Plant Soil (2024) 501:39–55
https://doi.org/10.1007/s11104-023-06190-5

RESEARCH ARTICLE

Phytopathogenic nematode communities infesting Moroccan olive agroecosystems: impact of agroecological patterns

Salah-Eddine Laasli · Fouad Mokrini · Driss Iraqi · Munqez J. Y. Shtaya · Said Amiri · Abdelfattah A. Dababat · Timothy Paulitz · Khalid Khfif · Rachid Lahlali

Received: 9 April 2023 / Accepted: 24 July 2023 / Published online: 3 August 2023

Abstract
Background and aims Olive trees are one of the most important crops in the Mediterranean, especially in Morocco, and they are vulnerable to various soil-borne pathogens that can cause significant yield losses and economic damage. This study aimed to investigate the diversity, abundance, and community composition of phytopathogenic nematodes in Moroccan olive agroecosystems, and to evaluate the impact of agroecological patterns on their abundance.

Methods Soil and root samples were collected from 13 olive-growing localities across 7 Moroccan regions (43 nurseries/22 orchards), and nematodes were ecologically assessed through the calculation of several diversity indices (e.g., Shannon Index, Evenness, and Plant Parasitic Index). In addition, the main nematode genera were evaluated in terms of soil types, irrigation regimes, and landscape complexity.
Results The obtained results revealed the presence of a diverse and complex community of phytopathogenic nematodes represented by 25 genera, including *Meloidogyne*, *Pratylenchus*, and *Helicotylenchus* among others. The abundance and diversity of

Responsible Editor: Guiyao Zhou.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s11104-023-06190-5.

S.-E. Laasli · S. Amiri · R. Lahlali
Department of Plant Protection and Environment, Ecole Nationale d'Agriculture de Meknes, km. 10, Route Haj Kaddour, B.P. S/40, 50001 Meknès, Morocco

S.-E. Laasli
Crop Protection Unit, Agronomic and Veterinary Institute IAV, Rabat, Morocco

S.-E. Laasli · F. Mokrini · D. Iraqi
Biotechnology Unit, Regional Center of Agricultural Research, INRA, Rabat, Morocco

M. J. Y. Shtaya
Department of Plant Production and Protection, Faculty of Agriculture and Veterinary Medicine, An-Najah National University, P.O. Box 7, Nablus, Palestine

A. A. Dababat
International Maize and Wheat Improvement Center (CIMMYT), P.O. Box 39, Emek, Ankara 06511, Turkey

T. Paulitz
Wheat Health, Genetics and Quality Research Unit, United States Department of Agriculture, Agricultural Research Service, Washington State University, Pullman, WA 99164-6430, USA

K. Khfif
Research Unit on Nuclear Techniques, Environment, and Quality, National Institute for Agricultural Research, INRA-Tangier, Tangier 90010, Morocco

R. Lahlali (✉)
Plant Pathology Laboratory, AgroBioSciences, College of Sustainable Agriculture and Environmental Sciences, Mohammed VI Polytechnic University, Lot 660, Hay Moulay Rachid, 43150 Ben Guerir, Morocco
e-mail: rlahlali@enameknes.ac.ma

nematodes varied significantly between the different regions and agroecological patterns, with higher densities observed in simple landscapes and higher irrigation regimes. Moreover, the community of dominant nematodes was influenced by soil types. Root-knot nematodes were the most prevalent in sandy soils, while root-lesion nematodes were significantly present in the clayish setting. The occurrence and severity of nematode damage were also correlated with the overall taxonomic richness shaped in different olive landscape modes.

Conclusion This study provides updated information and prospects into nematode sustainable monitoring and management in North African olive agroecosystems.

Keywords Agro-ecological patterns, diversity · *Meloidogyne* · Olive · Phytopathogenic nematodes

Introduction

Olive trees (*Olea europaea* L.) have a long and rich history in the Mediterranean region and have played an important role in the economy and culture of the area for centuries. Olives and their by-products are a crucial component of the Mediterranean diet, providing the primary source of dietary fats and vegetable oils (El and Karakaya 2009). In Morocco, olive trees have been cultivated for thousands of years, and today the country is one of the largest producers of olive oil in the world, with over 1.2 million hectares, making up to 65% of the total cultivated agricultural land with an annual production of over 1.9 Mt (FAOSTAT 2022). These trees are predominantly found in arid and semi-arid regions with inconsistent rainfall patterns (Breton et al. 2009).

However, the Moroccan production pattern of olives is facing numerous challenges caused by soil-borne pathogens including the infestation by phytopathogenic nematodes (PPNs). These microscopic pathogens cause extensive damage to crops worldwide estimated at 14.6% (157 billion US$/year) (Nicol et al. 2011). They can have negative effects on cultivated olive trees, reducing tree growth and causing yield losses of 5–10% (Koenning et al. 1999; Nico et al. 2002). Intensive cultivation systems and nurseries are more susceptible to the negative effects of nematode reproduction due to favorable irrigation conditions (Castillo et al. 2010). Research has discovered that olive trees, whether in orchards, nurseries, or even some wild areas, are hosts to 153 PPN species belonging to 56 genera (Ali et al. 2014). Several PPN genera have been reported in Moroccan olive nurseries and orchards (Ali et al. 2014, 2015, 2016; Hamza et al. 2017). For instance, root-knot nematodes (RKNs, *Meloidogyne* spp.), root lesion nematodes (RLNs, *Pratylenchus* spp.), and spiral nematodes (SNs, *Helicotylenchus* spp.) are the most dominant PPNs across olive-growing regions. The genus *Meloidogyne* has the largest economic importance in infesting olive areas as it occurs with four devastating species (*Meloidogyne javanica*, *M. incognita*, *M. arenaria*, and *M. spartelensis*) (Ali et al. 2015; Hamza et al. 2017, 2018). Furthermore, *Pratylenchus* genera are mainly represented by *Pratylenchus neglectus*, and *P. pinguicaudatus* (Ali et al. 2015; Hamza et al. 2017), and they are widely distributed with high densities. *Helicotylenchus* genera are also abundant with a large spectrum of species including *Helicotylenchus vulgaris*, *H. dihystera*, *H. digonicus*, and *H. canadensis* (Hamza et al. 2018). The impact of PPNs on olive trees can result in reduced growth, stunted plant development, and decreased fruit yield and quality. These effects can be compounded by agroecological factors, such as soil type, cropping system, water regime, and landscape complexity, which can all impact PPN distribution and biodiversity (Altaf et al. 2017).

The importance of soil type and irrigation on Phytopathogenic nematode communities in olive trees cannot be overstated. Soil characteristics and water availability are crucial factors influencing the distribution, abundance, and activity of nematodes in agricultural systems, including olive groves (Guesmi–Mzoughi et al. 2022; Barbera et al. 2013; Hamza et al. 2017; 2018; Laasli et al. 2023). Recent research studies have highlighted the influence of soil texture on the abundance and diversity of soil nematodes (Kekelis et al. 2022; Landi et al. 2022). These studies elucidated the significant affinity of these microorganisms in sandy and clayey soils. This affinity is strongly dependent on nematode genera. Specifically in olive groves, Guesmi–Mzoughi et al. (2022) demonstrated that sandy soils are more suitable for the multiplication of sedentary endoparasitic genera (e.g., *Meloidogyne* and *Heterodera* spp.), while the *Pratylenchus* genus was more prevalent in clay soils. These findings imply that soil is the most influential factor driving PPN communities when interacting with their respective host.

Irrigation practices significantly influence the population dynamics and distribution of olive PPNs (Guesmi–Mzoughi et al. 2022). The availability of water in the soil is a critical factor for the survival, movement, and infection process of these nematodes (Nicol et al. 2011; Mohawesh and Karajeh 2014). Nematode populations are sensitive and variable to changes in soil moisture, and the irrigation regime can be manipulated to reduce nematode infestation to recover the plant's health and productivity (Reddy 2017). In that manner, studies conducted by Song et al. (2016) and Bristol et al. (2023) found that increased rainfall, simulated through irrigation, led to a rise in PPN populations, likely due to enhanced plant productivity. The effect of vegetation complexity on PPN communities is another area of growing interest. Complex vegetative cover can provide diverse habitats and resources for nematode populations, potentially influencing their abundance, diversity, and impact on different crops (Šalamún et al. 2017; Brustolin et al. 2018). In that sense, soil nematodes could be significantly impacted by landscape change (Porazinska et al. 2021).

Despite the recent progress made in understanding the effects of agroecological patterns on PPNs, there remain significant knowledge gaps in this area (especially in Morocco). One such gap is the influence of drip irrigation-based regimes (configured by evapotranspiration levels) and their subsequent effects on olive nematodes. In addition, vegetation patterns have not been studied yet on olive PPNs. These gaps constitute the main objectives of this study alongside further insights on soil type influence and nematode diversity in all potential olive areas in Morocco. The studied agroecological factors are hypothesized to have a significant effect on nematode entities, by creating distinct microenvironments that support specific nematode genera. This study will provide ecological insights into the dynamics of nematode communities in relation to their environment, which is crucial for their sustainable management.

Materials and methods

Survey description and sampling

An extensive survey was conducted in potential olive agroecosystems (nurseries and orchards) located in seven regions of Morocco (North: Rabat-Salé-Kenitra, Fes-Meknes, and Settat-Casablanca), (South: Draa-Tafilalet and Souss-Massa), (West: Marrakesh-Safi), and (East: Beni Mellal-Khenifra), divided in 13 localities (Fig. S1; Table 1). These regions are characterized by important olive production and were chosen based on their proximity to each other, their altitude range, and the presence of PPN damage signs. The climate in these regions ranged from arid to subhumid while the soil types are represented by all key components (sand, clay, and loam) (Table 1). Twenty-two olive orchards were surveyed, and 10 trees per orchard were considered for the sampling procedure. To collect soil and root samples, a zigzag pattern was followed in the top 25 cm layer of soil depth, covering approximately 100 m^2 per orchard, using a 25 mm diameter auger. After collection, subsamples were combined to form a representative 2 kg sample, consisting of 20 soil and 15 root subsamples per olive orchard/nursery. In the case of nurseries, a total of 43 entities were prospected for PPN infestation, based on their geographic location, growth substrates, and cultivar diversity (Table 1). The majority of substrates used were loamy-cropped soils, and the five primary olive cultivars adopted were Picholine Marocaine (Morocco), Menara (Morocco), Haouzia (Morocco), Picholine Languedoc (France), and Arbequina (Spain). Following the same sampling procedure, we placed samples in polyethylene bags to prevent water loss and transported them immediately to the Nematology laboratory at INRA-Rabat for nematode extraction and processing.

