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EMERGING HARMONY AND BIODYNAMIC INTERACTIONS

Phytoparasitic nematodes of organic vegetables in the Argan Biosphere of Souss-Massa (Southern Morocco)

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Abstract

Agroecological productivity of the Arganeraie Biosphere Reserve of Morocco is limited by the wide spread and dynamics of plant parasitic nematodes (PPN). Ecological studies of nematode communities are required to develop effective biological management of these bioagressors as conventional control methods of PPN are inadequate and have persistent harmful effects. Fifty-nine organic vegetable soils in Souss-Massa were nematologically sampled, and assessment of taxonomic proliferation was made in relation to host species, geographical origin, and climatic and microclimatic factors. Twenty-four nematode genera were identified as obligate and facultative plant feeders. Taxonomic diversity increased from Chtouka to Taroudant and Tiznit provinces. Soil texture, organic matter, pH, nitrogen, zinc, magnesium, copper, altitude, and humidity and temperature were seen to effect driving roles in the abundance, distribution, and community structures of nematodes. The most prevalent taxa posing a high risk to organic agriculture of Souss Massa were needle nematodes (*Longidorus* spp.) and root-knot nematodes (*Meloidogyne* spp.). Edaphic and climatic variables effected nematode populations greatly. A combination of biological treatments and appropriate agroecological practices restricting important economic PPN growth and enhancing soil quality are required to achieve sustainable management in the area.

Keywords Plant-parasitic nematodes · Organic · Vegetables · Biodiversity · Soil ecology

Introduction

Organic agriculture is undergoing a rapid global transformation in response to demands for healthier foods and more environmentally friendly production (Olle and Williams 2012). Global growth of the sector is estimated at 30% due to market forces (Ashley et al. 2007). Statistics show a significant increase in organic land surfaces, over the last two decades, with organically farmed areas increased from 11 to 71.5 million hectares (ha) worldwide (Willer et al. 2020). In Morocco, in 2020, cultivated organic production areas were planned to widen to 40 000 ha (MAPMDREF 2018). Further, vegetable producing areas covering more than 2160 ha were supplemented with an additional 365 ha in 2018

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(Willer et al. 2020). Recently, with the launch of the new ministerial development strategy for agricultural in Morocco dubbed "Green Generation 2020–2030", certified organic farming is receiving considerable attention and has been allocated extra land to benefit a greater diversity of crops. Agronomic species, including those grown using organic methods, are exposed to plant-parasitic nematodes (PPN), the most common and destructive pests of the soil with ambiguous pathological symptoms (Khalil 2013; Seinhorst 1982; Noling 1986; Koenning et al. 1999; Plowright and Coyne 2002). Root knot nematodes (RKN) alone cause an average yield loss of 10% in vegetables (Barker and Koenning 1998; Koenning et al. 1999; Regnault-Roger et al. 2008), and their global economic impact is valued at 60% of crop losses, equating to more than €80 billion per year (Sasser 1989; Blok et al. 2008). Nematodes increase the vulnerability and susceptibility of plant hosts to attack from biotic agents including fungi and bacteria, resulting in 5 to 12% yield loss by year (Powell 1971; Taylor 1971). The extent of damage depends on the genera and population density of PPN (Ornat and Sorribas 2008). Crops may become severely vulnerable to PPN over time as nematode species emerge, or those previously viewed as benign become more harmful pests as cropping patterns change (Nicol 2002).

In most agroecosystems, efficiency of PPN control strategies remains limited and world yield losses are significant (Sasser 1989). Current PPN control methods, included in integrated pest management (IPM) strategies, are insufficient; specific PPN species are targeted as opposed to the community or mixture of species. Control methods effectively change communities via biotic gaps, re-arrangements, insurgence of virulent races, and potential increased aggressiveness of minor species. However, they do not necessarily modify their overall pathogenicity. From the perspective of soil health, such approaches affect the complexity of parasite communities, their multiple responses to environmental disturbances or stresses, and their role in crop production. Eco-epidemiological approaches based on community ecology (diversity, competitive elements, biological and edaphic constraints) plus focus on longer term, ecomanagement of PPN soil biodiversity are promising sustainable strategies.

Though some interesting nematological researches have been conducted in Morocco, focus concerns only key PPN such as *Meloidogyne*, *Heterodera*, or *Pratylenchus* species; nematodes diversity has been neglected in organic farming systems. Functional appreciation of nematodes and ecological drivers, which affect their community composition and abundance, requires clarification of links between the structure and distribution of PPN communities including interaction with biotic and abiotic factors (van Den Hoogen et al. 2019; van Den Hoogen et al. 2020). The latter is crucial in determining preventive ecological measures for controlling risks from emerging aggressor species of nematodes.

The objective of the current study was to reveal the assemblages and distribution of PPNs in organic vegetable farmlands of Souss-Massa in Morocco, across environmental and climatic gradients. Further, we aimed to clarify how the demographics of PPNs associated with organic vegetables are related to soil physicochemical and climatic variables in the core of the vegetable-producing region of the Argan Biosphere Reserve, in order to maximize productivity and ensure its environmentally sustainable management.

Materials and methods

Sampling areas, survey, and methodological details

Nematological surveys were undertaken during March and December 2018 in Sousss-Massa in Southern Morocco (Fig. 1), where vegetables are produced. The region is located in the Mediterranean climatic zone. Climatic data for the sites were unpublished internal data and were based on a 2019 study of the Agence du Bassin Hydraulique de Souss-Massa (ABHSM 2019), provided through personal communication with the Chief Engineer of Water and Forests of the Regional Directorate of Water and Forests and the Fight Against Desertification of the South West in Agadir (DREFLCD-SO). The temperatures are mild and regular with an annual average of 20 °C. Annual mean rainfall of the surveyed region varies between 201 and 220 mm in the center and reaches 250 mm in the northwest. In the south, average rainfall decreases to 148 mm per year. The sites were situated at altitudes ranging from 69 to 756 m.

A total of 59 soil samples were collected from seven rural and urban communes in Taroudant (TRD), Tioute (TIE), Tamaloukte (TLK), Biugra (BGR), Arhbalou (ARL), Belfaa (BLA), and Regada (RGD) (Table 1). Sampling was carried out in a systematic zig-zag pattern, from fields managed according to traditional, organic farming methods. Samples were collected from the root environment of 20 types of vegetables by coring, using a 2-cm diameter auger at a depth of 25 cm. Ten subsamples were collected from each site and kept in polyethylene bags to form 1-kg reference soil samples.

Nematode extraction, identification, and enumeration

Nematodes were extracted in the Laboratory of Biotechnology and Valorization of Natural Resources, Faculty of Sciences of Agadir, Ibn Zohr University (Agadir, Morocco) from 200 mL volumes of composite soil from each site by using the normalized elutriation technique (Oostenbrink 1960; ISO 2007). Plant feeders belonging to Dorylaimida, Triplonchida, Tylenchida, and Rhabditida orders were enumerated in counting dish using a stereomicroscope and identified at genus level using dichotomous keys (Mai and Mullin 1996; and Bongers 1988). The

