes were distributed widely, while BF had a more localized distribution across the surveyed orchards (Fig. 2B).

Regarding nematode densities per sample (Fig. S2), it ranged from 512 to 1120 nematodes per 100 cm^3 soil across 43 nurseries (Fig. S2A), and from 520 to 1188 nematodes per 100 cm^3 soil across 22 orchards (Fig. S2B). The nematode genera density, relative abundance, and frequency aspects in the representative olive regions were calculated and computed (Fig. S3, Fig S4). Of the 63 nematode genera detected, 17 taxa were dominant, including *Rhabditis*, *Meloidogyne*, *Pratylenchus*, *Panagrolaimus*, *Eudorylaimus*, *Mononchus*, and *Aphelenchus* spp. Additionally, 19 taxa were frequent across the study areas, including *Diplogasteriana, Prionchulus, Paratylenchus, Thornenema,* and *Ditylenchus* spp. Eleven taxa were detected as occasional (e.g., *Eumonhystera, Xiphinema, Clarkus, Dorylaimoides,* and *Tylolaimophorus* spp.). Furthermore, 17 taxa, including *Cruznema*, *Filenchus*, *Mylonchulus*, *Labronema*, and *Tylencholaimus* spp., were considered rare (Fig. S4).

3.2. Soil health-based diversity patterns of olive nematodes

Diversity indices were calculated for all surveyed olive agroecosystems to assess soil health aspects (Fig. S5). In terms of the MI, most olive-producing regions were significantly more prevalent ($F_{1,6} = 78.5$; $P < 0.05$). The highest values were obtained for BK (2.71), DT (2.53), and RSK (2.51) (Fig. S5A), whereas the lowest values were recorded for SM, MS, and SC regions. Regarding the PPI, significant differences were detected between some of the studied areas ($F_{1,6} = 67.04$; $df = 6$; $P < 0.05$) (Fig. S5B), with the highest value recorded in the MS region (3.22). The decomposition patterns of the nematode TGs (especially BF and FF) were represented by a significant trend in the CI ($F_{1,6} = 85.2$; $P < 0.05$). The DT and FM regions both had high CI values compared with the other regions (Fig. S5C), whereas the SC region had the lowest value (17.54). Furthermore, there was a significant fluctuation in the BI across the

studied areas ($F_{1,6} = 71.3$; $df = 6$; $P < 0.05$). Three regions (DT, FM, and RSK) exhibited high values ($15 < BI < 20$), whereas the SM region exhibited the lowest value of 8 (Fig. S5D).

Nematode communities in different olive agroecosystems were used to assess soil health status through food web analytics (Fig. 3). FWA was used to evaluate the soil health of each region based on nematode community structure and function using EI and SI (Fig. 3). In terms of these indices, nematode faunal structure is separated into four quadrants. In our study, most of the olive soils (35) derived from all surveyed regions remained restricted in quadrant B. The soils from this quadrant are characterized by low to moderate disturbance with balanced decomposition channels and maturing food web conditions. Twelve soil systems encompassing MS (5), FM (3) DT (2), and BK (2) regions were grouped towards the quadrant C which is known for undisturbed characteristics translated by structured and suppressive soil web conditions. The MS region had the majority of soils (11), followed by BK (3), and SC (2) categorized in quadrant A with high disturbance, bacterial decomposition, and conducive (i.e., a condition in which few higher TGs in the soil food web result in minimal predation on opportunists, allowing or not restricting their increase) aspects. On the other hand, only two sites from the RSK and FM regions showed degraded olive soils (Fig. 3).

To delve deeper into nutrient allocation to different processes that occurred in undisturbed and disturbed olive soils, a detailed MFA was conducted for both olive nurseries and orchards and visualized (Fig. 4). In undisturbed conditions, Bacterivore (Transformed $MF_{Bact} = 12.44$; $P = 0.0003$; CIn [0.001; 0.0005]), fungivore (Transformed $MF_{Fung} = 7.036$; $P = 0.0009$; CIn [0.001; 0.0007]), predator (Transformed $MF_{Pred} = 5.732$; $P = 0.0009$; CIn [0.0009; 0.0006]), and structure (Transformed $MF_{Struc} = 8.218$; $P = 0.0005$; CIn [0.0008; 0.0004]) footprints were slightly higher in orchards and have shown statistical differences (Fig. 4A). On the other hand, herbivore (Transformed $MF_{Herb} = 11.50$; $P = 0.0004$; CIn [0.0006; 0.0003]) and enrichment footprints (Transformed $MF_{Enri} = 17.00$; $P = 0.0001$; CIn [0.0005; 0.00009]) were significantly prevailing in disturbed conditions, especially in the surveyed nurseries (Fig. 4B). Nutrient allocation in soil food webs in undisturbed areas was larger in the decomposer food web (i.e., large fungivore/omnivore MF) than in the primary production channel (small herbivore MF). This was conversely observed in disturbed areas as nutrient allocation was relatively shifted towards a small fungivore MF which led to a bacterial decomposition channel (Fig. 4B). Regarding persisting nematode groups, omnivore and predator footprints were significantly greater in undisturbed soils than in disturbed ones ($P < 0.001$) (Fig. 4). Furthermore, The degree of enrichment and structural characteristics were indicated by the enrichment and structure MF (EMF and SMF). It was noticed that most of the surveyed localities had EMF ≫ SMF with either regulated or conducive proprieties.