Nematode extraction and diagnosis

The soil and root samples were processed for nematode isolation within 48 h of collection using the modified Baermann method as described by Hooper (1986). Nematodes were extracted from 100 cm^3 of soil and 20 g of root samples over a 72-hour incubation period. The nematode suspension was then examined under a stereomicroscope (Olympus CH-2, Japan) to measure the abundance of each genus. To preserve the samples, the nematodes were killed and fixed with hot formaldehyde (4%) and then transferred to a solution consisting of formaldehyde (4%) and glycerin (99/1; v/v). The nematodes were placed on a square watch glass with a diameter of 7 cm in a desiccator containing approximately 1/10 ethanol volume. The following day, the nematodes were removed from the desiccator and incubated at 37 °C.

Table 1 Agroecological regions surveyed for phytopathogenic nematodes in Moroccan olive nurseries and orchards

Localities	Bioclimate	Soil Type	A_R (mm)	A_T (°C)	Site N° (N/O)	SPS	GPS Coordinates (Lat, Long)	Code
Benslimane	Semi-arid	Sandy loam	66.5	13.5	2/1	5	33.6168709,-7.123036	BN
Chichaoua	Semi-arid	Clay loam	300.1	17.5	4/2	6	31.5469033,-8.759546	CH
Essaouira	Mediterranean	Medium loam	316.3	18.7	4/2	6	31.5118281,-9.762090	ES
Fes	Mediterranean	Sandy loam	393.3	17.8	3/2	12	34.0346534,-5.016192	FS
Gharb	Sub-Humid	Sandy clay loam	320.1	19.6	3/1	5	34.264570,-6.5701690	GA
Haouz	Arid	Clay loam	422.9	18.7	3/1	10	31.460070,-7.6236078	HZ
Marrakesh	Arid	Clay loam	288	18.5	3/1	20	31.625825,-7.9891608	MA
Meknes	Mediterranean	Sandy loam	371.3	17.4	2/3	15	33.8984131,-5.532158	MK
Ouarzazate	Arid	Clay loam	95.9	21.8	3/1	6	30.920193,-6.9109230	OU
Sidi Kacem	Sub-Humid	Medium loam	305.2	17.2	2/1	3	34.226412,-5.7114340	SK
Souss-Massa	Semi-arid	Sandy clay loam	160.6	28.7	5/3	22	30.4205162,-9.583853	SM
Tadla	Semi-arid	Medium loam	267.9	19.6	5/2	8	33.6887649,-7.392079	TA
Tafilalet	Arid	Sandy loam	122.1	27.6	4/2	6	31.2456745,-4.266280	TF

A_R: Annual rainfall; A_T: Annual temperature; N/O: Nurseries/Orchards; SPS: Samples Per Site

Within 3 h, a solution consisting of ethanol (96%) and glycerin (95/5; v/v) was added in triplicate to a watch glass partially covered with a glass slide to promote evaporation. Finally, a solution of ethanol (96%) and pure glycerol (50/50; v/v) was added, and the watch glass was placed in an incubator at 37 °C overnight according to De Grisse's method (De Grisse 1969).

The nematodes were identified based on their morphological characteristics, such as body size, shape, and stylet features using diagnostic keys (Mai and Lyon 1975; Mai and Mullin 1996). The glycerin-ethanol method was used for species identification using specific keys (Ryss 1988; Siddiqi 2000; Castillo 2007; Brzeski 1991; Andrássy 2005; Geraert 2008, 2010, 2011) under a light microscope (Nikon Eclipse E200, Tokyo, Japan). For *Meloidogyne* species, perineal samples were used for identification, and five samples were prepared and placed in glycerin for microscopy according to Taylor and Netscher (1974). *Heterodera* species (CNs) were extracted using the flotation method according to Hooper et al. (2005), and vulval cones were used for identification as described by Handoo (2002).

Nematode assessment

Following the evaluation of PPN densities (per 100 cm³ and 20 g of soil and root matrices, respectively), a taxonomic assessment of PPNs was established by calculating different ecological indices based on the total number of nematodes (N_{total}), generic richness (G) stating the number of genera per each community. These indices include Plant Parasitic Index ($PPI = \sum (vi) \times (fi)$), where vi involves the p-p (plant-parasitic) values of nematode genus i, and fi is the relative frequency of genus i occurring in a sample (Bongers 1990). Shannon–Weaver diversity index $H' = -\sum_{i-1}^{s} pi \ln pi$, where s depicts the richness of nematode genera, pi is the genera proportion, and the Evenness $E = H/Hmax, Hmax = \log_2 s$ (Krebs 1985). In addition, specific indices of nematode species were calculated considering their feeding level: ectoparasites (I_{ecto}), migratory endoparasites (I_{endo_mig}), and sedentary endoparasites (I_{endo_sed}). Each index highlights specifically the extent of the corresponding nematode species in their ecological niche (Guesmi-Mzoughi et al. 2022).

Agro-ecological relationships to phytopathogenic infestations of nematodes

To investigate the relationships between PPN infestation in olive areas (orchards and nurseries) and agro-ecological patterns, three main nematode genera (*Meloidogyne* spp., *Pratylenchus* spp., and *Helicotylenchus* spp.) were assessed for their abundance according to progressive levels of soil substrates, irrigation regime, and landscape complexity.

Nematode genera abundance was assessed in four soil types i.e., sandy, sandy-clay-loam, medium loam, and clay. For irrigation regime (IR), these genera were evaluated in olive nurseries at three levels according to the evapotranspiration percentage (ETP) (Low = 25%, Moderate = 50%, and High = 75%) in a drip irrigation setting (Fig. 1). Five olive varieties were considered including Picholine Marocaine (P_m), Picholine Languedoc (P_L), Arbequina (A_{rb}), Menara (M_n), and Haouzia (H_z). The experiment was conducted in a fully randomized block design (FRBD) and repeated 3 times (n = 3) for data validation. A negative control (C) plot was considered for all varieties with a regular IR and no nematode infection.

In olive orchards, main PPN feeding types (e.g., sedentary endoparasites, migratory endoparasites, and ectoparasites) were further assessed as a function of the associated landscape complexity (LC). This parameter highlights the amount of vegetation presented within olive cultivation and it ranged from low to complex (Fig. S2). Intercropping events were observed in intermediate and complex landscape levels.

Statistical data analytics

In the surveyed areas, the dominance parameter was determined for each nematode genera, and their frequencies were recorded. To analyze the abundance variables, a distribution diagram of nematode communities was generated after transforming the values to $\log_{10}(X+1)$. To examine the distribution of PPN communities in different olive agroecosystems, Principal Component Analysis (PCA) was carried out using *sklearn.decomposition.PCA* module implemented in Python. The datasets involving nematode abundances for each factor were first normalized using the Anderson-Darling normality test (Stephens 1974), and the PPN variables associated with the PCA were analyzed using a one-way ANOVA with the XLSTAT 2016.02.28451 software (Addinsoft, New York, NY, USA). To determine the significant differences among the variables at $P < 0.05$, Fisher's protected least significant difference (LSD), Tukey, and Duncan tests were employed. Score plots were performed to visualize and assess the homogeneity of the prospected olive sites in terms of PPN distribution patterns. Furthermore, a correlation matrix (Pearson type) was generated to highlight the relationship strengths between different nematode genera using the package *corrplot* (ver. 0.92) in R (ver. 4.0.5) software (Wei et al. 2017).

For agroecological patterns, a Violin plot was generated using *seaborn.violinplot* module in Python to compare different nematode abundance values between IR levels. In addition, exponential regression analysis was produced to predict the linkage between nematode taxonomic richness (G), the total number

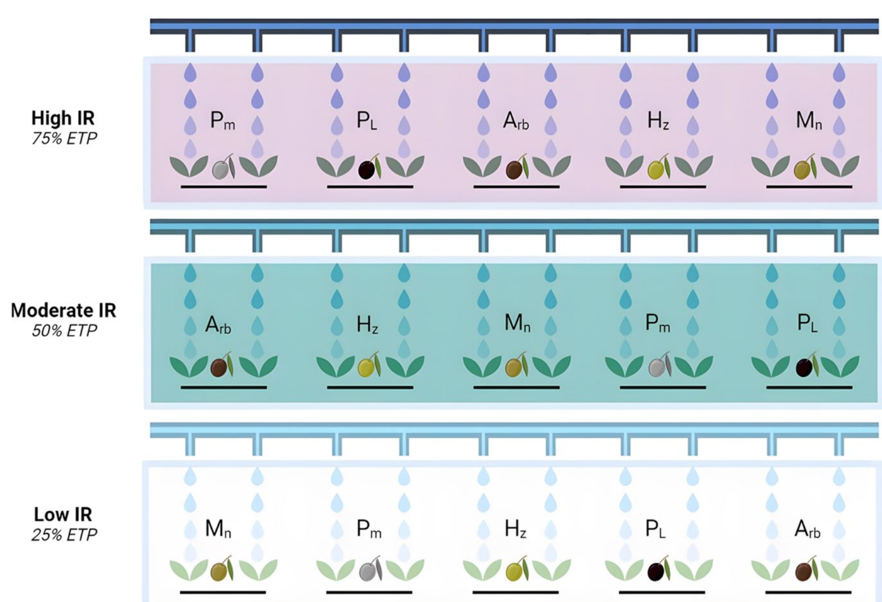

Fig. 1 Experimental design of irrigation regime (IR) influence on phytopathogenic nematode infestations in Moroccan olive nurseries. The IR levels were organized in a fully randomized block design (FRBD) and were based on evapotranspiration percentages (ETP) incorporated into a drip irrigation system. Abbreviations for olive cultivars stand for Picholine Marocaine (P_m), Picholine Languedoc (P_L), Arbequina (A_{rb}), Menara (M_n), and Haouzia (H_z)

of genera, and land complexity levels that occurred within olive orchards.