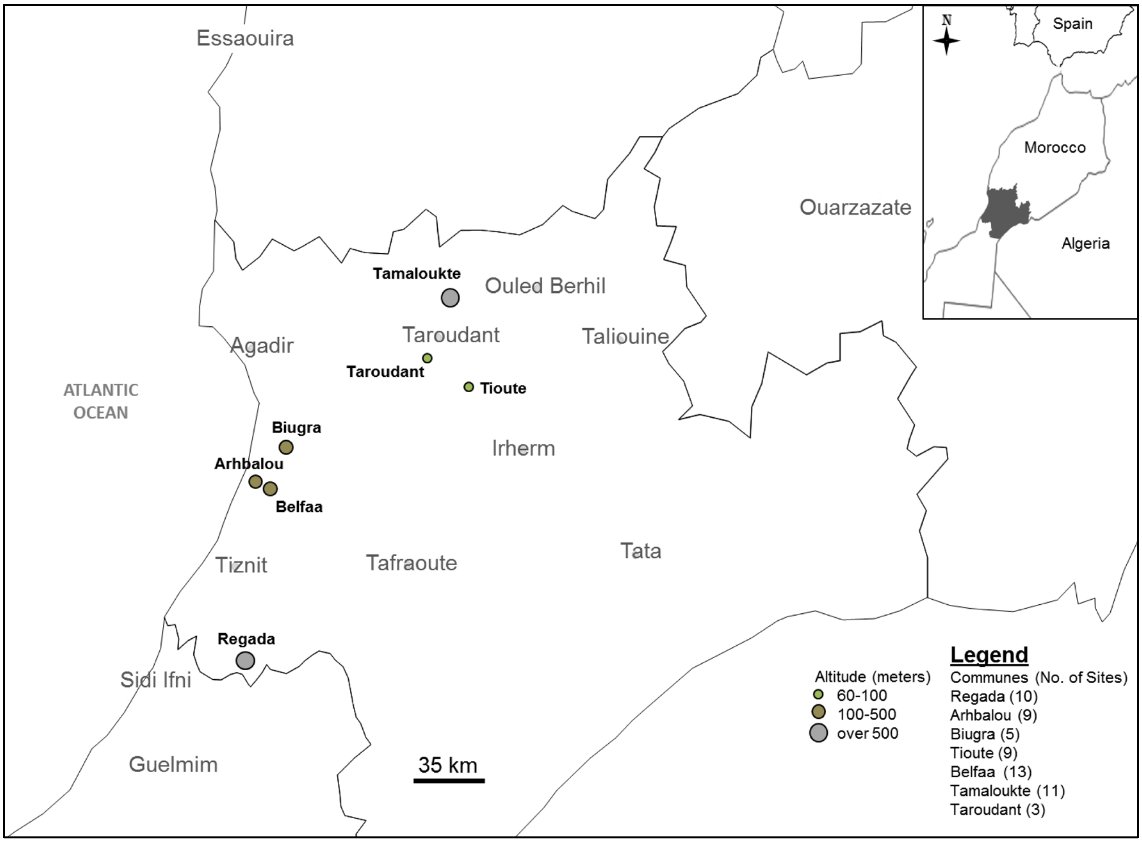

Fig. 1 Distribution map of the sampling sites in Souss-Massa region (Southern Morocco)

genera were expressed as the number of individuals per dm^3 of fresh soil.

Assessment of taxonomic diversity

Taxonomic diversity was assessed using indices based on the total number of nematodes in a community (Nt) and generic richness (G) that represents the number of species per community. Calculations were made according to Ali et al. (2017). The Shannon-Wiener diversity index was calculated as follow:

$$H' = -\sum p_i \ln p_i \quad (1)$$

Table 1 Location and characteristics of sampling sites

Provinces	Localities	Geographic position (Lat., Lon.)	Altitude (m)	Crops	Number of samples
Chtouka	Arhbalou	+30° 3′ 52″ −9° 37′ 40″	86	pumpkin, cabbage, lettuce, spinach, beet	9
	Biugra	+30° 10′ 34″ −9° 30′ 40″	80	leek, radish, sweet potato	5
	Belfaa	+30° 2′ 29″ −9° 33′ 16″	69	aubergine, carrot, potato, lettuce, beet, pea, sweet pepper	12
Tiznit	Regada	+29° 27′ 34″ −9° 42′ 25″	671	potato, carrot, zucchini, hot pepper, pumpkin, onion, radish	10
Taroudant	Tioute	+30° 23′ 16″ −8° 42′ 15″	451	onion, tomato, pumpkin, marrow, green bean, melon	9
	Tamaloukte	+30° 42′ 15″ −8° 47′ 14″	756	radish, onion, pumpkin, pea, hot pepper, tomato, marrow	11
	Taroudant	+30° 28′ 33″ −8° 53′ 29″	234	potato, pumpkin, hot pepper	3

where H′ is the Shannon-Weiner index, and p_i is the proportion of individuals in each genus. Equation 1 was calculated to quantify the local diversity. Evenness was calculated following:

$$E = H'/\ln G \quad (2)$$

where E is evenness, H′ is the Shannon-Weiner index, ln is logarithm, and G is the generic richness. Equation 2 was used to evaluate the regularity of species distributed within each community. The detected genera were allocated to life strategy groups with the colonizer-persister (c-p value) classification (Bongers 1990).

The plant-parasitic index (PPI) was calculated as:

$$PPI = \Sigma\, cp_{i*}\, n_i/N \quad (3)$$

where cp_i is the cp value assigned to family $_i$, n_i is the number of individuals in family $_i$, and N is the total number in the community (sample). Equation (3) was used as a measure of environmental disturbance to determine the plant feeding taxa diversity in each community (Bongers 1990). Frequency (F = percentage of samples where the genus was detected) and abundance (A = mean number of nematodes in the positive samples where the genus was spotted) were modelled according to Fortuner and Merny (1973) to estimate dominance in each of the genera was detected.

Physicochemical analyses of soil samples

Soil physicochemical analyses were carried out at the Soil-Plant-Water Laboratory of the Agronomic and Veterinary Institute Hassan II (IAV, Agadir, Morocco). The soil samples were dried and sieved using a 2-mm mesh. Measurements were determined on the proportion of clay (0–2 μm), fine (2–20 μm) and coarse (20–50 μm) silt, and fine (50–200 μm) and coarse (200–2000 μm) sand according to the sedimentation method (Hedges and Oades 1997). The organic matter (OM) was estimated using the (Walkley and Black 1934) technique with improvements by (Allison 1960). Total nitrogen (N) was quantified using the Kjeldahl nitrogen method (Barbano et al. 1990). Assimilated phosphorus (P), iron (Fe), copper (Cu), zinc (Zn), sodium (Na), manganese (Mn), magnesium (Mg), potassium (K), and limestone ($CaCO_3$) were analyzed using atomic absorption spectrophotometry (Lindsay and Norvell 1978; Sims and Johnson 1991). Conductivity (EC = μS/cm) (Richards 1954) and pH were also determined.

Statistical analysis

A principal component analysis (PCA) was implemented to explore community patterns for PPN diversity indices and genera through Ade4 packages (Chessel et al. 2004; Dray and Dufour 2007). Multiblock partial least squares method (MBPLS, mbpls {*Ade4*) (Bougeard et al. 2011) was performed to highlight the interaction between taxa with climatic variables (rainfall, maximum temperature, and humidity) and soil physicochemical properties. The relationship between taxa and crops was assessed by correspondence analysis (CA) with *FactoMineR* and *factoextra* packages (Wickham 2009; Lê et al. 2008). Additionally, a correlation matrix was produced to check the correspondence between different nematode genera using the package *corrplot* (Falissard 2012; Wei and Simko 2017). All statistical methods were carried out using open source software R version 3.2.4.

Results

Diversity of PPN

Twenty-four genera of PPN were identified in the organic vegetable sites surveyed (Table 2). Obligate (OPF) and facultative (FPF) plant feeders were observed in 98.3% and 86.4% of fields, respectively. The total number of OPF was greater than that of FPF with values of 68.9% and 31.1%. Among 13 families detected, Hoplolaimidae was the most diversified with five genera. Genera such as *Aphelenchus*, *Longidorus*, *Meloidogyne*, *Pratylenchus*, *Tylenchorhynchus*, *Tylenchus*, and *Telotylenchus* were extensively spread throughout the sites. *Aphelenchus*, *Longidorus*, *Paratylenchus*, and *Tylenchus* were observed in all communities within TRD, Tiznit (TZN), and Chtouka (CHK) provinces. *Helicotylenchus*, *Heterodera*, *Paratylenchus*, and *Xiphinema* were moderately disseminated in the sampling geographical range. In contrast, *Dolichodorus* was only found in ARL while *Pararotylenchus*, *Radopholus*, and *Rotylenchulus* were detected in two communes. RGD and TIE comprised 20 genera, which represented 83% of PPN detected.