3.3. Relationships between olive nematodes and soil physicochemical proprieties

The correlation between nematode assemblages and soil physicochemical characteristics was assessed by coinertia (COI) analysis and the Mantel test (Fig. 5; Fig. S6). The COI score plot indicated that most nematode TGs (e.g., BF, FF, and O) were positively

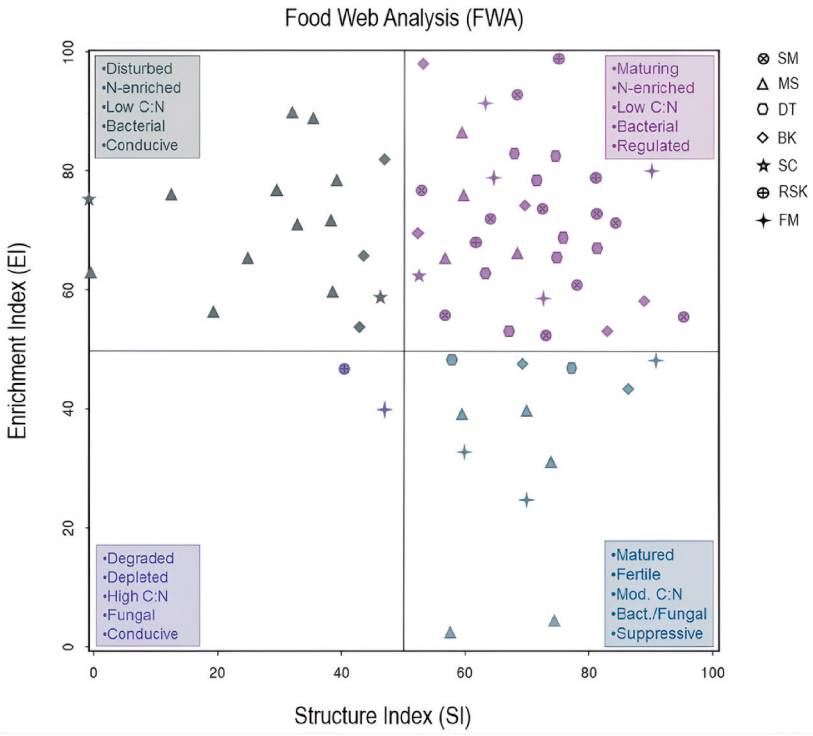


Fig. 3. Food web analytics of terrestrial nematodes and their role as soil health bioindicators in olive agroecosystems.

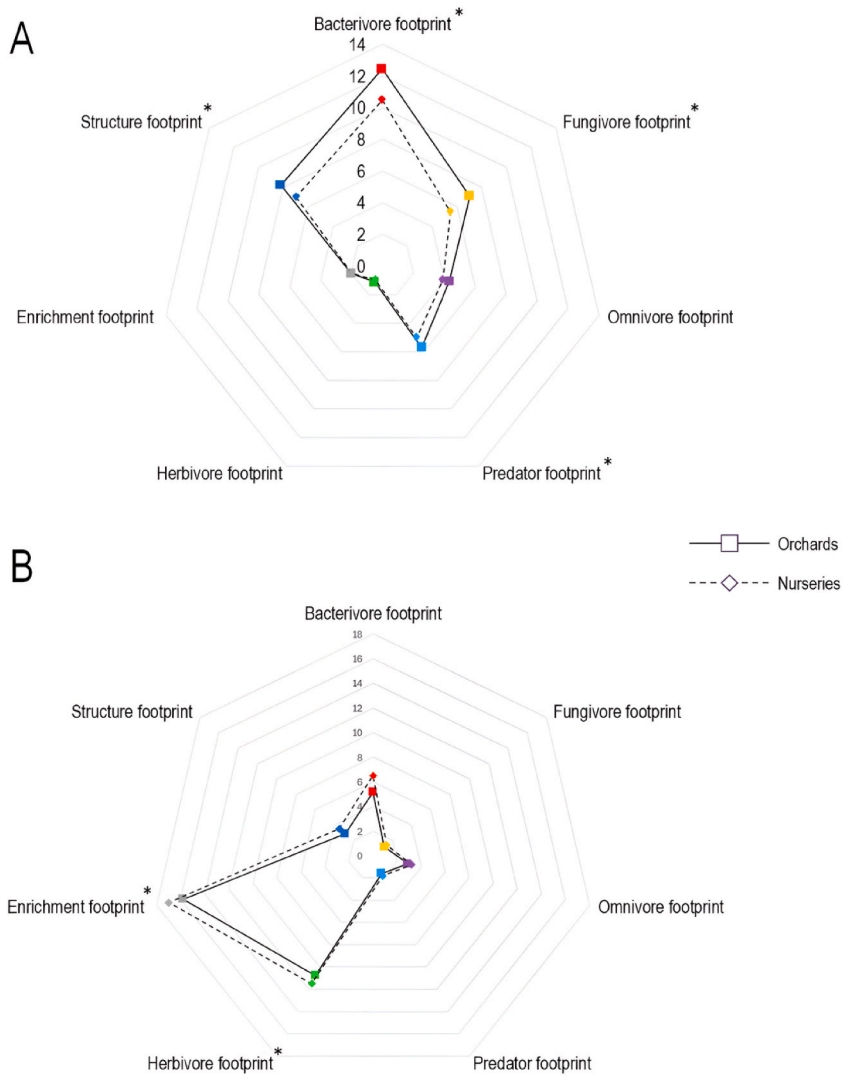


Fig. 4. Radar plots showcasing metabolic footprints performed by each nematode trophic group in (A) undisturbed soils and (B) disturbed soils of Moroccan olive nurseries and orchards. Asterisks (*) represent significant differences obtained from the Welch Two Sample *t*-test at $P < 0.001$. Values were log-transformed to meet normal distribution assumptions.