Results

Nematode community composition and ecological distribution in moroccan olive agroecosystems

The collected soil and root samples from the olive orchards contained a total of 25 different genera of phytopathogenic nematodes. The most common species found were *Meloidogyne* spp., *Pratylenchus* spp., and *Helicotylenchus* spp. (Table 2). The diversity of nematode communities varied between nurseries/orchards, with some localities showing high levels of diversity and others showing low levels (Fig. S3). The highest PPN density rates were recorded in MK, FS, OU, and CH. In terms of feeding behavior, sedentary endoparasites (*Meloidogyne* and *Heterodera* spp.) were significantly dominant in CH, FS, MK, OU, SM, and TA (up to 895 nematodes per 100 cm³ of soil and 20 g of roots) (F_{index} = 150.6; $df = 12$; $P < 0.05$) (Fig. S3). Migratory endoparasites (e.g., *Pratylenchus* spp.) were significantly present in CH, FS, and MK (up to 720 nematodes), while ES, SK, SM, and TA recorded lower values (down to 256 nematodes) (F_{index} = 124.3; $df = 12$; $P < 0.05$). Furthermore, significant densities of ectoparasites were also recorded in ES, MA, MK, OU, and TF (up to 149 nematodes) ($F_{index} = 81.5$; $df = 12$; $P < 0.05$) (Fig. S3).

At the genus level, the RKN (*Meloidogyne* spp.) had the highest average density in the olive root matrix (750.4 nematodes) (F_{index} = 102.9; $df = 24$;

Table 2 Phytopathogenic nematode genera identified in Moroccan olive nurseries and orchards

PPN Genera	cp. value	Localities													Code
		HZ	TA	SM	MA	CH	OU	TF	ES	FS	MK	SK	GA	BN	
Aphelenchoides	2	+	-	+	+	+	-	-	-	+	+	-	-	+	*Aphe*
Aphelenchus	2	+	-	-	+	-	+	-	-	+	-	-	+	+	*Aph*
Coslenchus	2	-	-	-	+	-	-	-	-	+	-	-	-	-	*Cos*
Criconema	3	-	-	+	-	+	-	-	+	-	+	-	+	+	*Cri*
Criconemoides	3	+	-	-	-	-	-	+	-	-	-	-	+	-	*Crid*
Ditylenchus	2	-	-	+	+	-	+	-	+	+	+	-	+	-	*Dit*
Filenchus	2	+	+	-	-	-	+	-	-	-	+	-	-	-	*Fil*
Helicotylenchus	3	+	+	+	+	+	+	+	+	+	+	+	+	+	*Hel*
Heterodera	3	-	-	+	+	+	+	-	-	+	+	-	+	-	*Het*
Hoplolaimus	3	-	+	+	-	-	-	-	+	+	+	-	-	+	*Hop*
Longidorus	5	-	-	+	-	-	+	+	-	-	-	-	-	-	*Lon*
Meloidogyne	3	+	+	+	+	+	+	+	+	+	+	+	+	+	*Mel*
Merlinius	3	+	-	+	+	-	-	+	+	-	-	-	+	-	*Mer*
Paratylenchus	2	-	-	+	+	+	-	-	+	-	-	+	-	+	*Par*
Pratylenchoides	3	-	-	+	+	-	-	-	-	+	-	-	+	+	*Prad*
Pratylenchus	3	+	+	+	+	+	+	+	+	+	+	+	+	+	*Pra*
Rotylenchulus	3	-	-	-	+	+	-	-	-	+	+	-	-	-	*Rotl*
Rotylenchus	3	+	+	-	+	+	-	+	+	+	+	-	+	+	*Rot*
Telotylenchus	3	-	-	-	-	-	-	-	-	+	+	-	-	-	*Tel*
Trichorodrus	4	-	+	-	-	-	-	+	+	-	+	-	-	-	*Tri*
Trophurus	3	+	-	+	+	-	-	-	-	-	+	-	-	-	*Tro*
Tylenchorhynchus	3	+	+	+	+	-	-	+	+	+	-	+	+	-	*Tyle*
Tylenchus	2	+	+	+	-	+	+	+	-	-	-	-	+	+	*Tyl*
Xiphinema	5	-	-	+	+	-	-	-	-	-	+	+	-	-	*Xip*
Zygotylenchus	3	-	-	+	-	+	-	-	-	+	+	-	+	-	*Zyg*

(+) Presence; (-) Absence; (cp. value) colonizer-persister value

$P < 0.05$) followed by the *Pratylenchus* spp. (560.9 nematodes) and *Tylenchorhynchus* spp. (285.6 nematodes) (Fig. S4). On the other hand, *Pratylenchus* genera were significantly found in soil matrices at the highest rates (721.6 nematodes) (F_{index} = 111.2; $df = 24$; $P < 0.05$) followed by *Meloidogyne* spp. and *Helicotylenchus* spp. (566.2 and 480.1 nematodes, respectively). The lowest rates were recorded by 11 nematode genera in both matrices including *Aphelenchus*, *Aphelenchoides*, *Coslenchus*, *Criconema*, *Criconemoides*, *Ditylenchus*, *Filenchus*, and *Zygotylenchus* spp. (down to 9.4 nematodes) (Fig. S4).

The abundance and frequency of nematodes in each surveyed region were calculated. A total of 25 genera were identified, with *Meloidogyne*, *Pratylenchus*, and *Helicotylenchus* being the dominant and frequent ones. Ten genera were frequent but with lower abundance in the surveyed areas, namely *Aphelenchoides*, *Hoplolaimus*, *Rotylenchus*, *Ditylenchus*, *Heterodera*, *Paratylenchus*, and *Zygotylenchus*. Additionally, there were some occasional genera observed, including *Aphelenchus*, *Pratylenchoides*, *Longidorus*, and *Xiphinema*. However, 7 genera were rarely found, such as *Rotylenchulus*, *Filenchus*, *Trichodorus*, *Trophorus*, *Telotylenchus*, *Criconema*, and *Criconemoides* (Fig. 2).

At the species level, three distinct species of *Meloidogyne* spp. were identified according to the perineal patterns including *Meloidogyne incognita* (high presence), *M. javanica*, and *M. arenaria. Pratylenchus* spp. were represented in two species including *Pratylenchus thornei*, and *P. neglectus* (high presence) (Table S1). Similarly, *Helicotylenchus vulgaris* and *H. dihystera* were the two species recorded for *Helicotylenchus* genus. The stem nematode (*Ditylenchus* spp.) was represented by *D. dipsaci*, while the citrus nematode (*Rotylenchulus semipenetrans*) was also detected.

Diversity Trends of moroccan olive PPNs

The PCA showed a diverse pattern of PPN genera distributed differently in the sampling sites (Fig. S5). The first two PCA axes (PC1 and PC2) accounted for 39.8% and 23.1%, respectively of the total variance (Fig. S5A). The score plots (Fig. S5B) showed that the prospected sites are well separated and classified by PPN diversity.

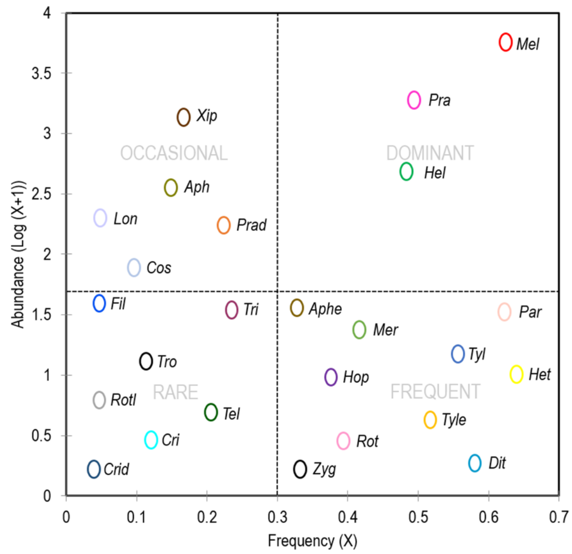

Fig. 2 Distribution Diagram (Abundance-Frequency) of phytopathogenic nematode communities found in Moroccan olive nurseries and orchards. Codes representing nematode genera are listed in Table 2

For instance, the TA region was distinctively separated from MA, ES, CH, and HZ by the absence or presence of the *Rotylenchus*, *Heterodera*, and *Merlinius* genera. The same goes for all localities.

Figure 3 showcased the attribution trends of the PPN ecological indices calculated for olive-growing locations. The first two PCA axes accounted for 52.3% and 39.8%, respectively of the total variance (Fig. 3A). The PCA plot showed that some diversity indicators (e.g., G, PPI, and E) were more important in the localities of FS, CH, TA, SM, HZ, and MK. The H', and H_{max} were of high weight in MK, ES, and HZ. In addition, specific indices of nematode species (I_{ecto}, I_{endo_mig}, and I_{endo_sed}) were highly indicated in the MK region (Fig. 3B).