With reference to the dominance model by Fortuner and Merny (1973) in Fig. 2, 75% of the PPN genera were found to be less distributed on the parcels sampled ($F < 30\%$) and 16.7% were considered to be occasional ($F < 5\%$). The frequent nematodes ($F \geq 30\%$) were *Aphelenchus*, *Meloidogyne*, *Longidorus*, *Tylenchorhynchus*, and *Tylenchus*. *Meloidogyne* and *Aphelenchus* represented 8.3% of PPN and were observed to be abundant and widespread in the study area. However, no dominant genus ($F \geq 30\%$ and $A \geq 200$ nematodes/dm^3 of soil) was observed in all samples.

The diversity assessed in nematodes revealed a G ranging from 1 to 13 PPN taxa. The H′ varied from 0.23 to 2.28; the highest was observed in RGD at a carrot field and the lowest in a pea field in BLA. The E was bounded between 0.48 and 0.97, indicating that the genera were generally widespread across sites.

Table 2 Variables studied and corresponding codes

Variables	Code	Variables	Code	Variables	Code
Feeding type		*Rotylenchulus*	Rol	Potassium	K
Obligate plant feeders	OPF	*Rotylenchus*	Rot	Sodium	Na
Facultative plant feeders	FPF	*Telotylenchus*	Tel	Zinc	Zn
Nematode genera		*Trichodorus*	Trd	Acidity	pH
Axonchium	Axu	*Tylenchorhynchus*	Tyo	Conductivity	EC
Anguina	Ang	*Tylenchulus*	Tys	Organic matter	OM
Aphelenchoides	Aps	*Tylenchus*	Tyu	Limestone	CaCO3
Aphelenchus	Aph	*Xiphinema*	Xip	Diversity indices	
Ditylenchus	Dit	Soil characteristics		Shannon-Wiener index	H′
Dolichodorus	Dol	Coarse sand	CS	Evenness index	E
Helicotylenchus	Hel	Fine sand	FS	Generic richness	G
Heterodera	Het	Coarse silt	Csi	Plant parasitic index	PPI
Hoplolaimus	Hps	Fine silt	Fsi	Total number	Nt
Longidorus	Lon	Clay	Cly	Climatic parameters	
Meloidogyne	Mel	Total Nitrogen	N	Average maximum temperature by year	T.max
Pararotylenchus	Pal	Copper	Cu	Average annual precipitation	AR
Paratrichodorus	Prd	Iron	Fe	Humidity	Hd
Paratylenchus	pTyl	Magnesium	Mg	Altitude	Alt
Pratylenchus	Pra	Manganese	Mn		
Radopholus	Rad	Phosphorus	P		

The PCA showed a variety of PPN taxa distributed differently in the sampling locations. The first two PCA axes accounted for 22% of the total variance in the dataset (Fig. 3). The loading plots (Fig. 3c) showed that TRD and TLK sites contained distinct communities.

Helicotylenchus, *Hoplolaimus*, and *Rotylenchus* contributed further to the first axis and were notably present in TLK whereas BGR and TIE were differentiated by *Longidorus*, *Rotylenchulus*, and *Anguina* (Fig. 3a and c). The genera *Heterodera*, *Trichodorus*, *Xiphinema*, *Axonchium*, and *Tylenchorhynchus* contributed more to the second axis and were generally associated with sites at TIE, TRD, and RGD.

Certain taxa contributed less to the analysis such as *Pararotylenchus*, *Aphelenchoides*, *Dolichodorus*, *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Radopholus*, *Tylenchulus*, and *Paratrichodorus*. Figure 4 PCA axes respecting diversity index values represented 67.7% of the total variance. The PCA plot showed that the diversity indicators were more important in the provinces of Taroudant and Tiznit than in Chtouka (Fig. 4a and b). The H′ index values and G were of a high weight in TRD,

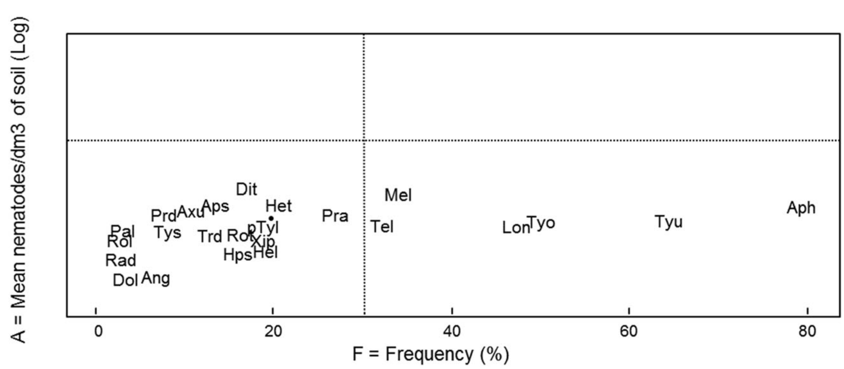

Fig. 2 Dominance diagram of plant-parasitic nematode genera detected in sites surveyed in Souss-Massa. Lines constitute delineation between low and high abundances (A) or frequencies (F), as described by Fortuner and Merny (1973); Axu, *Axonchium*; Ang, *Anguina*; Aps, *Aphelenchoides*; Aph, *Aphelenchus*; Dit, *Ditylenchus*; Dol, *Dolichodorus*; Hel, *Helicotylenchus*; Het, *Heterodera*; Hps, *Hoplolaimus*; Lon, *Longidorus*; Mel, *Meloidogyne*; Pal, *Pararotylenchus*; Prd, *Paratrichodorus*; pTyl, *Paratylenchus*; Pra, *Pratylenchus*; Rad, *Radopholus*; Rol, *Rotylenchulus*; Rot, *Rotylenchus*; Tel, *Telotylenchus*; Trd, *Trichodorus*; Tyo, *Tylenchorhynchus*; Tys, *Tylenchulus*; Tyu, *Tylenchus*; Xip, *Xiphinema*