correlated with HOM and TOM (Fig. S6). The same trend was observed for the soil texture contents (clay, loam, and sand). Therefore, *Rhabditis, Diphterophora*, *Aporcelaimus*, *Heterodera*, and *Meloidogyne* spp. were more closely related to sandy soils, whereas *Aphelenchus*, *Prionchulus*, and *Pratylenchus* spp. had more affinity for clay soils. Except for O (e.g., *Aprocelaimus*, *Dorylaimus*, and *Thornenema* spp.) and some PF taxa (e.g., *Longidorus*, *Trichodorus*, and *Xiphinema* spp.), most nematode entities were affiliated with loam content (Fig. 5). For soil mineral contents, Fe and Mg were positively correlated with some nematode TGs (e.g., BF and P), whereas the rest (Cu, Ca, Mn, Na, and Zn) were not very closely associated with these nematodes. For the NPK content, positive correlations were detected with several nematode taxa. Therefore, BF (e.g., *Mesorhabditis* spp.), FF (e.g., *Aphelenchoides* spp.), O (*Dorylaimoides* spp.), P (*Mononchus* spp.), and PF (*Heterodera* spp.) had positive associations with K content, whereas the rest, excluding some FF, O, and PF, showed prominent abundance at high N and P soil concentrations (Fig. 5; Fig. S6). Soil EC was shown to be negatively correlated with almost all nematode taxa, whereas soil pH positively affected some nematode entities (e.g., *Anaplectus*, *Tripyla*, and *Tylenchus* spp.).

3.4. Ecological nematode dynamics in olive agroecosystems

3.4.1. Structural dynamics

To gain deeper insight into the potential of terrestrial nematodes as soil health bioindicators, a taxa contribution analysis (TCA) was performed by considering both the SIMPER and ANOSIM findings. This analytical approach emphasizes the key factors that influence soil health in both disturbed and undisturbed olive soils (Fig. 6). In the undisturbed soils, BF contributed more to the population, with

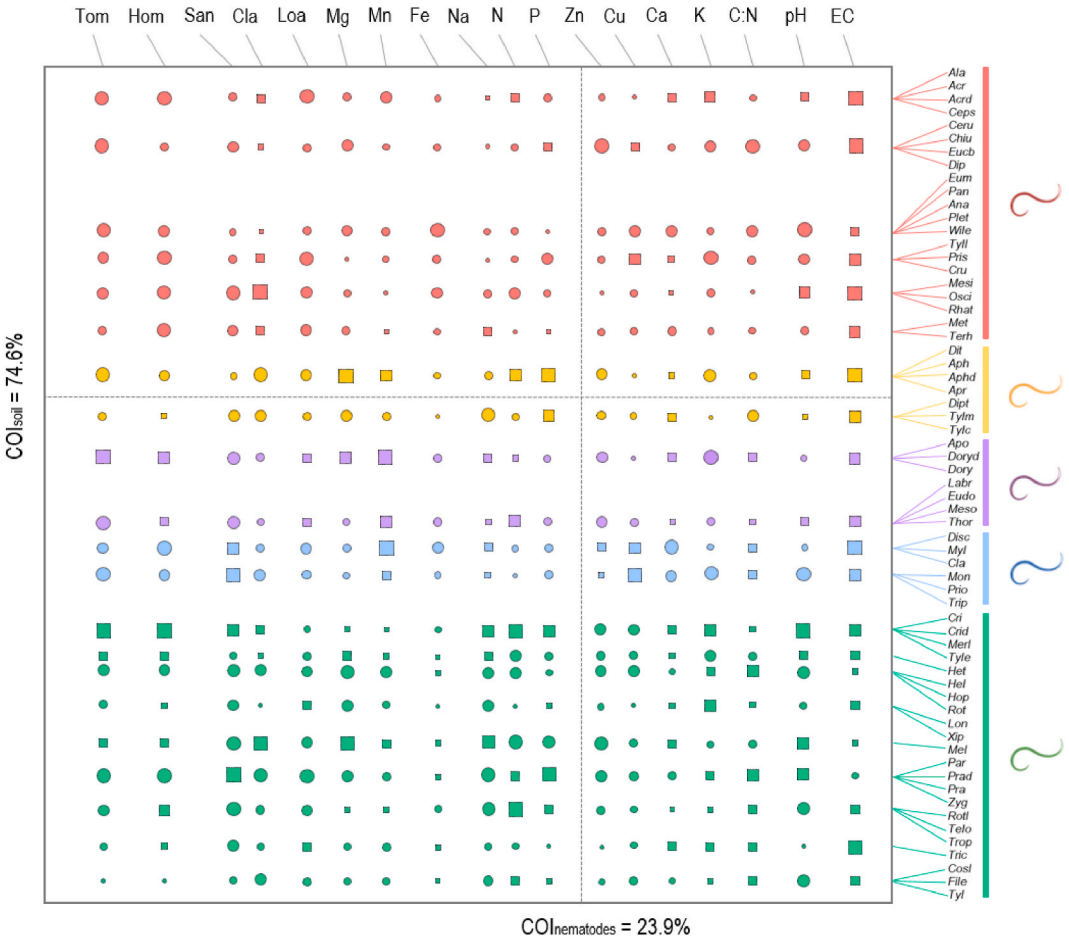


Fig. 5. Coinertia score plot depicting positive (circles) and negative (squares) correlations between soil nematodes identified in olive agroecosystems and soil physicochemical characteristics. Eigenvalues are represented in the coinertial contribution between terrestrial nematodes ($COI_{nematodes}$) and soil patterns (COI_{soil}). The nematode assemblages were clustered based on Ward's algorithm model. The magnitude of the correlation is proportional to the relative strength of the correlation.

five nematode taxa, namely, *Plectus* (40 %), *Rhabditis* (28 %), and *Eucephalobus* spp. (13 %) (Fig. 6A). The structural contribution of PF was attributed to 5 nematode taxa, mainly *Meloidogyne* (38 %), *Helicotylenchus* (32 %), and *Pratylenchus* spp. (15 %). FF contributed slightly less than PF, as *Aphelenchus* spp., *Aphelenchoides* spp., and *Tylolaimophorus* spp. led the assemblage. Therefore, two TGs were shown to have a low contribution to undisturbed soil status, as O (e.g., *Aporcelaimus* and *Eudorylaimus* spp.) and P (e.g., *Tripyla* and *Mononchus* spp.) shaped their respective nematode consortia. In disturbed olive soils, PF (e.g., *Helicotylenchus*, *Tylenchorhynchus,* and *Merlinius* spp.) contributed more than BF (e.g., *Cephalobus*, *Teratocephalus*, and *Plectus* spp.). Furthermore, O (e.g., *Eudorylaimus*, *Dorylaimus*, and *Dorylaimoides* spp.) were contributing the most in disturbed soils despite their low abundance, whereas FF (*Diphterophora*, *Aphelenchoides*, and *Aphelenchus* spp.) and P (*Clarkus*, *Discolaimus*, and *Mononchus* spp.) were the least common contributors (Fig. 6B).