The relationship patterns between PPNs identified in Moroccan olive agroecosystems were established through a correlation analysis (Fig. S6). Significant positive correlations were detected including those between *Aphelenchus* and *Zygotylenchus* ($r = 0.72$), *Criconema* and *Paratylenchus* ($r = 0.83$), and *Rotylenchulus* and *Tylenchorhynchus* ($r = 0.86$). Furthermore, *Hoplolaimus* was moderately associated with *Paratylenchus* ($r = 0.54$) while *Trichodorus* was similarly linked with *Tylenchorhynchus* ($r = 0.46$). On the other hand, *Ahelenchus* had a significant negative correlation with *Tel* ($r = -0.87$). The same was recorded

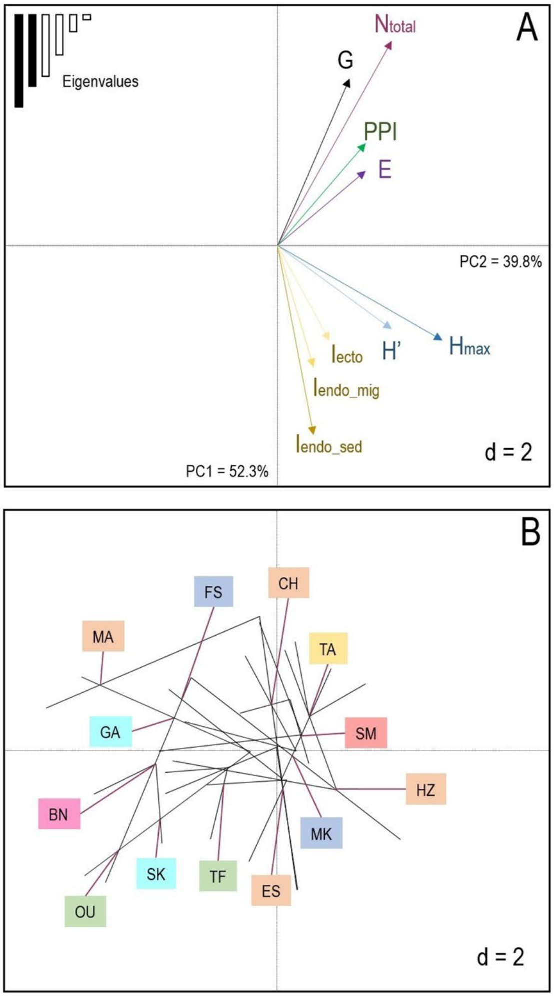

Fig. 3 Principal component analyses (PCA) of diversity indices of olive PPNs in Morocco; **A** PCA main plot of ecological indices; **B** score plot for the prospected locations. The value d represents the dimensionality of the PCA. Plots were generated using *sklearn.decomposition.PCA* module implemented in Python. Codes representing the surveyed regions are listed in Table 1

with *Xiphinema* and *Rotylenchulus* (r = −0.76), and *Telotylenchus* and *Xiphinema* (r = −0.69) (Fig. S6). In other cases, many nematode genera didn't have any association with each other.

Impact of agroecological factors (soil type, irrigation regime, and landscape complexity) on olive PPNs

The abundance of dominant PPN genera detected in Moroccan olive orchards (*Meloidogyne*, *Pratylenchus*, and *Helicotylenchus* spp.) was assessed in terms of four soil types (sandy, clay, medium loam, and sandy-clay-loam). *Meloidogyne* was significantly abundant in sandy, sandy-clay-loam, and medium loam types (60–70%) (F_{index} = 72.9; df=3; P<0.05). Oppositely, *Pratylenchus* significantly prevailed in clay and medium loam soils compared to the others (F_{index} = 87.5; df=3; P<0.05). No significant differences were obtained between soil types in terms of *Helicotylenchus* abundance (F_{index} = 56.1; df=3; P>0.05) (Fig. 4A).

The dominant nematode genera in olive nurseries were also assessed as a function of three irrigation regimes (IRs) levels according to the evapotranspiration percentages (ETP) performed in drip irrigation mode. *Meloidogyne* genera were significantly abundant starting from the moderate regime to the higher one (F_{index} = 71.2; df=2; P<0.05) (Fig. 4B). Furthermore, *Pratylenchus* genera showed to be in significant abundance in the higher IRs (especially in 75% ETP regime) (F_{index} = 76.5; df=2; P<0.05). Furthermore, *Helicotylenchus* genera were relatively less abundant in the three IRs compared to the other genera. In addition, these nematodes are seemingly unaffected by the higher IRs (F_{index} = 56.8; df=2; P<0.05) (Fig. 4B).

Throughout the experiment, plant parameters such as plant height and root length were assessed to see the impact of PPNs functioning within progressive IR levels (Fig. 5). In terms of irrigation regimes, plant height was significantly reduced in the low and high IRs (25 and 75% ETP), while the moderate IR showed high values (F_{index} = 103.5; df=2; P<0.05). However, the values were significantly lower than the negative control (C) (F_{index} = 123.4; df=3; P<0.05) (Fig. 5A). The same trend was more or less observed with the root length (F_{index} = 96.1; df=3; P<0.05) (Fig. 5B). As for nematode genera factor, *Meloidogyne* and *Pratylenchus* seem to have a significant impact on plant height (F_{index} = 120.6; df=2; P<0.05) and root length (F_{index} = 104.3; df=2; P<0.05). Noticeably, all olive varieties were negatively and prominently affected by *Meloidogyne* compared to *Pratylenchus* and *Helicotylenchus* (Fig. 5).

Phytopathogenic nematodes, grouped into main feeding aspects were thoroughly assessed in different olive landscape complexity (LCs) levels (simple, intermediate, and complex). Sedentary (*Endo_sed*) and migratory (*Endo_mig*) endoparasites were

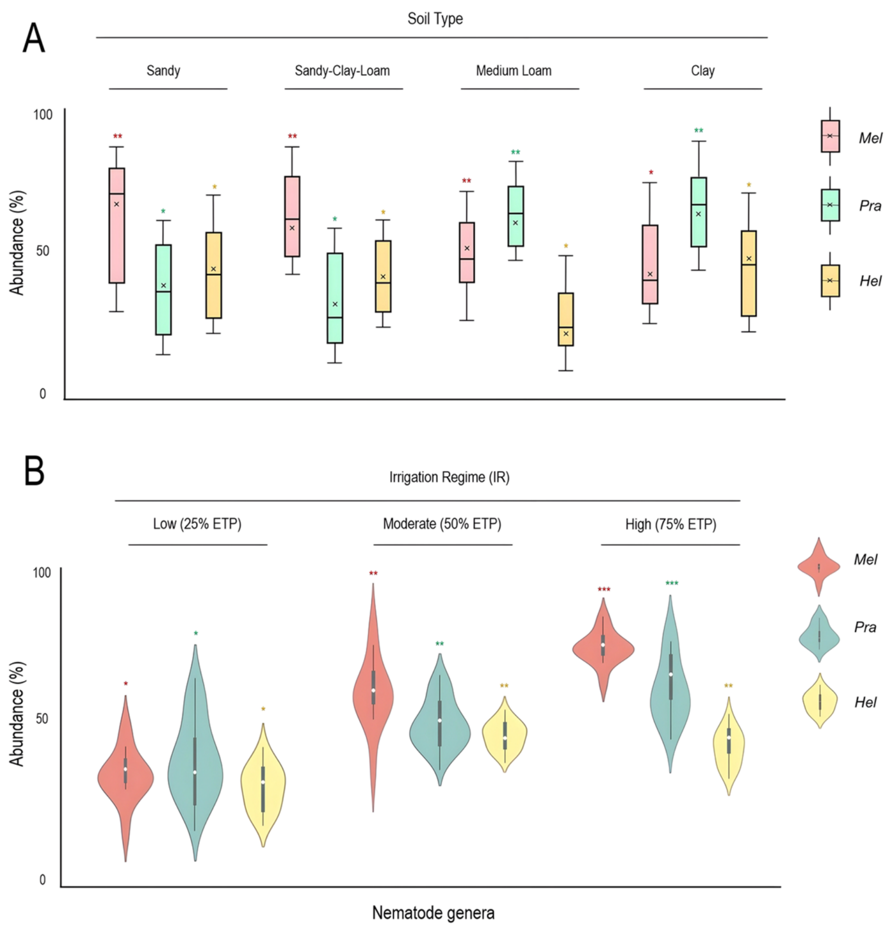

Fig. 4 Impact of soil types and irrigation regime (IR) on the abundance of dominant phytopathogenic nematodes in Moroccan olive agroecosystems. **A** Box plot showing the effect of soil types; Violin plot depicting the effect of IR. Soil types were based on the overall granulometry observed in olive fields. Irrigation levels were based on evapotranspiration percentage (ETP) integrated into a drip irrigation setting. Stars represent homogeneous groups (colored for each nematode genus) based on the protected LSD test for each variable at $P<0.05$. Error lines on bars represent the standard error ($n \geq 3$). The plots were generated using *seaborn.boxplot* and *seaborn.violinplot* modules implemented in Python

significantly abundant in simple and intermediate landscapes (F_{index} = 88.9; $df=2$; $P<0.05$), while lower values were observed in complex structured orchards (Fig. 6). Similarly, ectoparasites (*Ecto*) showed a significant abundance (70%) in simple landscapes compared to the diversified ones (F_{index} = 71.2.9; $df=2$; $P<0.05$). Interestingly, the *Pratylenchus* genus was more dominant than *Meloidogyne* in all landscape settings except for the intermediate one, while genera including *Xiphinema*, *Longidorus*, and *Trichodorus* were less redundant in the complex landscapes (Fig. 6).

By going deep into the landscape complexity mechanics in the distribution of olive PPNs, the relationship between taxonomic richness (G) and the total number of species (N_{total}) was elaborated using exponential regression analysis (Fig. S7). Overall, a strong association was obtained between the two parameters (R^2 = 0.74) that highlighted PPN distribution patterns based on different LCs. For instance, the studied parameters were significantly increased in complex landscapes followed by intermediate, and then came the samples orchards (Fig. S7).