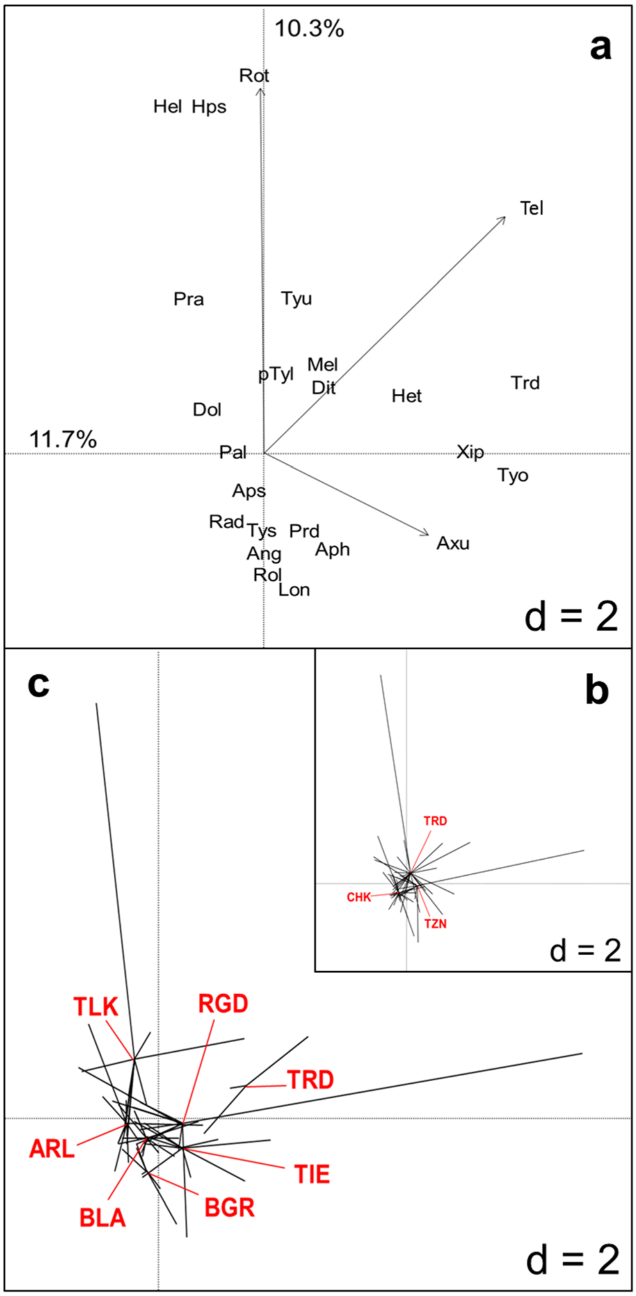

Fig. 3 Principal component analyses of PPN genera associated with vegetable crops: (a) PCA loading plot of PPN genera; (b) score plot for the survey provinces; (c) score plot of the study sites; Axu, *Axonchium*; Ang, *Anguina*; Aps, *Aphelenchoides*; Aph, *Aphelenchus*; Dit, *Ditylenchus*; Dol, *Dolichodorus*; Hel, *Helicotylenchus*; Het, *Heterodera*; Hps, *Hoplolaimus*; Lon, *Longidorus*; Mel, *Meloidogyne*; Pal, *Pararotylenchus*; Prd, *Paratrichodorus*; pTyl, *Paratylenchus*; Pra, *Pratylenchus*; Rad, *Radopholus*; Rol, *Rotylenchulus*; Rot, *Rotylenchus*; Tel, *Telotylenchus*; Trd, *Trichodorus*; Tyo, *Tylenchorhynchus*; Tys, *Tylenchulus*; Tyu, *Tylenchus*; Xip, *Xiphinema*; TLK, Tamaloukte; ARL, Arhbalou; BLA, Belfaa; BGR, Biugra; TIE, Tioute; RGD, Regada; TRD, Taroudant; TZN, Tiznit; CHK, Chtouka

RGD, TLK, and TIE sites (Fig. 4a and c). The obligate PPN were found to be more abundant than FPF nematodes and both were widespread in fields in Taroudant and Tiznit provinces (Fig. 4a and b). The plant-parasitic index (PPI) was generally associated with diversity (H′, G, and E).

Co-occurrence between taxa

Relationships between different PPN genera detected in survey of the current study were assessed using a correlation matrix (Fig. 5). A high positive correlation (r = 0.75) was found between *Longidorus* and *Paratylenchus*. A similar correlation was observed between *Pararotylenchus* and *Radopholus*. *Paratrichodorus* was found to be strongly positively correlated with *Xiphinema* and *Rotylenchulus*. Moreover, *Tylenchulus* had a moderate association with *Aphelenchoides* and *Helicotylenchus* (r = 0.5 and r = 0.52). The correlation matrix shows negative r values of −0.39 and −0.37 for *Aphelenchus* with *Ditylenchus* and *Meloidogyne*, respectively. *Axonchium* with *Helicotylenchus* and *Tylenchus* with *Hoplolaimus* were similarly correlated at −0.34 and −0.43.

Correspondence between PPN taxa and vegetables

In the current study, onion and pumpkin soils were found to be infested with 18 genera representing more than 73% of the PPN detected. Over half of the herbivorous genera detected were recovered from potato, marrow, carrot, tomato, and green bean fields (Table 3). Certain PPN genera were observed in specific sites, *Ditylenchus*, *Meloidogyne*, and *Tylenchus* occurred on sites with pea; *Aphelenchus* and *Tylenchorhynchus* occurred in sites with sweet potato while *Meloidogyne* and *Rotylenchus* occurred in sites with aubergine. *Radopholus*, known to be mainly associated with banana in Souss-Massa, was detected in bean and cabbage fields. *Aphelenchus* was the most frequent nematode detected in the crop sites followed by *Tylenchus* and *Tylenchorhynchus* (Fig. 2 and Table 3). *Aphelenchus*, *Tylenchus*, and *Tylenchorhynchus*, respectively, infested the rhizospheric zones of 90%, 75%, and 75% of vegetable crops surveyed (Fig. 6). *Longidorus*, *Meloidogyne*, *Tylenchorhynchus*, and *Tylenchus* genera existed in the majority of surveyed locations. Three genera (*Dolichodorus*, *Radopholus*, and *Rotylenchulus*) were detected in two vegetable sites each (Table 3), whereas *Pararotylenchus* appeared only in green bean soils.

The first two axes of the correspondence analysis of Fig. 7 accounted for 52.9% of the total variance. Genera and crops of a frequency less than 10% has a low contribution to the analysis and were excluded prior to running second analysis. The latter showed that *Meloidogyne*, *Radopholus*, and *Rotylenchus* were linked with sites of aubergine, pumpkin, and green bean (Fig. 7). *Pararotylenchus* and *Tylenchus* and green bean sites had an insignificantly weighted contribution to the analysis. *Tylenchulus*, *Tylenchorhynchus*, *Paratylenchus*, *Aphelenchus*, *Axonchium*, *Anguina*, and

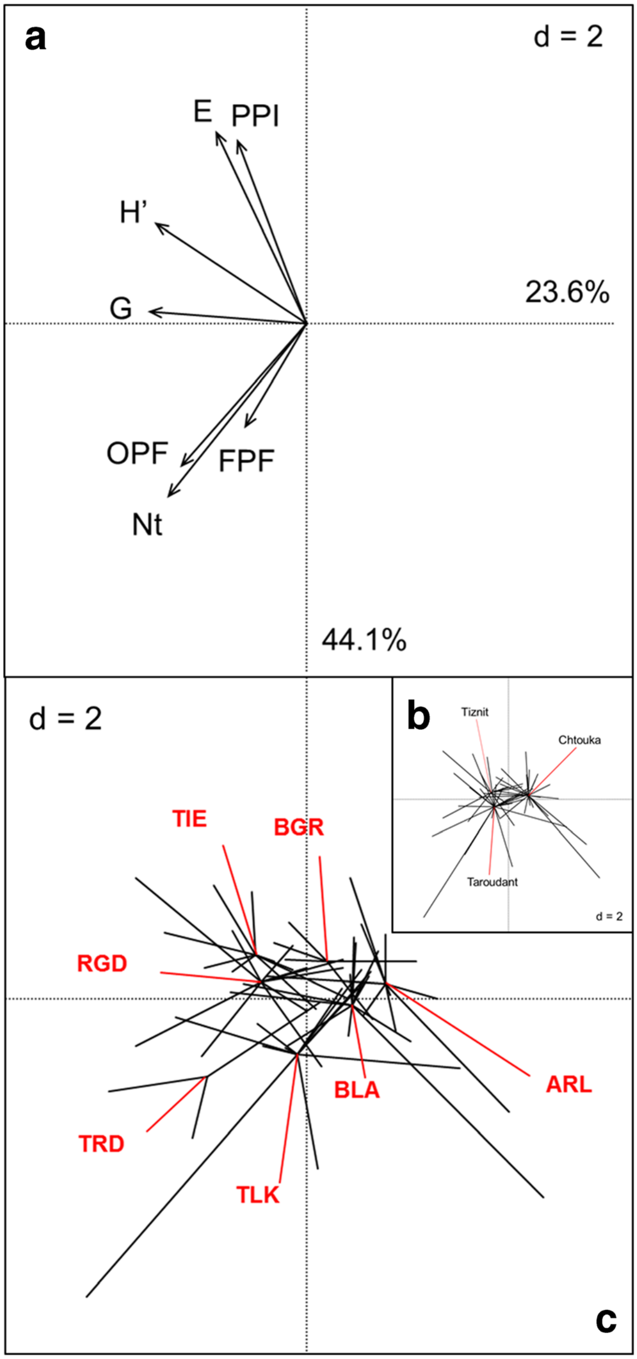

Fig. 4 Principal component analyses of diversity indices: (a) PCA loading plot of the taxonomical diversity indices; (b) score plot for the survey sites; (c) score plot for the prospection provinces; H′, Shannon-Wiener index; E, Evenness index; G, generic richness; PPI, Plant parasitic index; Nt, total number; OPF, obligate plant feeding; FPF, facultative plant feeding; TLK, Tamaloukte; ARL, Arhbalou; BLA, Belfaa; BGR, Biugra; TIE, Tioute; RGD, Regada; TRD, Taroudant

Hoplolaimus were found to be globally associated with the rhizospheres of onion, beet, cabbage, tomato, melon, carrot, and leek. *Aphelenchoides*, *Xiphinema*, *Helicotylenchus*, *Heterodera*, *Paratrichodorus*, and *Rotylenchulus* were also associated with these crops. A high correlation was observed between *Ditylenchus* with pea sites and between *Paratylenchus* with melon sites.