The structural successions were predicted using a machine learning related approach to understand the importance of these successions for indicating soil disturbance profiles in olive agroecosystems (Fig. 7). Venn diagrams depict the possible trophic group combinations that could prevail in soil profiles (Fig. 7). In undisturbed olive soils, the most representative successions were PF↔FF (WSRP = 45 %; $P < 0.001$), PF↔BF (WSRP = 32 %; $P < 0.001$), and BF↔O (WSRP = 25 %; $P < 0.001$) (Fig. 7A). On the other hand, the disturbed soils are somehow similar to the undisturbed soils, except for prominent successions in BF↔FF (WSRP = 24 %; $P < 0.001$) and BF↔FF↔O (WSRP = 19 %; $P < 0.001$) (Fig. 7B). Interestingly, only 15 % and 11 % of the complete successions (PF↔FF↔BF↔O↔P) were present in the same habitat matrices (soil and/or root systems) under undisturbed and disturbed conditions, respectively.

3.4.2. Functional dynamics

The contribution of nematode FGs was visualized using lollipop plots (Fig. 8). This contribution referred to nutrient cycling, decomposition, predation, and mutualistic interactions in terms of soil disturbance status. In undisturbed soils, the BF group was

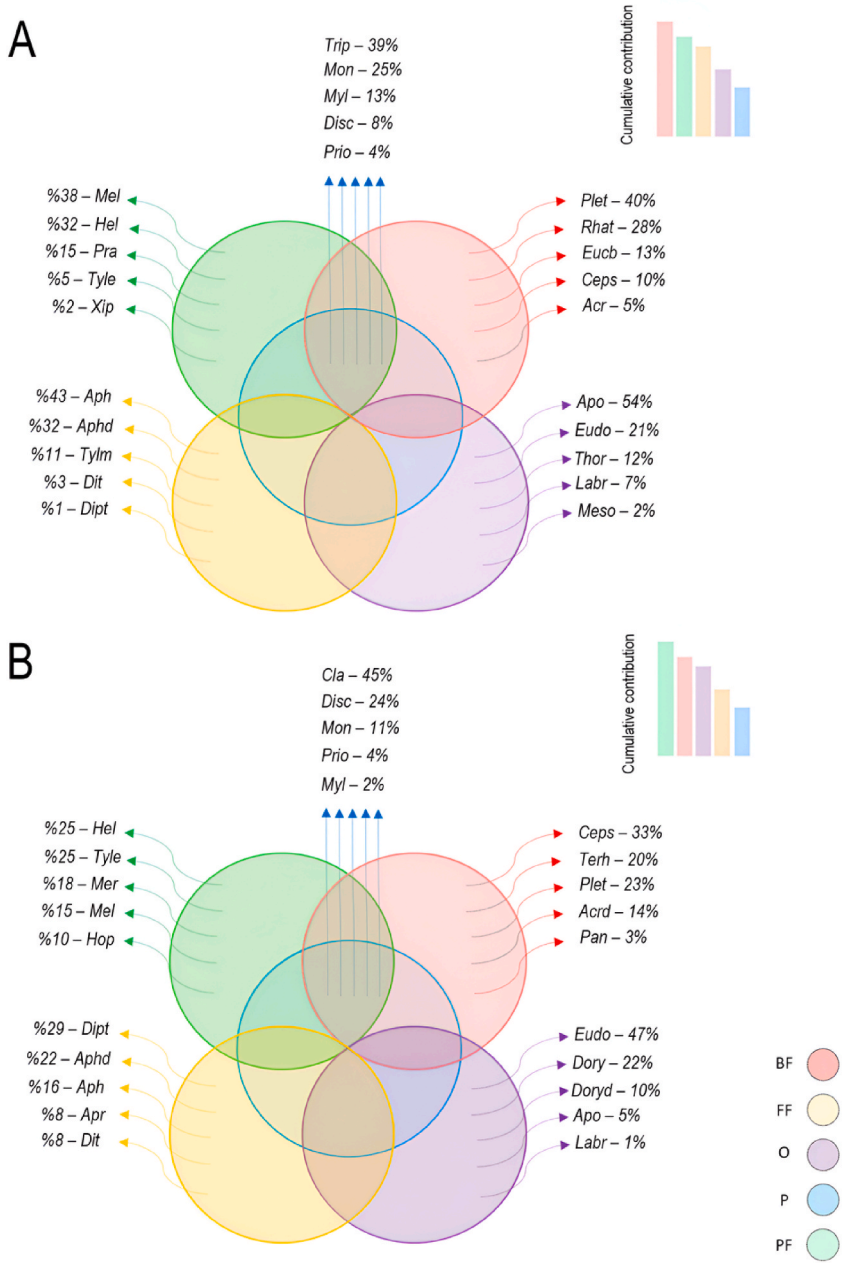


Fig. 6. Taxa contribution analysis showing spatial nematode contribution patterns to soil health in Moroccan olive agroecosystems. (A) Undisturbed soils. (B) Disturbed soils.

positively contributing with all respective FGs (Ba1 to Ba4), while the same trend was recorded with the P group (Pr3 to Pr5). The FF group (Fu2 to Fu4) had a positive contribution over the decomposition channels, while the main production channels were not prominently presented as He2, He3, and He5 were negatively contributed (Fig. 8A). On the other hand, disturbed soils displayed different contribution patterns. Most of the persisters represented by O (Om4 and Om5) and P (Pr4 and Pr5) groups negatively contributed. Similarly, colonizers represented by BF (Ba1 and Ba2) and FF (Fu2) did not positively contribute to the disturbance. Furthermore, all herbivore FGs (He2 to He5) were prominently presenting the production channels with positive contributions (Fig. 8B).