Discussion

Diversity of phytopathogenic nematodes in moroccan olive agroecosystems

The biodiversity of phytopathogenic nematodes in olive nurseries and orchards has extensive trends worldwide. These pathogens represent a prominent threat to both agronomic and socioeconomic sectors of olive-producing areas (Pandey and Mukerji 2006; Fernández-Escobar et al. 2013; Laasli et al. 2023). In most cases, PPN damages cause significant yield

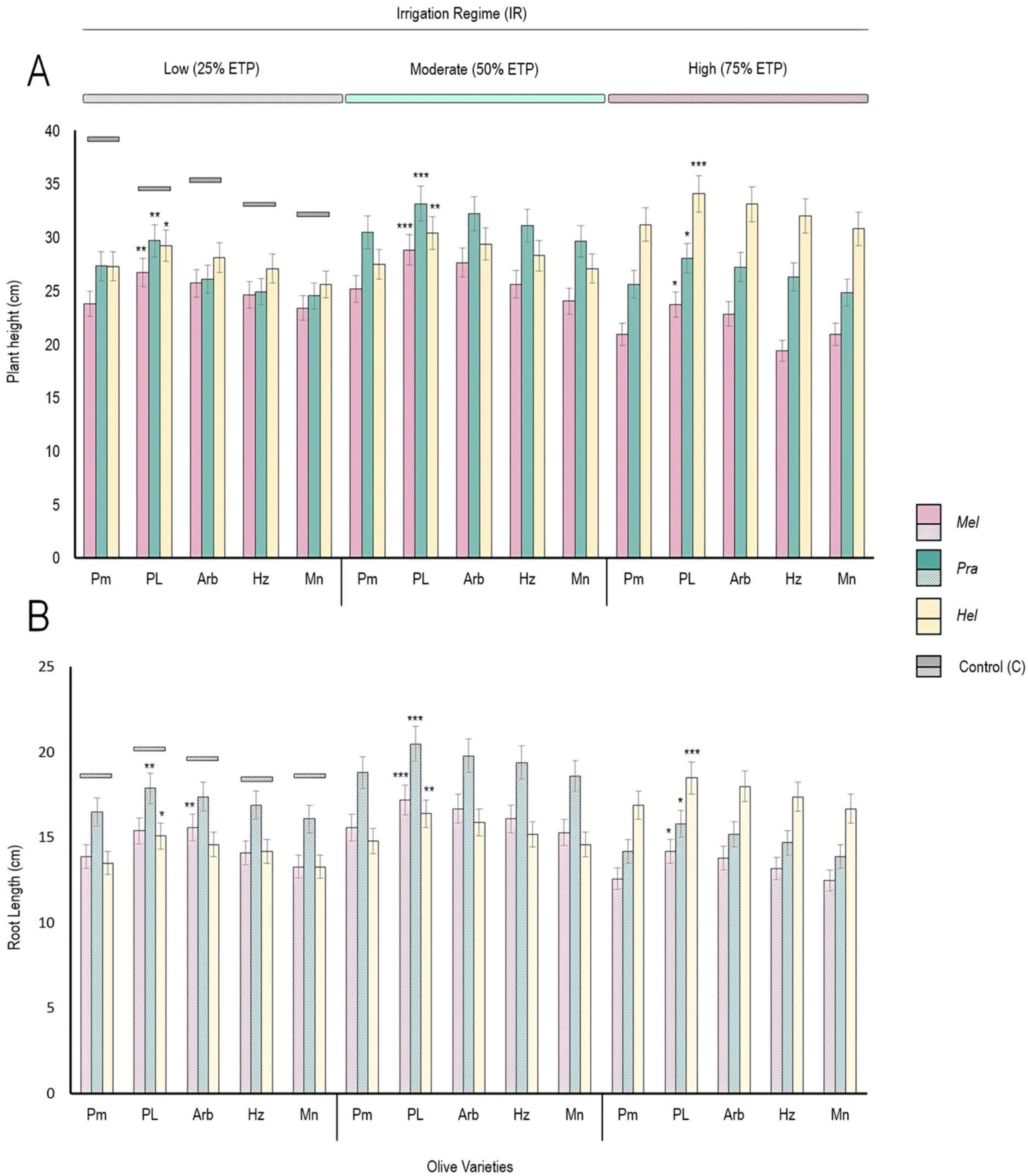

Fig. 5 Effect of irrigation regime (IR) on plant parameters impacted by nematode infestations. **A** Plant height; **B** Root length. All measurements were conducted in cm. The Control (C) represents standard IR without nematode infestation. Asterisks (*) represent homogenous groups showcasing the significant differences between the treatments according to the Duncan test at $P < 0.05$. Error lines on bars represent the standard error ($n = 3$)

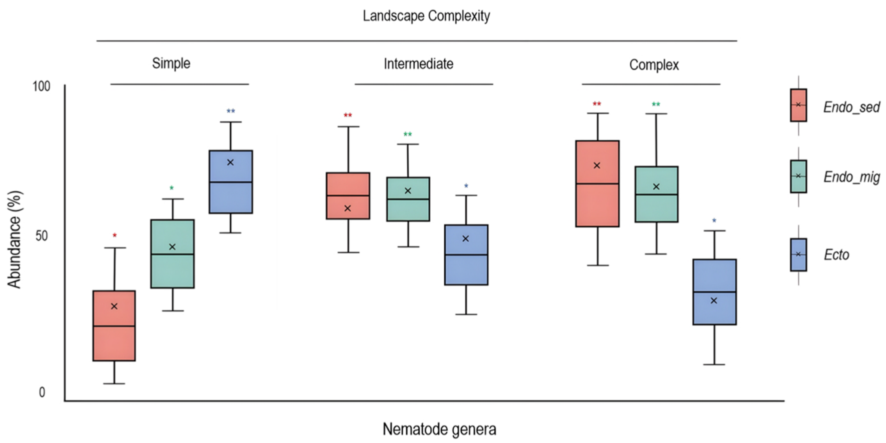

Fig. 6 Box Plot showcasing the impact of landscape complexity (LC) on the abundance of the main feeding groups of phytopathogenic nematodes in Moroccan olive orchards. LC levels were based on vegetation diversity that occurred for olive landscape areas. Stars represent homogeneous groups (colored for each nematode genus) based on the protected LSD test for each variable at $P < 0.05$. Error lines on bars represent the standard error (SE) ($n \geq 3$). The plot was generated using *seaborn.boxplot* module implemented in Python

loss, especially for susceptible olive varieties which require immediate interventions targeting sustainable PPN management (Nico et al. 2003; Abbas and Mohammad 2005; Palomares–Rius et al. 2019). This study provides insights and updated information on the biodiversity of PPN communities in Moroccan olive nurseries/orchards and their linkage to agroecological patterns.

Across 43 prospected olive nurseries and orchards, twenty-five PPN genera were detected and identified. *Meloidogyne* spp., *Pratylenchus* spp., and *Helicotylenchus* spp. were abundant and frequent in all olive-growing areas. In the same manner, Hamza et al. (2018) discussed the diversity of phytopathogenic nematode communities found in Moroccan olive nurseries and the potential impacts of these communities on the environment. They found that the nematode communities in the olive nurseries were diverse, with a mix of native and introduced species. Thirteen nematode families were shown to be linked with olives including Telotylenchidae, Pratylenchidae, Longidoridae, and Hoplolaimidae. The latter had the highest number of species identified. In our study, *Pratylenchus* spp., *Helicotylenchus* spp., and *Meloidogyne* spp. had the highest infestation frequencies. The same findings were obtained in Tunisia (Guesmi–Mzoughi et al. 2022), Algeria (Chafaa et al. 2014; Belahmar et al. 2015), Libya (Buarousha et al. 2020), and Egypt (Ibrahim et al. 2010; Abdel–Baset et al. 2022).

Meloidogyne genera are significant pathogens of olive trees, causing damage in many olive nurseries around the world (Martelli et al. 2000). In our study, three species were encountered including *Meloidogyne javanica*, *M. incognita*, and *M. arenaria*. Several studies highlighted the occurrence of the same species across multiple olive agroecosystems worldwide (Nico et al. 2002; Wesemael et al. 2011; Archidona-Yuste et al. 2018; Keshari and Mallikarjun 2022). *Pratylenchus* genera are migratory endoparasites that are widely distributed and capable of infecting a diverse range of plant species (Vovlas et al. 2000). Among the species identified in our study, *Pratylenchus neglectus*, and *P. thornei* were the most prevalent. Other studies have highlighted the diversity of the same RLN species alongside the presence of others including *P. zeae*, *P. mediterraneus*, *P. crenatus*, and *P. vulnus* (Lamberti and Vovlas 1993; Cilbircioğlu 2007). As for *Helicotylenchus* spp., it has been well-established in most Moroccan olive nurseries and orchards surveyed. Two distinct species (*H. vulgaris*, and *H. dihystera*) have shown a prominent presence. However, A total of 11 species have been found previously in Morocco including *H. crassatus, H. digonicus*, and *H. varicaudatus* which were the most dominant (Hamza et al. 2018). *Helicotylenchus digonicus* is a dominant spiral nematode species in many olive orchards, with high prevalence in many regions (Archidona-Yuste et al. 2020), while other species (e.g., *H. oleae*) were found across Mediterranean countries (Inserra et al. 1979).

Impact of soil type on olive PPN distribution patterns

Soil type can have a significant impact on the distribution and abundance of nematodes (Nisa et al. 2021). Understanding the relationship between soil type and nematode populations can help farmers and researchers develop effective management strategies to reduce crop damage and increase yields (Neher 2001). In our study, *Meloidogyne*, *Pratylenchus*, and *Helicotylenchus* are the main genera of PPNs that have been extensively studied with four soil types (sandy, sandy-clay-loam, medium loam, and clay) due to their representative dominance throughout all localities. *Meloidogyne* was abundant in sandy soils while *Pratylenchus* was highly present in clayish and loam settings. Similarly, previous studies have shown that the distribution of *Meloidogyne* and *Pratylenchus* was significantly influenced by soil texture (Griffin 1996; Trinh et al. 2009; Hamza et al. 2018; Mokrini et al. 2019). In Tunisia, Guesmi–Mzoughi et al. (2022) found that *Meloidogyne* genera were more abundant in sandy soils, while *Pratylenchus* were more abundant in clay soils within olive orchards. Another study conducted in Benin found that the abundance of *Helicotylenchus dihystera* was positively linked to the soil's organic properties and negatively affiliated with soil granulometry (Baimey et al. 2009).