Correspondence between plant-parasitic nematode taxa with climatic and soil factors

The MBPLS analysis showed that *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Tylenchus*, and *Heterodera* genera were positively correlated with Zn and negatively correlated with Fe, Mn, T.max, and pH (Fig. 8). *Tylenchorhynchus*, *Xiphinema*, *Hoplolaimus*, *Helicotylenchus*, *Pratylenchus*, *Rotylenchus*, and *Telotylenchus* were observed to be mainly associated with coarse sand (CS) and fine sand (FS). A negative correlation was recorded between these genera with Mg, N, and OM. *Rotylenchulus*, *Tylenchulus*, and *Longidorus* were positively correlated with Mn. The loading plots of Fig. 8a and b show *Dolichodorus*, *Axonchium*, and *Anguina* occurrence positively corresponded with T.max, pH, and coarse silt (Csi) while they were negatively correlated with Hd. Genera had no correlation with Cu with the exceptions of *Longidorus*, *Tylenchulus*, and *Rotylenchulus* which had a weak association. *Dolichodorus*, *Axonchium*, and *Anguina* were linked to Csi and T.max. *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Tylenchus*, *Heterodera*, *Aphelenchus*, *Trichodorus*, and *Aphelenchoides* were present in clay and moist soils. Variables of P and K, altitude (Alt), EC, Na, and $CaCO_3$, and the presence of *Pararotylenchus* and *Radopholus* did not have a great effect on the analysis.

The multiblock analysis for diversity indices showed that OPF nematodes effected diversity indices (H′, G, E, and Nt), Alt, and T.max and were generally associated with $CaCO_3$, Cly, OM, Hd, N, Mg, and P (Fig. 9). The PPI index was linked to T.max, pH, fine silt (Fsi), and Mn and also generally related to the diversity index values (H′), G, and E. FPF genera were associated with Zn, Hd, and clay. Coarse silt and OPF were negatively correlated.

Discussion

Organic soils were found to be infested with variable genera assemblages. Those strongly positively correlated included *Longidorus* and *Paratylenchus*; *Pararotylenchus* with *Radopholus*; *Paratrichodorus* with *Xiphinema* and *Rotylenchulus*; and *Tylenchulus* with *Aphelenchoides* and *Helicotylenchus*. PPN often parasitize plants in mixed species communities (Jones and Perry 1978). Eisenback (1993) suggested that there are synergistic interactions in species through similar feeding behaviors and persistence resulting in an increase or inhibition of species proliferation. High negative correlations included *Aphelenchus* with *Ditylenchus* and *Meloidogyne*, *Axonchium* with *Helicotylenchus*, and *Tylenchus* with *Hoplolaimus*. Such negative associations are

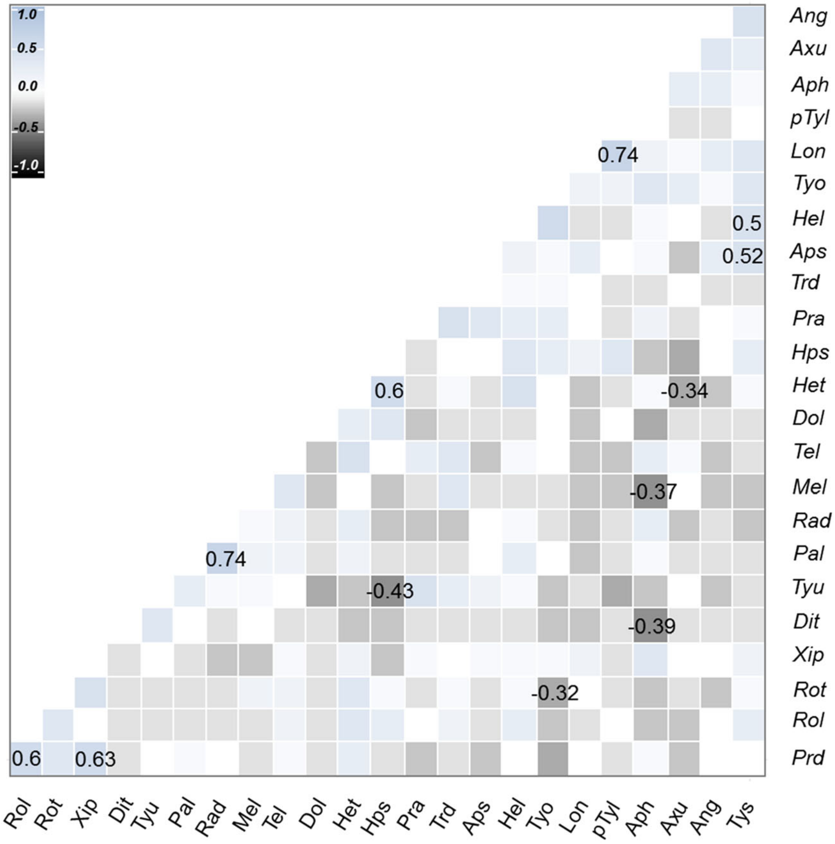

Fig. 5 A correlation matrix between different PPN genera detected in the organic vegetable soils in the Arganeraie Biosphere of Souss-Massa (South of Morocco); Axu, *Axonchium*; Ang, *Anguina*; Aps, *Aphelenchoides*; Aph, *Aphelenchus*; Dit, *Ditylenchus*; Dol, *Dolichodorus*; Hel, *Helicotylenchus*; Het, *Heterodera*; Hps, *Hoplolaimus*; Lon, *Longidorus*; Mel, *Meloidogyne*; Pal, *Pararotylenchus*; Prd, *Paratrichodorus*; pTyl, *Paratylenchus*; Pra, *Pratylenchus*; Rad, *Radopholus*; Rol, *Rotylenchulus*; Rot, *Rotylenchus*; Tel, *Telotylenchus*; Trd, *Trichodorus*; Tyo, *Tylenchorhynchus*; Tys, *Tylenchulus*; Tyu, *Tylenchus*; Xip, *Xiphinema*

related to the adverse effect among taxa. Disturbance of the relationships between PPN and other soil organisms allows PPN to develop rapidly (Aït Hamza et al. 2018), and hence to compete with other species in persistent and wide distribution (Oostenbrink 1966). Further, intergeneric inhibition has been reported (Ross 1964; Amosu and Taylor 1974).

The current study identified eight of the most economically important genera of PPN (Jones et al. 2013). These were *Meloidogyne*, *Ditylenchus*, *Heterodera*, *Pratylenchus*, *Xiphinema*, *Aphelenchoides*, *Radopholus* and *Rotylenchulus*. Although these taxa were found to be non-dominant, their presence in the organic vegetable fields of Souss-Massa represents a risk of PPN to crops due to their prevalence.