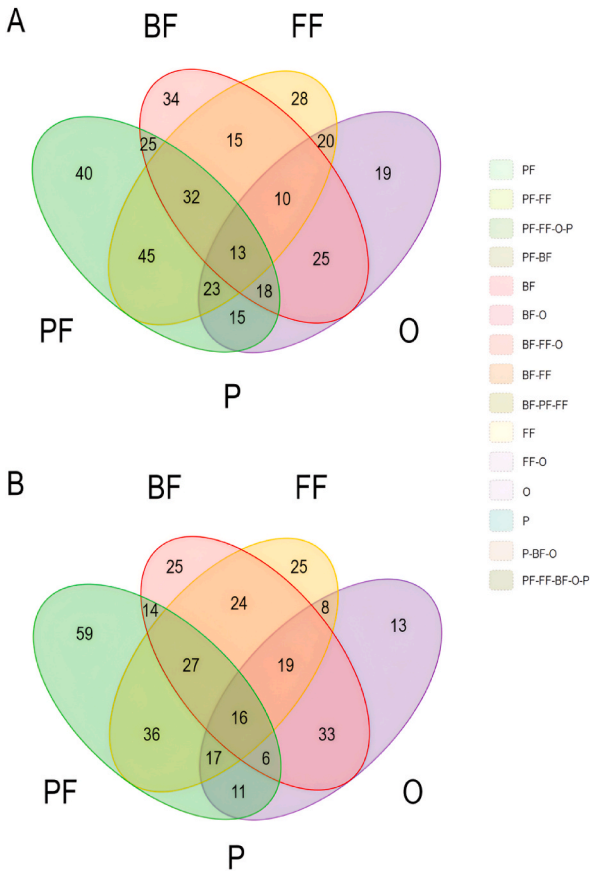


Fig. 7. Venn plots showing structural nematode TG successions predicted in olive agroecosystems in terms of disturbed profile. (A) Undisturbed soil profiles and (B) disturbed soil profiles.

4. Discussion

4.1. Olive nematode distribution patterns in Moroccan agroecosystems

Terrestrial nematodes, as one of the key organisms in the soil, are crucial entities for soil health in many cropping agroecosystems including olives [59–61]. It is important to emphasize that scientific research on olive nematology has focused mostly on PPNs, ignoring FLNs, while soil health concepts also depend on beneficial organisms that govern potential decomposition channels present within soil ecosystems. In this context, the identification and classification of these microorganisms in olive orchards can provide new insights into the integration of these concepts for sustainable olive production [62]. In our study, 63 nematode taxa were detected across different Moroccan olive nurseries and orchards. These taxa were categorized into 5 distinct TGs: 21 BF, 7 FF, 7 O, 6 P, and 22 PF. A recent study conducted in Central and South Italy identified multiple nematode genera in olive orchards (i.e., 12 BF, 4 FF, 10 O, 4 P, and 13 PF), derived from 19 taxon families [57], while Palomares-Rius et al. [63] identified 24 taxa associated with soil and root matrices of a 16 olive cultivar collection planted in southern Spain (i.e., 7 BF, 4 FF, 1 O, and 12 PF).

Nine families of the BF group were found to be predominated by Cephalobidae, Plectidae, and Rhabditidae. In addition, general opportunists (Ba2) were the most prevalent. These findings are consistent with the work conducted by Öztürk [64], who indicated that *Acrobeloides, Acrobeles, Cephalobus,* and *Eucephalobus* taxa exhibit significant and dominant abundances compared to the other FGs in Turkish olive orchards. Moreover, Dimou et al. [65] emphasized that olive ecosystems can generally enhance the spread of BF nematodes, specifically those from the Cephalobidae family [66]. Furthermore, *Aphelenchoides*, *Aprutides,* and *Ditylenchus* FF taxa were abundant across some structured olive agroecosystems. Sánchez-Moreno et al. [67] reported the same results in Spanish olive orchards, in which a prominent abundance of FF nematodes was detected in areas without tillage. These nematode TGs are extremely important for their decomposition proprieties in undisturbed cropping systems, where soil OM is more nutrient-poor (high C:N ratio) [68]. The genus *Ditylenchus* is often considered fungivorous due to its members' ability to feed on fungal hyphae [69]. This feeding behavior is facilitated by their specialized stylets, which allows them to pierce fungal cells and extract nutrients. Omnivores and predators had low to moderate abundances in the surveyed olive nurseries and orchards. This can be explained by their low abundance in topsoil (15 cm level) and the disrupted food sources especially in the disturbed areas [70]. In addition, these persisting nematodes have an extensive body size and are sensitive to disturbance and environmental constraints, which explains their low densities [71].