Meloidogyne species prefer sandy soils due to their larger particle sizes, which result in high permeability and rapid drainage. Sandy soils have low water-holding capacity, limited nutrient availability, and reduced competition from other soil organisms, all of which favor survival and reproduction. These nematodes can easily migrate through sandy soil particles, access plant roots, and cause root damage (Perry et al. 2009; Nyczepir and Thomas 2009; Nicol et al. 2011). Conversely, *Pratylenchus* species prefer clayish and loam soils due to their smaller pore spaces and higher water-holding capacities. These soils allow nematodes to move more freely and provide a suitable environment for their life cycle (Luc et al. 2005). Clayish and loam soils also retain organic matter, promoting microbial communities that support nematode populations. The compact structure of these soils facilitates the nematodes' feeding processes and leads to root damage and plant decline (Sundararaju and Jeyabaskaran 2003; Nicol et al. 2011).

Irrigation regime influence on olive PPN abundance and plant interactions

The effect of irrigation regimes on PPNs has been studied extensively, and the results have shown that different nematode species respond differently to different IRs based on ETP percentages. For instance, *Meloidogyne* and *Pratylenchus* genera were significantly abundant in high IR levels. In that manner, *Meloidogyne* spp. is known to prefer moist soil conditions for their survival and reproduction (Evans and Perry 2009). Hence, continuous and heavy irrigation regimes promote their growth and reproduction (Porazinska et al. 1998; Majić et al. 2021). Studies have shown that increasing levels of drip irrigation, which provides water directly to the plant roots, increase PPN populations in the soil compared to traditional flood irrigation (Okasha et al. 2020; Choudhary and Bhambri 2013; 2021). In addition, some *Pratylenchus* species are known to prefer drier soil conditions for their survival and reproduction without relying on a rhizospheric biota (Castillo and Vovlas 2010). Studies have shown that reduced irrigation regimes can help in reducing the populations of *Pratylenchus* in the soil (Kuchta et al. 2021; Phani et al. 2021). For instance, a study conducted on cotton crops in Brazil showed that the reduction in irrigation from 60 to 30% of the crop's water requirement resulted in a significant reduction in RLN populations in the soil (Ribeiro et al. 2012). On the other hand, *Helicotylenchus* spp. has shown mixed responses to different IRs. Studies have shown that under water-stressed conditions, their populations decrease, while under excessive irrigation, their populations increase (Ko et al. 1997; Eissa et al. 2003; Majić et al. 2021). For instance, a study conducted on tomato crops in Egypt showed that *Helicotylenchus* populations increased with increasing irrigation levels (Taha 2020). Therefore, these abundance trends are dependently affiliated with plant growth parameters as they affect the tendencies of plant height and root length values (Cadet et al. 2004; Da Silva et al. 2017). These values are essentially dependent on the Plant × Nematode interaction (Wilschut and Geisen 2021).

Varied effects of landscape complexity on olive PPN

Understanding how landscape complexity affects these nematodes is crucial in developing effective management strategies to minimize their impact (Brustolin et al. 2018). Our findings revealed that nematode abundance was significantly decreased going from simple landscapes to complex ones. In simple landscapes, such as monoculture fields or urban areas, the nematode populations may be higher due to the lack of natural predators and other factors that could limit their growth (Jackson et al. 2019; Porazinska et al. 2021). In contrast, complex landscapes with more diverse plant communities and varied topography can provide a habitat for natural enemies of nematodes, such as predatory mites and fungi (Porazinska et al. 2021). Therefore, nematode populations may be lower in complex landscapes. For instance, a study conducted in a complex landscape in France found that the nematode community could have some diversity limitations in areas characterized by high land complexity. These limitations are attributed to the homogeneity of vegetation in the landscape rather than the presence of multiple plant genera within (Duyck et al. 2012).

Moreover, a study by Flores et al. (2014) found that increasing landscape complexity (i.e., increasing the number of landscape elements such as hedgerows, woodlands, and ponds) decreased the abundance of *Meloidogyne* spp., in agricultural soils. Similarly, a study by Tarno et al. (2021) found that increasing landscape complexity reduced the abundance of *Pratylenchus* spp., in agricultural soils. However, the effects of landscape complexity on PPNs can be complex and may depend on the specific nematode species and the surrounding landscape (Flores et al. 2014). For instance, a study conducted by Cavigelli et al. (2005) found that landscape complexity did not affect the abundance of the dagger nematode, *Xiphinema* spp., in maize-based soils. This may be because these nematodes have a specific host range and are less affected by the diversity of vegetation types in the surrounding landscape (Cavigelli et al. 2005).

Future research implications

The study of phytopathogenic nematode communities infesting Moroccan olive agroecosystems and the impact of agroecological patterns presents significant implications for future research. A comprehensive understanding of these communities and their influence on olive crop productivity is essential for developing effective, sustainable management strategies (Ali et al. 2014). Recent studies have started to uncover the complex interactions between nematode communities, agroecosystem characteristics, and environmental factors in Moroccan olive orchards (Laasli et al. 2023). However, more extensive research is needed to fully grasp the ecological processes shaping these communities and the potential consequences of agroecological patterns on crop health and disease management. Future studies should consider expanding the geographic scope and incorporating advanced molecular techniques to characterize nematode diversity and their functional roles within the agroecosystem. Additionally, research should focus on understanding the effects of land use change, agricultural practices, and climate change on nematode community dynamics to help inform policy and decision-making in the context of sustainable agriculture.

Conclusion

This study provides updated information and insights on the incidence of phytopathogenic nematode communities in Moroccan olive agroecosystems. Twenty-five PPN genera were detected, with *Meloidogyne*, *Pratylenchus*, and *Helicotylenchus* being the most prominent. Their positive/negative interaction with soil, irrigation, and landscape complexity was revealed, offering opportunities for sustainable management. Future research should focus on the dynamics of all soil nematode communities, employing metagenomics, transcriptomics, and proteomics for deeper insights into their functional dynamics and interactions. Additionally, a comprehensive soil health mapping of olive-growing regions is recommended to develop sustainable agricultural practices for effective nematode population management and disease control.

Acknowledgements The authors are grateful to the farmers and stakeholders for assisting by giving the required information during field surveys.

Author contribution Conceptualization: SEL, FM, AAD and RL; Methodology: SEL, RL and FM; Formal analysis and investigation: SEL, FM, and RL; Writing - original draft preparation: SEL; Writing - review and editing: SEL, FM, DI, MS, SA, AAD, TP, KK, and RL; Funding acquisition: RL; Resources: SA, and RL; Supervision: FM, AAD and RL.

Funding This work was funded by SIRAM (Sustainable Innovations for Regenerative Agriculture in the Mediterranean Area) Project affiliated with PRIMA.

Data availability The data that supports the findings of this study are available on request from the corresponding author.

Declarations

Competing interests 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.

References

Abbas HS, Mohammad RM (2005) Reaction of olive cultivars to *Meloidogyne javanica*. C R Réunion 28(9):141–145

Abdel–Baset SH, Khalil AE, Mohamed S (2022) Plant–parasitic nematodes associated with certain fruit trees and vegetable crops in the northeastern Egypt. Egypt J Agron 21(2):110–121. https://doi.org/10.21608/ejaj.2022.267637

Ali N, Chapuis E, Tavoillot J, Mateille T (2014) Plant–parasitic nematodes associated with olive tree (*Olea europaea* L.) with a focus on the Mediterranean Basin: a review. C R Biol 337(7–8):423–442. https://doi.org/10.1016/j.crvi.2014.05.006

Ali N, Tavoillot J, Mateille T, Chapuis E, Besnard G, El Bakkali A, Palomares–Rius JE (2015) A new root–knot nematode *Meloidogyne spartelensis* n. sp. (Nematoda: Meloidogynidae) in Northern Morocco. Eur J Plant Pathol 143(1):25–42. https://doi.org/10.1007/s10658-015-0662-3

Ali N, Tavoillot J, Chapuis E, Mateille T (2016) Trend to explain the distribution of root–knot nematodes *Meloidogyne* spp. associated with olive trees in Morocco. Agric Ecosyst Environ 225:22–32. https://doi.org/10.1016/j.agee.2016.03.042

Altaf J, Qureshi NA, Siddiqui MJI (2017) Terrestrial snails as bioindicators of environmental degradation. J Biodivers Environ Sci 10:253–264

Andrássy I (2005) Free-living nematodes of Hungary: (Nematoda errantia), I. In: C. Csuzdi & S. Mahunka (Eds.), Pedozoologica Hungarica No. 3. Hungarian Natural History Museum. Budapest, Hungary. pp 518

Archidona-Yuste A, Cantalapiedra-Navarrete C, Liebanas G, Rapoport HF, Castillo P, Palomares Rius JE (2018) Diversity of root-knot nematodes of the genus *Meloidogyne Göeldi*, 1892 (Nematoda: Meloidogynidae) associated with olive plants and environmental cues regarding their distribution in southern Spain. PLoS One 13(6):e0198236. https://doi.org/10.1371/journal.pone.0198236

Archidona-Yuste A, Cantalapiedra-Navarrete C, Palomares-Rius JE, Castillo P, Tzortzakakis EA (2020) Plant-parasitic nematodes associated with cultivated and wild olive trees in Crete, Greece. Hell Plant Prot J 13(1):24–28. https://doi.org/10.2478/hppj-2020-0003

Baimey H, Coyne D, Dagbenonbakin G, James B (2009) Plant-parasitic nematodes associated with vegetable crops in Benin: relationship with soil physico-chemical properties. Nematol Mediterr 37(2):227–236

Barbera AC, Maucieri C, Cavallaro V, Ioppolo A, Spagna G (2013) Effects of spreading olive mill wastewater on soil properties and crops, a review. Agric Water Manag 119:43–53. https://doi.org/10.1016/j.agwat.2012.12.009