During the sampling, interviews with the growers confirmed the occurrence of *Meloidogyne* spp. damage to organic vegetables of Souss-Massa. Solanaceae and Fabaceae were remarked as being more vulnerable due to their prolific rooting systems. Nematodes were associated with 12 of the organic vegetables (60%) in the current study, indicating their wide distribution. Low population densities of *Meloidogyne* spp. were previously recorded in carrot, sweet pepper, green beans, and pumpkin (Baimey et al. 2009); indeed in the current study, organic carrot sites contained a low prevalence of 18 nematodes per dm^3 of soil, and green pepper soils were found to be free from the taxon. Additionally, no soil infestation with *Meloidogyne* was found in radish, cabbage, lettuce, spinach, beet, sweet potato, and melon. Conversely, sweet pepper and pumpkin had significant average densities of *Meloidogyne* (103 and 222 individuals per dm^3 of soil). The current study shows moderate infestation of onion rhizospheres by RKN with an average of 36 individuals per dm^3 of soil, while no plant infection was reported in previous studies (Baimey et al. 2009). This could be explained by the existence of different *Meloidogyne* species (Afouda et al. 2008; Baimey et al. 2009) or the low susceptibility of resistant crop varieties (Roberts and Ulloa 2010; Starr and Roberts 2004; Starr et al. 2010). Grower's management (rotation, types of manure, and intercropping plans) against *Meloidogyne* may explain the absence or low abundance of the PPN populations in Souss-Massa.

Radopholus is known for its prevalence in tropical and subtropical regions (Loof 1991); however, in the current study, frequency of the genus was estimated at 10% and only appeared in soils of lettuce and green bean in the sampled sites. Presence of this genus can be attributed to crop susceptibility (EFSA PLH Panel 2014) and/or to previous cultivation of the main host plants, namely, banana, a good host for *R. similis* (Haegeman et al. 2010). The present survey revealed that *Pratylenchus* spp. were prevalent in fields with nine (45%) of the vegetable crops. Association of *P. penetrans* and *R. similis* with vegetables has been reported to limit yields worldwide (Anwar and McKenry 2012; Sehgal and Gaur 1999).

Table 3 Mean population density of the 10 most frequent PPN genera detected in organic vegetable crop soils in Taroudant, Tiznit, and Chtouka regions between March and December 2018

Crops	NS	NG	Lon	Mel	Hps	Aph	Tyu	Tyo	Pra	Het	pTyl	Xip	P*	N*
Potato (*Solanum tuberosum* L.)	10	17	14	65	43	144	27	68	72	8	11	14	71	17
Zucchini (*Cucurbita pepo* L.)	1	8	0	40	30	95	63	0	0	0	10	0	33	8
Pumpkin (*Cucurbita maxima* D)	10	18	3	222	40	39	55	12	11	12	4	3	73	18
Marrow (*Cucurbita pepo* L.)	2	11	10	10	0	60	173	10	80	0	0	10	46	11
Carrot (*Daucus carota* L.)	3	15	13	18	0	90	25	40	33	3	20	13	63	15
Hot pepper (*Capsicum frutescens* L.)	3	9	0	107	0	58	83	25	10	0	0	0	38	9
Tomato (*Solanum lycopersicum* L.)	4	13	26	10	0	119	45	106	30	0	10	26	54	13
Onion (*Allium cepa* L.)	4	18	8	36	31	33	43	16	28	38	15	8	75	18
Radish (*Raphanus sativus* L.)	3	9	0	0	20	87	113	20	73	0	10	0	38	9
Cabbage (*Brassica* sp.)	2	8	65	0	20	135	40	0	0	20	0	65	33	8
Lettuce (*Lactuca sativa* L.)	3	9	0	0	20	156	1	6	0	20	0	0	38	9
Spinach (*Spinacia oleracea* L.)	1	6	0	0	0	20	0	20	0	20	20	0	25	6
Beet (*Beta vulgaris* L.)	2	7	0	0	10	95	0	63	0	28	0	0	29	7
Sweet potato (*Ipomoea batatas* L.)	1	2	0	0	0	60	0	5	0	0	0	0	8	2
Leek (*Allium porrum* L.)	2	9	0	8	0	123	28	30	0	0	0	0	38	9
Sweet pepper (*Capsicum annuum* L.)	2	6	10	0	0	75	40	0	0	0	0	10	25	6
Green bean (*Phaseolus vulgaris* L.)	1	14	0	103	22	97	112	20	7	20	0	0	58	14
Aubergine (*Solanum melongena* L.)	1	2	0	170	0	0	0	0	0	0	0	0	8	2
Pea (*Pisum sativum* L.)	3	3	0	20	0	0	140	0	0	0	0	0	13	3
Melon (*Cucumis melo* L.)	1	5	0	0	0	85	0	40	0	0	180	0	21	5
Percentage infested crop soils (%) [a]			70	60	45	90	75	75	45	45	45	40		
Nematode occurrence frequency in all sites (%)			47.4	33.9	32.2	79.7	64.4	49.1	27.1	18.6	18.6	18.6		

NS, number of samples; *NG*, number of nematode genera; [(a)] percentage of infested crop soils with a nematode genus compared to twenty crop kinds; P* percentage genera in crop soils (%); N* number of genera in crop soils; *Lon*, *Longidorus*; *Mel*, *Meloidogyne*; *Hps*, *Hoplolaimus*; *Aph*, *Aphelenchus*; *Tyu*, *Tylenchus*; *Tyo*, *Tylenchorhynchus*; *Pra*, *Pratylenchus*; *Het*, *Heterodera*; *pTyl*, *Paratylenchus*; *Xip*, *Xiphinema*

Aphelenchus avenae, *Helicotylenchus dihystera*, *Hoplolaimus columbus*, *Tylenchorhynchus claytoni*, as well as *Xiphinema* species have all been recovered from crops of tomato, chili, and bell peppers (Anwar et al. 2013). Conversely, *Helicotylenchus* did not appear during our survey in any sampling sites of these vegetables. The remaining genera were all observed in tomato fields. In addition to their occurrence in bell pepper soils, *Aphelenchus* was also detected in hot pepper soils. *Tylenchorhynchus* was also associated with the latter. However, *Xiphinema* was detected only bell pepper fields.

The diversity indices were significantly higher in TRD and TZN provinces than in CHK. This may be due to the importance

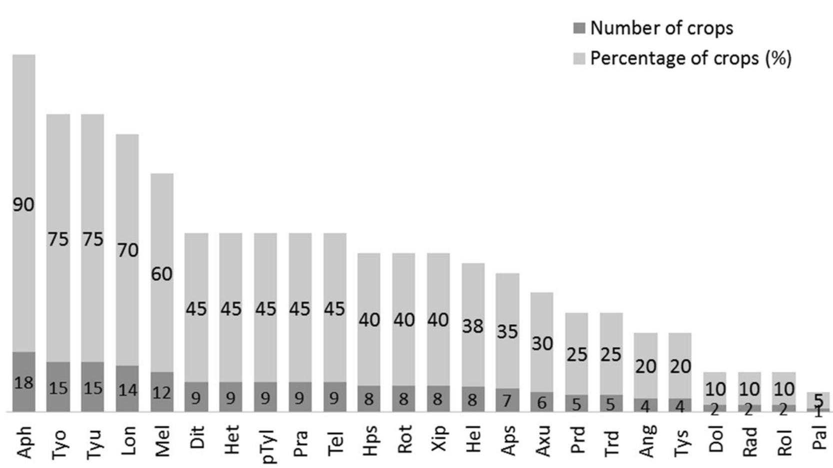

Fig. 6 Percentage and number of organic vegetables associated with PPN in the Arganeraie Biosphere of Souss-Massa (South of Morocco); See encoding in Table 2