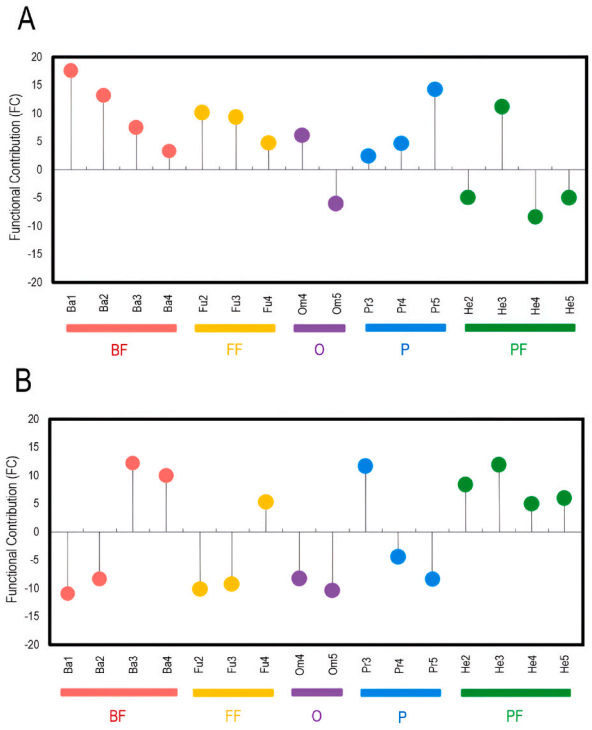


Fig. 8. Lollipop plots depicting the dynamics of nematode functional guilds detected in olive agroecosystems in terms of soil disturbance status. Dynamics were expressed in positive and negative functional contributions in (A) undisturbed and (B) disturbed soil profiles.

Among PPNs, 22 were detected and identified. Several nematode taxa have been reported in Moroccan olive areas [4,12]. RKNs, RLNs, and spiral nematodes (SNs) are the most abundant [72]. Recently, Laasli et al. [72] discovered a complex and diverse PPN community represented by 25 taxa in olive nurseries and orchards, including *Meloidogyne*, *Pratylenchus*, *Helicotylenchus, Paratylenchus, Heterodera*, and *Tylenchus* spp. The classification of *Tylenchus* genera as PPNs is primarily based on their observed feeding behavior (as root hair feeders), and morphological adaptations. Most *Tylenchus* species are associated with grasses, shrubs, and tree roots [73].

The spatial distribution of nematode TGs in olive nurseries and orchards often varies due to differences in soil structure, root density, and microbial diversity associated with these environments [74]. In our study, nematodes had a patchily distribution mode overall. This aspect was also highlighted by Sánchez-Moreno and Yuste [75] holm-oak forests. In olive nurseries, soils tend to be more disturbed and managed with regular inputs. This would promote a homogenous environment that may support a wider spatial distribution for certain TGs, such as BF and O [74]. However, FF and PF often show narrower distribution in nurseries, possibly due to limited fungal growth and young root structures, respectively, which can restrict the niches available to these groups [10,12]. In contrast, olive orchards, which are less frequently disturbed and have more established root systems, typically display a wider spatial distribution for FF and PF, as these groups thrive in matured soils rich in fungal networks and plant roots [76]. The Predator group, which relies on stable environments and diverse prey availability, often has narrower distributions in both settings due to limited ecological niches and sensitivity to environmental changes [77].

4.2. Ecological diversity of terrestrial nematodes in olive soils

The diversity indices calculated for the surveyed olive agroecosystems reveal significant variations across different regions. The MI was notably higher in some soils across BK, DT, and RSK regions, which can be attributed to favorable agronomic practices and optimal climatic conditions that promote soil health and biodiversity [78]. Recent studies highlight that factors such as soil texture, OM content, and irrigation practices significantly influence MI [78,79]. Regions with higher MI values likely benefit from well-managed soil conditions that support a diverse nematode community, enhancing soil fertility and structure [80]. Conversely, some soils in SM, MS, and SC regions exhibited lower MI values, which may be due to less favorable soil conditions or suboptimal agricultural practices. Soil compaction, lower OM, and inadequate irrigation can negatively impact soil biodiversity, leading to reduced MI [81]. As for PPI, it was higher in the MS region, indicating a balanced proportion of higher cp entities among the PPNs, which can be detrimental to soil health. This could also be linked to monoculture practices that favor the proliferation of parasitic species [82].

The CI and BI further illustrate the decomposition dynamics and basal metabolic activity within these ecosystems. DT and FM regions, which exhibit high CI values, likely indicate a potential prevalence of fungal over bacterial decomposition [18]. In contrast, the low CI value in the SC region indicates a less efficient decomposition process, possibly due to lower microbial diversity or unfavorable soil conditions [18,46]. Similarly, the high BI values in some soils in FM, and RSK regions suggest robust basal metabolic

activity, indicative of a depleted and degraded soil ecosystem. The low BI value in the SM region points to a less active soil microbial community, which could be a result of poor soil management or adverse environmental conditions [46,81].

4.3. Soil health bioindication in olive agroecosystems

The soil health status of the Moroccan olive agroecosystems was assessed using nematode community analyses. Most of the soils derived from the MS region have shown high disturbance. This region is characterized by mixed traditional (manual harvesting) and modern practices (Table S1) that could be attributed to this situation by the dominance of enrichment opportunists (c-p1), which are primarily BF with high metabolic activity. The BF group is also tolerant of pollutants and products of OM decomposition [60]. Furthermore, most of the soil ecosystems (derived from all surveyed regions) were classified as maturing with regulated properties that could be related to the climatic, edaphic, and management aspects within respective nurseries and orchards (Table S1). This soil category according to Ferris et al. [18] has low to moderate disturbance with a nitrogen enrichment mode. In addition, It is dominated by both r-strategists (c-p1 and c-p2) and has a balanced decomposition channel (bacterial/fungal) [18,46,60,61]. The involved nematodes have short/longer generation times, and are tolerant of adverse conditions, mainly BF and FF [18]. On the other hand, some undisturbed soils (from FM, MS, DT, and BK regions) were detected and characterized by a considerable abundance of persisters (c-p4 and c-p5) known as structure indicators. These nematodes (mainly from the O and P groups) have a long generation time and are very sensitive to pollutants and other disturbances [18,60]. The ecological aspects surrounding these regions including water and soil management could significantly contribute to enhancing soil stability and structuring (Table S1).