Belahmar M, Elkfel F, Mihoub M, Abdewahab S, Mateille M, Sellami S (2015) Plant parasitic nematodes associated with olive in Algeria. Acta Phytopathol Entomol Hung 50(2):187–193. https://doi.org/10.1556/038.50.2015.2.4

Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19. https://doi.org/10.1007/BF00324627

Breton C, Terral JF, Pinatel C, Médail F, Bonhomme F, Bervillé A (2009) The origins of the domestication of the olive tree. C R Biol 332(12):1059–1064. https://doi.org/10.1016/j.crvi.2009.08.001

Bristol D, Hassan K, Blankinship JC, Nielsen UN (2023) Responses of nematode abundances to increased and reduced rainfall under field conditions: a meta-analysis. Ecosphere 14(1):e4364. https://doi.org/10.1002/ecs2.4364

Brustolin MC, Nagelkerken I, Fonseca G (2018) Large-scale distribution patterns of mangrove nematodes: a global meta-analysis. Ecol Evol 8(10):4734–4742. https://doi.org/10.1002/ece3.3982

Brzeski MW (1991) Review of the genus *Ditylenchus* Filipjev, 1936 (Nematoda: Anguinidae). Rev Nematol 14(1):9–59

Buarousha N, Adam M, Ehwaeti M (2020) A survey and identification of plant parasitic nematodes associated with wild olive trees *olea europaea* var. Oleaster in El JabelAlakther, Libya. AAU J 6(1):1–13

Cadet P, Guichaoua L, Spaull VW (2004) Nematodes, bacterial activity, soil characteristics and plant growth associated with termitaria in a sugarcane field in South Africa. Appl Soil Ecol 25(3):193–206. https://doi.org/10.1016/j.apsoil.2003.10.001

Castillo P, Vovlas N (2007) *Pratylenchus* (Nematoda: Pratylenchidae): diagnosis, biology, pathogenicity and management. Brill, Leiden, The Netherlands

Castillo P, Vovlas N (2010) Biology and ecology Of *Pratylenchus*. In Castillo P, Vovlas N (eds) *Pratylenchus* (Nematoda: Pratylenchidae): diagnosis, biology, pathogenicity and management. Brill, Leiden, pp 302–321. https://doi.org/10.1163/ej.9789004155640.i-523.104

Castillo P, Nico AI, Navas–Cortes JA, Landa BB, Jimenez–Diaz RM, Vovlas N (2010) Plant–parasitic nematodes

attacking olive trees and their management. Plant Dis 94(2):148–162. https://doi.org/10.1094/PDIS-94-2-0148
Cavigelli MA, Lengnick LL, Buyer JS, Fravel D, Handoo Z, McCarty G, Rabenhorst M, Cavigelli MA, Lengnick LL, Buyer JS, Fravel D, Handoo Z, McCarty G, Millner P, Sikora L, Wright S, Vinyard B, Rabenhorst M (2005) Landscape level variation in soil resources and microbial properties in a no-till corn field. Appl Soil Ecol 29(2):99–123. https://doi.org/10.1016/j.apsoil.2004.12.007
Chafaa S, Si Bachir A, Boukhadra M, Achi A (2014) Inventory and global stand dynamics of plant parasitic nematodes (Nematoda: Secernentea) of olive trees (*Olea europeae*) in an arid region of the Northeast of Algeria. J Anim Plant Sci 23(3):3637–3645
Choudhary VK, Bhambri MC (2013) Crop productivity, water use and weed control efficiency of capsicum (*Capsicum annum* L.) under drip irrigation and mulching. J Agric Phys 13:133–138
Choudhary V, Kumar KK, Sahu B, Muthappa SK, Das ADA (2021) Agronomic innovations in biotic stress management and its combined effect with abiotic stresses in crop production. Indian J Agron 66(5):237–257
Cilbircioğlu C (2007) Plant Parasitic Nematodes Associated with *Olea europea* L. Fauna of Turkey. J Agric Urban Entomol 24(4):227–231. https://doi.org/10.3954/1523-5475-24.4.227
Da Silva LMA, Pedrosa EMR, da Silva Vicente TF, de Oliveira Cardoso MS, Castro DB, Rolim MM (2017) Seasonal variation of plant-parasitic nematodes and relationship with nutritional and growth properties of sugarcane plantations. Trop Plant Pathol 42:132–136. https://doi.org/10.1007/s40858-017-0129-5
De Grisse AT (1969) Redescription ou modification de quelques techniques utilisés dans l'études des nématodes phytoparaires. Meded Rijks Fakulteit Landbouwwet 34:351–356
Duyck PF, Dortel E, Tixier P, Vinatier F, Loubana PM, Chabrier C, Quénéhervé P (2012) Niche partitioning based on soil type and climate at the landscape scale in a community of plant-feeding nematodes. Soil Biol Biochem 44(1):49–55. https://doi.org/10.1016/j.soilbio.2011.09.014
Eissa MFM, El Gindi AY, Abdel Gawad MM, Ismail AE, El Nagdi WMA (2003) Vertical and horizontal distributions of plant–parasitic nematodes associated with banana CV. Williams under flood irrigation regime. Bull Natl Res Cent 28(4):453–460
El SN, Karakaya S (2009) Olive tree (*Olea europaea*) leaves: potential beneficial effects on human health. Nutr Rev 67(11):632–638. https://doi.org/10.1111/j.1753-4887.2009.00248.x
Evans AA, Perry RN (2009) Survival mechanisms. In: Perry RN, Moens M, Starr JL (eds) Root-knot nematodes. CABI Publishing, Wallingford, UK, pp 201–222
Fernández-Escobar R, De la Rosa R, Leon L, Gomez JA, Testi L, Orgaz F, Masallem M (2013) Evolution and sustainability of the olive production systems. Options Mediterr 106:11–42
Flores L, Dussi MC, Fernández C, Azpilicueta C, Aruani C, Sugar D (2014) Impact of alleyway management and vegetation diversity on nematode abundance in pear agroecosystems. In XII International Pear Symposium 1094 (pp. 341–349)
Food and Agriculture Organization Corporate Statistical Database (FAOSTAT) (2022) New Food Balances. http://www.fao.org/faostat/en/#data/FBS.Accessed 23 Feb 2023
Geraert E (2008) The Tylenchidae of the World: identification of the Family Tylenchidae (Nematoda). Academia Press, Ghent, Belgium
Geraert E (2010) The Criconematidae of the World: identification of the family Criconematidae (Nematoda). Academia Press.Ghent, Belgium
Geraert E (2011) The Dolichodoridae of the World: identification of the Family Dolichodoridae (Nematoda). Academia Press, Ghent, Belgium
Griffin GD (1996) Importance of soil texture to the pathogenicity of plant-parasitic nematodes on rangeland grasses. Nematropica 26(1):27–37
Guesmi–Mzoughi I, Tabib M, Sellami F, Hadj–Naser F, Regaieg H, Kallel S, Horrigue–Raouani N (2022) Diversity of plant–parasitic nematode communities infesting olive orchards in Tunisia in relation to agronomic factors. Eur J Plant Pathol 164(4):479–494. https://doi.org/10.1007/s10658-022-02572-0
Hamza MA, Ali N, Tavoillot J, Fossati–Gaschignard O, Boubaker H, El Mousadik A, Mateille T (2017) Diversity of root–knot nematodes in moroccan olive nurseries and orchards: does *Meloidogyne javanica* disperse according to invasion processes? BMC Ecol 17(1):1–13. https://doi.org/10.1186/s12898-017-0153-9
Hamza MA, Moukhli A, Ferji Z, Fossati–Gaschignard O, Tavoillot J, Ali N, Mateille T (2018) Diversity of plant–parasitic nematode communities associated with olive nurseries in Morocco: origin and environmental impacts. Appl Soil Ecol 124:7–16. https://doi.org/10.1016/j.apsoil.2017.10.019
Handoo ZA (2002) A key and compendium to species of the *Heterodera avenae* group (Nematoda: Heteroderidae). J Nematol 34:250
Hooper DJ (1986) Extraction of free-living nematode stages from soil. In: Southey JF (ed) Laboratory methods for work with plant and soil nematodes. Her Majesty's Stationery Office, London, UK, pp 5–22
Hooper DJ, Hallmann J, Subbotin SA (2005) Methods for extraction, processing and detection of plant and soil nematodes. In: Luc M, Sikora RA, Bridge J (eds) Plant parasitic nematodes in subtropical and tropical agriculture. CABI Publishing, Wallingford, UK, pp 53–86
Ibrahim IKA, Mokbel AA, Handoo ZA (2010) Current status of phytoparasitic nematodes and their host plants in Egypt. Nematropica 40:239–262
Inserra RN, Vovlas N, Golden AM (1979) Helicotylenchus oleae n. sp. and H *neopaxilli* n. sp. (Hoplolaimidae), two new spiral nematodes parasitic on olive trees in Italy. J Nematol 11(1):56
Jackson LE, Bowles TM, Ferris H, Margenot AJ, Hollander A, Garcia-Palacios P, Sánchez-Moreno S, Jackson LE, Bowles TM, Ferris H, Margenot AJ, Hollander A, Garcia-Palacios P, Daufresne T, Sánchez-Moreno S (2019) Plant and soil microfaunal biodiversity across the borders between arable and forest ecosystems in a Mediterranean landscape. Appl Soil Ecol 136:122–138. https://doi.org/10.1016/j.apsoil.2018.11.015
Kekelis P, Papatheodorou EM, Terpsidou E, Dimou M, Aschonitis V, Monokrousos N (2022) The free-living nematodes as indicators of the Soil Quality in Relation to the clay content, when Coffee Waste is Applied. Agronomy 12(11):2702. https://doi.org/10.3390/agronomy12112702

Keshari N, Mallikarjun G (2022) Plant Parasitic Nematodes: A Major Constraint in Fruit Production. In: Bellé C, Kaspary T (eds) Nematodes-Recent Advances, Management and New Perspectives. IntechOpen, pp 1–33. https://doi.org/10.5772/intechopen.101696