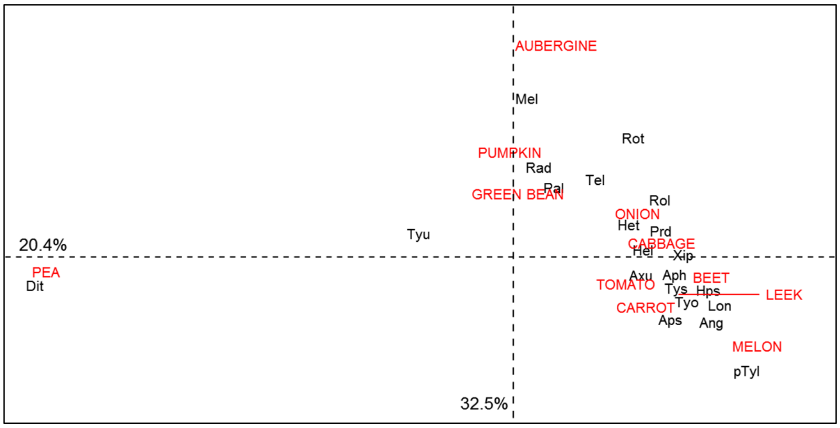

Fig. 7 Correspondence analysis between PPN genera with vegetables: (**a**) PCA loading plot of the nematode genera; (**b**) score plot for the crop types; Axu, *Axonchium*; Ang, *Anguina*; Aps, *Aphelenchoides*; Aph, *Aphelenchus*; Dit, *Ditylenchus*; Hel, *Helicotylenchus*; Het, *Heterodera*; Hps, *Hoplolaimus*; Lon, *Longidorus*; Mel, *Meloidogyne*; Pal, *Pararotylenchus*; Prd, *Paratrichodorus*; pTyl, *Paratylenchus*; Rad, *Radopholus*; Rol, *Rotylenchulus*; Rot, *Rotylenchus*; Tel, *Telotylenchus*; Tyo, *Tylenchorhynchus*; Tys, *Tylenchulus*; Tyu, *Tylenchus*; Xip, *Xiphinema*

of sustainability in these areas and resilience of soil ecosystems (Yeates 2007), which result from organic farming system practiced in the two provinces. Although altitude had no impact on the nematode richness under most conditions (Popovici and Ciobanu 2010), the current study indicated a significant relationship between diversity indices and elevation.

The occurrence of ectoparasitic nematodes was confirmed in commercially farmed vegetable fields (Maqbool 1992; Barker et al. 1998). Presence of these genera in organic vegetable growing sites should be taken into account by growers and can be anticipated as a risk for vegetable production in Souss-Massa. Important correlations between the distribution of PPN genera with climatic and soil variables were underlined in the present study. The studied sites indicated a high relation between OM and PPN. Genera were detected in soils with a low OM, namely, *Tylenchorhynchus*, *Xiphinema*, *Hoplolaimus*, *Helicotylenchus*, *Pratylenchus*, *Rotylenchus*, and *Telotylenchus*. According to Hominick (1999) and Qi and Hu (2007), most genera had a negative correlation with OM that results in a direct decrease of nematode abundance probably due to increased microbial antagonism of PPN with accumulation of soil OM (De Guiran et al. 1980; Widmer et al. 2002).

In the current study, PPN such as *Longidorus*, *Tylenchulus*, and *Rotylenchulus* were associated with Cu. *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Tylenchus*, and *Heterodera* were found to be positively correlated with Zn. Cu and Zn lead to a decrease of the G index in nematodes and the maturity of soils (Georgieva et al. 2002). This assumes that levels of Zn and Cu disrupt nematode community structures as well as species biological characteristics, which promote development of some adapted nematodes. Impact of Mg on the PPN abundance has been reported (Cadet and Thioulouse 1998; Benjlil et al. 2020) in addition to positive correlations with *Heterodera* spp. (Francl 1993). Our results indicated a negative correlation of *Tylenchorhynchus*, *Xiphinema*, *Hoplolaimus*, *Helicotylenchus*, *Pratylenchus*, *Rotylenchus*, and *Telotylenchus* with Mg. Conversely, Robinson et al. (1987) and Zoon et al. (1993) confirmed that *Helicotylenchus* spp. were related to Mg. Earlier, it was reported that PPN increase with enhanced levels of K (Kincaid et al. 1970; Badra and Yousif 1979; Yavuzaslanoglu et al. 2012) that affects some genera (Kandji et al. 2001). The present study did not allow clarifying the role that plays K in the distribution of PPN. Except *Aphelenchoides*, *Ditylenchus*, and *Criconema*, most genera identified (*Tylenchorhynchus*, *Xiphinema*, *Hoplolaimus*, *Helicotylenchus*, *Pratylenchus*, *Rotylenchus*, and *Telotylenchus*) showed a negative correlation with total N (Benjlil et al. 2020), and that could possibly be the result of accumulation of NO_3^- and NH_4^+-N through nitrogen degradation considered toxic to PPN (Rodriguez-Kabana 1986). However, Treonis et al. (2018) reported that the abundance of Tylenchidae and Cephalobidae both revealed positive correlations with nitrogen. Population and diversity of soil nematodes are proven to be affected by pH value (Zhong et al. 2010). The majority of genera in the sampling sites were observed to be influenced by pH in agreement with previous research (Cadet and Thioulouse 1998; Wang et al. 2009; Benjlil et al. 2020).

Nematodes detected in this study had different distributions in response to soil texture. Genera such as *Tylenchorhynchus*, *Xiphinema*, *Hoplolaimus*, *Helicotylenchus*, *Pratylenchus*, and *Rotylenchus* found to be mainly associated with CS and FS soils. Benjlil et al. (2020) indicated that a high abundance of PPN was observed in loamy soils while clayey soils exhibited lower abundance. Although *Pratylenchus* spp. were often observed in sandy soils (Zirakparvar et al. 1980; Yavuzaslanoglu et al. 2012; Choshali et al. 2015), higher reproduction rates in the clay substrate were reported (McSorley and Frederick 2002); the only exceptions are *P. thornei*, *P. neglectus*, and *P. helophilus* (Grandison and Wallace 1974; Thompson et al. 2010). Humid clay soils in the current study showed high