4.4. Relationships of terrestrial nematodes and olive soil functioning

In disturbed nurseries, nematode MF values were higher than those in disturbed orchards due to the specific management practices and growth conditions that nurseries entail (Table S1). Nurseries are often subject to frequent disturbances, such as transplanting, irrigation, and the application of fertilizers and pesticides, which accelerate microbial growth and lead to nutrient-rich soil environments [83]. This constant disturbance could provide a continual supply of OM and nutrients, which supports higher populations of BF and FF nematodes that thrive in conditions where microbial activity is boosted [84]. Unlike orchards, which may be disturbed only occasionally, nurseries undergo these interventions more regularly to support young plants' rapid growth, creating an ideal environment for fast-cycling nematode groups that capitalize on transient nutrient surges [85]. In MFA, EMF $\gg$ SMF patterns were observed in several soil agroecosystems. This common pattern could indicate a metabolic imbalance in nematode entities alongside a wealth of nutrients reaching the food web not being invested in creating complexity, thus reflecting disturbance [86]. Another possible explanation is the dominance of BF nematodes (including dauerlarvae formed from c-p1 nematodes) over the structure indicators [87], which was evident in our study. However, this nematode group could often have higher MF in undisturbed soils as resulted in our study. This is due to the diverse microbial community (serving as a food source) alongside the gradual accumulation and decomposition of OM, creating a nutrient-rich environment that promotes a steady growth of bacterial populations [88].

Conversely, MF values of undisturbed orchards were typically higher than those of undisturbed nurseries due to the more stable and mature ecosystems [18]. In undisturbed orchards, the well-established root systems of mature trees continuously support a complex soil food web [89]. This stability promotes higher predator, omnivore, and structure footprints, reflecting a balanced, mature ecosystem with stable nutrient cycling and long-term ecological relationships [90]. In contrast, undisturbed nurseries, which contain younger plants, lack the extensive root systems and ecological stability found in orchards [91]. As a result, They have lower predator and structure footprints, as their simpler ecosystems do not support the same level of trophic complexity and stability as undisturbed orchard soils [92].

The nutrient allocations of the soil food web were shifting towards the primary production channels (mainly operated by PF) and decomposition channels (mainly operated by FF) in the disturbed and undisturbed areas, respectively. This is supported by evidence showing that PF can benefit from conducive soil proprieties that create a favorable edaphic environment for their ecological functioning, leading to higher metabolic activity and footprint [93]. Conversely, Research has shown that FF nematodes contribute significantly to microbial diversity and carbon cycling in undisturbed soils which allow them to thrive and exhibit higher metabolic footprints [94,95].

4.5. Correlation between olive nematodes and soil patterns

The relationship between soil characteristics and the diversity of terrestrial nematodes is a critical area of research. Soil proprieties can directly or indirectly influence the development of nematodes, a key component of their life cycle [96,97]. Our research revealed a significant correlation between certain soil properties and nematode populations. Soil texture has affected the abundance aspects of nematodes. Hamza et al. [12] reported similar results, emphasizing a strong link between nematodes and different soil particles in Moroccan olive groves. The impact of sandy texture on the presence of soil nematodes in olive agroecosystems could be due to the negative relationship between sandy texture and soil EC [98]. Moreover, the EC is lower in sandy soils than in clay soils, which might explain the negative association of EC with overall nematode distribution. Dieng et al. [99] suggested that sandy conditions provide favorable conditions by enhancing nematode motility and increasing their reproduction. In terms of soil minerals, several parameters (e.g., Mg, Mn, Ca, Cu, Zn, etc.) were positively correlated with nematode entities. Numerous studies have reported a strong relationship between land-dwelling nematodes and soil mineral content [6,12,20]. However, other research has shown that the soil structure indicators (O and P groups) can be negatively affected by soil mineral content, leading to a decrease in both richness and MI

[81]. The spatial distribution of soil minerals can create heterogeneous environments that further influence nematode community structure. Nematodes in different TGs, such as BF, and FF exhibit varied responses to soil mineral gradients, reflecting their specific ecological niches and dietary requirements [81,100]. According to our results, NPK content had a significant effect on nematodes (especially PF). El-Deriny et al. [101] indicated that the presence of a high NPK content strongly affects most PF due to the optimal conditions it creates for plants to be more resilient to nematode attacks. Soil OM (HOM and TOM) was found to play a significant role in determining the structural dynamics of land-dwelling nematodes. For instance, higher levels of soil OM have been associated with increased abundance and diversity of nematode communities. This is because OM provides essential nutrients that support the growth of microbial populations, which serve as food sources for BF and FF [102]. Additionally, these microbial feeders are often positively correlated with soil nutrient concentrations, indicating that nutrient-rich soils can support more robust nematode populations [102, 103]. However, the accumulation of OM in soils could lead to a decrease in PF [104]. Indarti et al. [105] reported that OM significantly decreased the abundance of several PF nematodes due to the reduction in available food sources and the potential disruption of their habitat, leading to unfavorable conditions for their survival and reproduction.