Ko MP, Schmitt DP, Fleisch H, Sipes BS (1997) Re-establishment and resurgence of plant-parasitic nematodes in fumigated pineapple fields at different elevations and irrigation regimes in Hawaii. Australas Plant Pathol 26:60–68. https://doi.org/10.1071/AP97009

Koenning SR, Overstreet C, Noling JW, Donald PA, Becker JO, Fortnum BA (1999) Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. J Nematol 31(4S):587

Krebs CJ (1985) Ecology: the experimental analysis of distribution and abundance. Harper and row, New York, NY, USA

Kuchta S, Neilsen D, Zebarth BJ, Forge T, Nichol C (2021) Nitrogen, irrigation, and alley management affects raspberry crop response and soil nitrogen and root-lesion nematode dynamics. Soil Sci Soc Am J 85(4):1139–1156. https://doi.org/10.1002/saj2.20190

Laasli SE, Mokrini F, Dababat AA, Yüksel E, Imren M, Amiri S, Lahlali R (2023) Phytopathogenic nematodes associated with olive trees (*Olea europaea* L.) in North Africa: current status and management prospects. J Plant Dis Prot 26:1–8. https://doi.org/10.1007/s41348-023-00744-6

Lamberti F, Vovlas N (1993) Plant parasitic nematodes associated with olive. EPPO Bull 23(3):481–488. https://doi.org/10.1111/j.1365-2338.1993.tb01356.x

Landi S, d'Errico G, Papini R, Cutino I, Simoncini S, Rocchini A, Roversi PF, Landi S, d'Errico G, Papini R, Cutino I, Simoncini S, Rocchini A, Brandi G, Rizzo R, Gugliuzza G, Germinara GS, Nucifora S, Mazzeo G, Roversi PF (2022) Impact of super-high density olive orchard management system on soil free-living and plant-parasitic nematodes in central and south Italy. Animals 12(12):1551. https://doi.org/10.3390/ani12121551

Luc M, Sikora RA, Bridge J (2005) Plant parasitic nematodes in subtropical and tropical agriculture. CABI publishing, UK

Mai WF, Lyon HH (1975) Pictorial key to the genera of plant-parasitic nematodes, 4th edn. Cornell University Press, Ithaca, NY, USA

Mai WF, Mullin PG (1996) Plant-parasitic nematodes: a pictorial key to genera. Cornell University Press, Ithaca, NY, USA

Majić I, Sarajlić A, Raspudić E, Josipović M, Šarić GK (2021) Effects of Irrigation and Bioproducts of Microbial Origin on Nematode Community and Mycorrhizal Root Colonization in Soybean. In: C. Bellé, Kaspary TE (eds) Nematodes-Recent Advances, Management and New Perspectives. IntechOpen, London, pp 93. https://doi.org/10.5772/intechopen.99294

Martelli GP, Salerno M, Savino V, Prota U (2000) An appraisal of diseases and pathogens of olive. In: C. Vitagliano, Martelli GP (eds) Proceeding of the IV International Symposium on Olive Growing, ISHS Acta Horticulturae, Valenzano, Italy, pp 701–708. https://doi.org/10.17660/ActaHortic.2002.586.150

Mohawesh O, Karajeh M (2014) Effects of deficit irrigation on tomato and eggplant and their infection with the root-knot nematode under controlled environmental conditions. Arch Agron Soil Sci 60(8):1091–1102. https://doi.org/10.1080/03650340.2013.871385

Mokrini F, Laasli SE, Iraqui D, Wifaya A, Mimouni A, Erginbas-Orakci G, Dababat AA (2019) Distribution and occurrence of plant-parasitic nematodes associated with raspberry (*Rubus idaeus*) in Souss-Massa region of Morocco: relationship with soil physico-chemical factors. Russ J Nematol 27(2):107–121

Neher DA (2001) Role of nematodes in soil health and their use as indicators. J Nematol 33(4):161

Nico AI, Rapoport HF, Jiménez–Díaz RM, Castillo P (2002) Incidence and population density of plant–parasitic nematodes associated with olive planting stocks at nurseries in southern Spain. Plant Dis 86(10):1075–1079. https://doi.org/10.1094/PDIS.2002.86.10.1075

Nico AI, Jiménez–Díaz RM, Castillo P (2003) Host suitability of the olive cultivars Arbequina and Picual for plant–parasitic nematodes. J Nematol 35(1):29

Nicol JM, Turner SJ, Coyne DL, Nijs LD, Hockland S, Maafi ZT (2011) Current nematode threats to world agriculture. In: Jones J, Gheysen G, Fenoll C (eds) Genomics and molecular genetics of plant-nematode interactions. Springer, Dordrecht, pp 21–43

Nisa RU, Tantray AY, Kouser N, Allie KA, Wani SM, Alamri SA, Shah AA (2021) Influence of ecological and edaphic factors on biodiversity of soil nematodes. Saudi J Biol Sci 28(5):3049–3059. https://doi.org/10.1016/j.sjbs.2021.02.046

Nyczepir AP, Thomas SH (2009) Current and future management strategies in intensive crop production systems. In: Perry RN, Moens M, Starr JL (eds) Root-knot nematodes. Wallingford, CABI, UK, pp 412–443. https://doi.org/10.1079/9781845934927.0412

Okasha EM, El–Metwally IM, Taha NM, Darwesh RK (2020) Impact of drip and gated pipe irrigation systems, irrigation intervals on yield, productivity of irrigation water and quality of two common bean (*Phaseolus vulgaris* L.) cultivars in heavy clay soil. Egypt J Chem 63(12):5103–5116

Palomares–Rius JE, Belaj A, León L, de la Rosa R, Rapoport HF, Castillo P (2019) Evaluation of the phytopathological reaction of wild and cultivated olives as a means of finding promising new sources of genetic diversity for resistance to root–knot nematodes. Plant dis 103(10):2559–2568. https://doi.org/10.1094/PDIS-02-19-0322-RE

Pandey A, Mukerji KG (2006) Biological control of plant diseases (1st edn). CRC Press, pp 442

Perry RN, Moens M, Starr JL (2009) Root-knot nematodes. Wallingford, CABI, UK

Phani V, Khan MR, Dutta TK (2021) Plant-parasitic nematodes as a potential threat to protected agriculture: current status and management options. Crop Prot 144:105573. https://doi.org/10.1016/j.cropro.2021.105573

Porazinska DL, McSorley R, Duncan LW, Graham JH, Wheaton TA, Parsons LR (1998) Nematode community composition under various irrigation schemes in a citrus soil ecosystem. J Nematol 30(2):170

Porazinska DL, de Mesquita CPB, Farrer EC, Spasojevic MJ, Suding KN, Schmidt SK (2021) Nematode community diversity and function across an alpine landscape undergoing plant colonization of previously unvegetated soils. Soil Biol Biochem 161:108380. https://doi.org/10.1016/j.soilbio.2021.108380

Reddy PP (2017) Agro-ecological approaches to pest management for sustainable agriculture. Springer Singapore, Singapore
Ribeiro LM, Campos HD, Ribeiro GC, Neves DL, Dias-Arieira CR (2012) Effect of treating cotton seeds on the population dynamics of *Pratylenchus brachyurus* under water stress conditions. Nematropica 42(1):84–90
Ryss AY (1988) World fauna of the root parasitic nematodes of the family pratylenchidae (Tylenchida). St Petersburg, Russia, Nauka
Šalamún P, Hanzelová V, Miklisová D, Šestinová O, Findoráková L, Kováčik P (2017) The effects of vegetation cover on soil nematode communities in various biotopes disturbed by industrial emissions. Sci Total Environ 592:106–114. https://doi.org/10.1016/j.scitotenv.2017.02.238
Siddiqi MR (2000) Tylenchida, parasites of plants and insects, 2nd edn. CAB International, Wallingford
Song M, Li X, Jing S, Lei L, Wang J, Wan S (2016) Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Appl Soil Ecol 102:53–60. https://doi.org/10.1016/j.apsoil.2016.02.011
Stephens MA (1974) EDF statistics for goodness of fit and some comparisons. J Am Stat Assoc 69(347):730–737
Sundararaju P, Jeyabaskaran KJ (2003) Evaluation of different soil types on multiplication of *Pratylenchus coffeae* and growth of banana seedlings var. Nendran Nematol Medit 31:151–153
Taha EH (2020) Fluctuation of nematode populations in some vegetable hosts under drip and conventional irrigation systems. J Plant Prot Pathol 11(11):595–599. https://doi.org/10.21608/jppp.2020.128705
Tarno H, Marsudi EW, Widjayanti T, Setiawan Y (2021) Nematodes associated with robusta coffee plantations in Malang District, East Java, Indonesia. J Biol Diver 22(8):3306–3312. https://doi.org/10.13057/biodiv/d220825
Taylor DP, Netscher C (1974) An improved technique for preparing perineal patterns of *Meloidogyne* spp. Nematologica 20(2):268–269. https://doi.org/10.1163/187529274X00285
Trinh PQ, de la Peña E, Nguyen CN, Nguyen HX, Moens M (2009) Plant-parasitic nematodes associated with coffee in Vietnam. Russ J Nematol 17(1):73
Vovlas N, Castillo P, Rapoport HF, Jiménez-Díaz RM (2000) Parasitic nematodes associated with olive in countries bordering the Mediterranean Sea. In: C. Vitagliano, Martelli GP (eds) Proceeding of the IV International Symposium on Olive Growing, ISHS Acta Horticulturae, Valenzano, Italy, pp 857–860. https://doi.org/10.17660/ActaHortic.2002.586.186
Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J (2017) Package 'corrplot'. Statistician 56(316):e24
Wesemael W, Viaene N, Moens M (2011) Root-knot nematodes (*Meloidogyne* spp.) in Europe. Nematology 13(1):3–16. https://doi.org/10.1163/138855410X526831
Wilschut RA, Geisen S (2021) Nematodes as drivers of plant performance in natural systems. Trends Plant Sci 26(3):237–247. https://doi.org/10.1016/j.tplants.2020.10.006