4.6. Structural and functional dynamics of olive nematodes

The structural and functional contributions of nematode taxa from different TGs in olive agroecosystems provide valuable insights into soil health and ecosystem functioning [106]. The structural dynamics of nematodes (i.e., contribution patterns in nematode community composition, diversity, and population structure) can be assessed using various metrics, such as spatial contributions and TG succession percentages (i.e., progressive shifts in the composition and roles of nematode groups following soil status) within soil ecosystems [20]. These aspects reflect the relative structure and sequential patterns of different TGs and their sensitivity or resilience to soil disturbance [20]. In TCA, BF contributed more to the total biomass in undisturbed soils, whereas PF prevailed in disturbed soils. This could be explained by the fact that in undisturbed soils, BF benefits from a higher OM content and microbial biomass, which provide them with food resources and a favorable habitat [107], whereas in disturbed soils, PF thrive due to reduced competition from other TGs and an altered soil structure that disrupts microbial communities and lowers OM content, creating conditions that do not regulate their populations and favor their adaptations [107,108]. In that sense, Ferris et al. [18] stated that disturbed soils have characteristics that create favorable conditions for certain nematode groups (soil conduciveness). On the other hand, O, P, and FF nematodes were less contributing to disturbed soils. Persisting nematodes (especially from c-p4 and c-p5 groups) could face some predation pressure imposed by higher trophic-level organisms in the soil food web, such as microarthropods (mites (Acari) and springtails (Collembola)). These organisms can be resilient to some moderate disturbances and can continue to adapt even when the overall soil ecosystem is disrupted [18]. However, because O and P nematodes generally require stable conditions with high habitat complexity and a consistent prey base, their populations tend to be low, particularly in disturbed or simplified soils where their food sources or habitat conditions are limited [109]. FFs, on the other hand, face resource limitations and survival challenges due to reduced fungal biomass and diversity under disturbed conditions [110]. In our study, some individual genera from cp-4 nematodes (e.g., *Eudorylaimus* and *Clarkus*) were predicted to have some contributions under disturbance. The latter may temporarily create niches or microenvironments that allow these genera to establish and contribute to nutrient cycling or ecological functions in ways not observed under more stable conditions [111,112]. In addition, changes in their population can ripple through the soil food web, affecting other organisms that directly influence soil structure, such as earthworms or soil-dwelling insects [113]. Regarding TG successions, PF↔FF, PF↔BF, and BF↔O were more frequent in undisturbed soils, whereas BF↔FF and BF↔FF↔O successions were more common in disturbed soil ecosystems. These results can be explained by factors related to OM content compensation and bacterial/fungal biomass that favor the coexistence of different nematode TGs in the same complex [45,114].

The functional dynamics (i.e., nematode functional contribution to nutrient cycling and energy flow, influenced by trophic interactions in response to disturbance status) targeting the contribution of nematode FGs highlight the complexity of soil ecosystems and the need for a nuanced understanding of nematode functional roles [115,116]. Our study revealed that bacterial, predator, and fungal FGs had positive inputs in undisturbed soils, while herbivore FGs were the main contributors to disturbed conditions. Ferris [86] emphasized the functional roles of BF and P groups which are crucial in maintaining soil health and stability, while the positive role of FF in decomposition channels further emphasizes their importance in breaking down OM and facilitating nutrient availability [86,95]. In contrast, a shift towards production channels is expected by PF, possibly due to increased plant root exudates and OM inputs from disturbed vegetation [117,118]. These findings align with previous studies that have shown how soil disturbances resulting from agricultural practices and environmental changes, can alter nematode community structures and their functional roles [119,120]. The resilience of certain nematode TGs in undisturbed soils highlights their adaptability and essential functions in maintaining ecosystem stability [121]. Conversely, the altered contributions in disturbed soils highlight the need for sustainable soil management practices to mitigate the negative impacts of disturbances and promote soil health in olive agroecosystems [122].

5. Conclusion

This study provides genuine insights into the biodiversity and dynamics of terrestrial nematodes associated with Moroccan olive agroecosystems and their contributions as effective soil health bioindicators. Nematode taxa from various TGs were diverse and widely distributed across olive-surveyed areas. Among the latter, the majority of soil systems derived from all localities had low to moderate disturbance with enriched and balanced decomposition channels, whereas some derived from MS and SC regions had highly disturbed soils with bacterial and conducive aspects. Structural and functional analyses of nematode dynamics have revealed the spatial contributions of nematode TGs and FGs under different disturbance scenarios. BF (e.g., Cephalobidae and Rhabditidae) and PF (e.g.,

Meloidogynidae and Pratylenchidae) were the major contributors to undisturbed and disturbed soils, respectively. Organic and mineral characteristics within these soils have shown positive/negative relationships with olive nematode communities depending on their respective TG. This study can potentially be used as a model for other olive production systems in different countries (especially in the Mediterranean), shaping the importance of nematodes as soil health bioindicators. In addition, the predicted soil profiles provided insights into nematode interactions with biological processes to maintain soil health in olive agroecosystems. However, further research is needed to determine the relationships between climatic/edaphic gradients and nematode TGs within olive agroecosystems. This will strengthen the prospects of growers for managing disturbance events occurring in their soil habitats, thus helping them to achieve sustainable soil health and olive productivity.

CRediT authorship contribution statement

Salah-Eddine Laasli: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Rachid Lahlali:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Abdelfattah A. Dababat:** Writing – review & editing, Validation, Supervision, Resources, Conceptualization. **Timothy Paulitz:** Writing – review & editing. **Amine Assouguem:** Writing – review & editing, Funding acquisition. **Riaz Ullah:** Writing – review & editing, Funding acquisition. **Ahmed Bari:** Writing – review & editing, Funding acquisition. **Mustafa İmren:** Writing – review & editing. **Ebubekir Yüksel:** Writing – review & editing. **Jihane Kenfaoui:** Writing – review & editing. **Lucy Kiarie:** Writing – review & editing. **Driss Iraqi:** Writing – review & editing. **Fouad Mokrini:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Data availability statement

Available data are presented in the manuscript.

Funding

This work was funded by the Sustainable Innovations for Regenerative Agriculture in the Mediterranean Area (SIRAM) Project affiliated with PRIMA. The authors wish to thank the researchers supporting project number (RSP2024R146) at King Saud University, Riyadh, Saudi Arabia for financial support.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was financially supported by the Phytopathology Unit of the Ecole Nationale d'Agriculture de Meknes (Morocco). The authors are thankful to the farmers and stakeholders for their assistance in providing the needed information during field surveys. The authors also appreciate the important support received from the MCRDV 2023 Project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e40715.

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