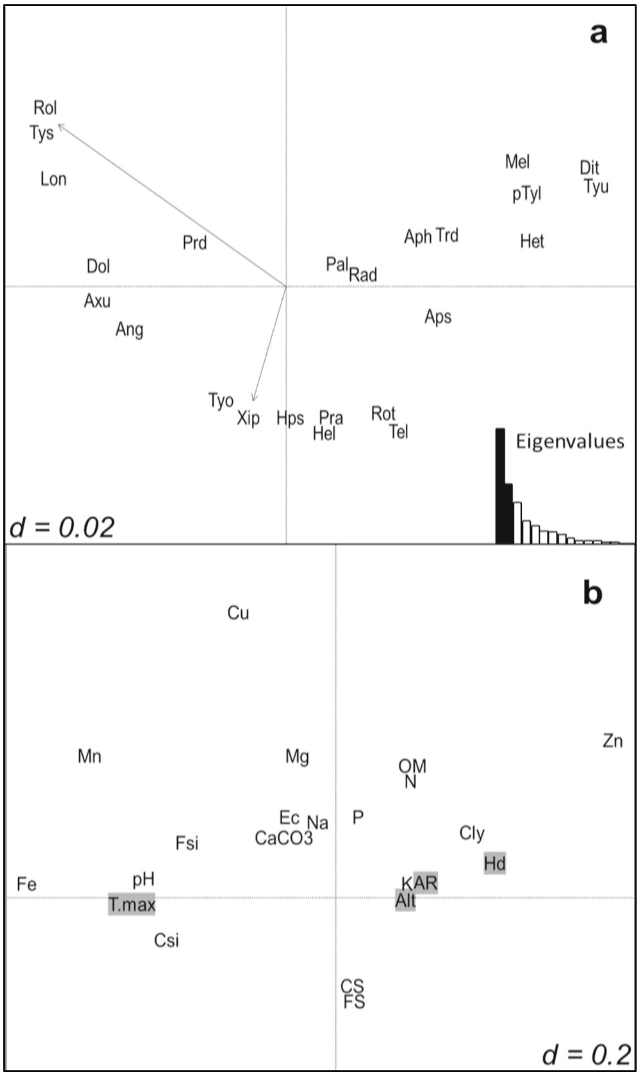

Fig. 8 Multiblock analysis between PPN communities, soil physicochemical and climatic parameters: (**a**) PCA loading plot of the nematode genera; (**b**) PCA loading plot of the soil physicochemical and climatic factors; Axu, *Axonchium*; Ang, *Anguina*; Aps, *Aphelenchoides*; Aph, *Aphelenchus*; Dit, *Ditylenchus*; Dol, *Dolichodorus*; Hel, *Helicotylenchus*; Het, *Heterodera*; Hps, *Hoplolaimus*; Lon, *Longidorus*; Mel, *Meloidogyne*; Pal, *Pararotylenchus*; Prd, *Paratrichodorus*; pTyl, *Paratylenchus*; Pra, *Pratylenchus*; Rad, *Radopholus*; Rol, *Rotylenchulus*; Rot, *Rotylenchus*; Tel, *Telotylenchus*; Trd, *Trichodorus*; Tyo, *Tylenchorhynchus*; Tys, *Tylenchulus*; Tyu, *Tylenchus*; Xip, *Xiphinema*; CS, coarse sand; FS, fine sand; Csi, coarse silt; Fsi, fine silt; Cly, clay; N, nitrogen; Cu, copper; Fe, iron; Mg, magnesium; Mn, manganese; P, phosphorus; K, potassium; Na, sodium; Zn, zinc; pH, acidity; Con, conductivity; OM, organic matter; $CaCO_3$, limestone; T.max, average maximum temperature by year; AR, average annual precipitation; Hd, humidity; Alt, altitude

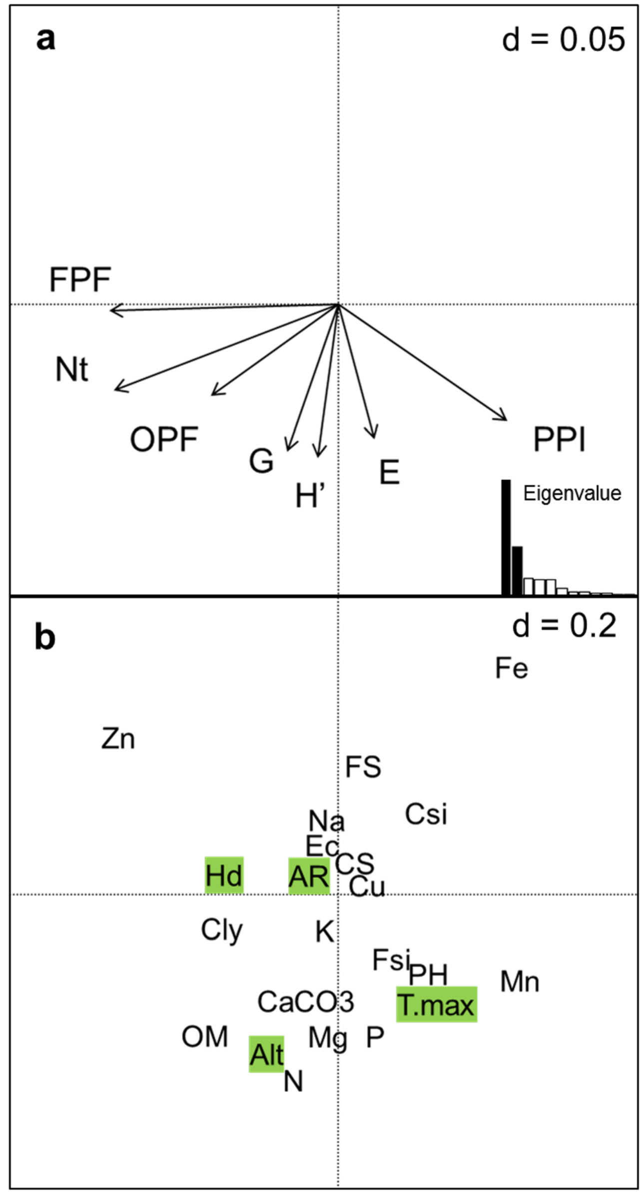

Fig. 9 Multiblock analysis of diversity index comonents with soil physicochemical and climatic factors: (**a**) PCA loading plot of the diversity index values components; (**b**) PCA loading plot of the soil physicochemical and climatic parameters; H′, Shannon-Wiener index; E, Evenness; G, generic richness; PPI, Plant parasitic index; Nt, total number; OPF, obligate plant feeding; FPF, facultative plant feeding; CS, coarse sand; FS, fine sand; Csi, coarse silt; Fsi, fine silt; Cly, clay; N, nitrogen; Cu, copper; Fe, iron; Mg, magnesium; Mn, manganese; P, phosphorus; K, potassium; Na, sodium; Zn, zinc; pH, acidity; Con, conductivity; OM, organic matter; $CaCO_3$, limestone; T.max, average maximum temperature by year; AR, average annual precipitation; Hd, humidity; Alt, altitude

prevalence of *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Tylenchus*, *Heterodera*, *Aphelenchus*, *Trichodorus*, and *Aphelenchoides* genera. An analogous tendency was observed for *Ditylenchus dipsaci* (Wallace 1962). Previous studies reported a positive correlation between sandy soils of rice, abundance, and pathogenicity of *Heterodera* spp. (Audebert et al. 2000). Additionally, *Meloidogyne javanica* has been reported to be positively correlated with sandy soils (Al-Hazmi et al. 2017).

Rainfall, humidity, and temperature contributed to the distribution of taxa and strongly influenced PPN determined in the current study. These climatic factors constitute major driving forces for abundance, community structure (Aït Hamza et al. 2018; Chowdhury et al. 2019; Benjlil et al. 2020), diversity, and distribution of soil nematodes (Neilson and Boag 1996; Bakonyi et al. 2007). *Dolichodorus*, *Axonchium*, and *Anguina* were related to T.max. Contrastingly, genera such as *Meloidogyne*, *Paratylenchus*, *Ditylenchus*, *Tylenchus*, and *Heterodera* have been found negatively correlated to T.max. Further, the increased reproduction rate of *Pratylenchus* has been linked to augmented temperature (Duyck et al. 2012). Precise optimal temperature is required for life processes of nematode species (Tzortzakakis and Trudgill 2005; Evans and Perry 2009), and it has been considered a determining factor in their ultimate geographical distribution range (Luc et al. 2005). This explains the deviation of genera within the study sites according to T.max. Most genera recovered from the sampling fields were significantly related to Hd directly affecting the nematode infestation rate in soils. The latter is in agreement with studies indicating that humid substrates are associated with proliferation of PPN (Nico et al. 2002; Castillo et al. 2010; Aït Hamza et al. 2015). Additionally, dryness of the soil affects the survival of PPN seeking root infection (Colagiero and Ciancio 2011). Reports suggest that soil Hd has no effect on the dissemination of nematodes in most agricultural soils in Northern Europe (Boag et al. 1991; Neilson and Boag 1996; Coakley et al. 1999); AR was shown to have a role in their distribution within the survey sites in Souss-Massa. Similarly, Mateille et al. (2016) indicated that precipitation rates influence the richness, variability, and taxonomic with functional diversity of nematodes.

Conclusion

The current study shows that in organically farmed soils, diversity of PPN is important, especially in Taroudant and Tiznit provinces. Eight taxa found in Souss-Massa are among the top 10 most damaging PPN. Soil texture, OM, pH, N, Zn, Cu, and Mg as well as climatic variables (moisture and T.max) and host crops were key drivers of the abundance, distribution, and community structure of soil nematodes in the organic vegetable fields in the region. Changes in geographic distribution of PPN due to these drivers may take a long time, but their movement between fields may occur over short periods through exchange of planting materials among farmers and is probably increased with other human activities. Nematological insight achieved in the current study contributes to geographical databases of soil nematodes at both national and global scale. Nematodes, including those of economic impact should be identified up to the species level, to allow screening of available crop cultivars and understand nematode species interactions. Attention should be focused on agroecological practices leading to resilient soils with suppressive effects to key soil-borne pathogens, in order to increase productivity of organic crops. The Argan Biosphere is a UNESCO reserve, a unique territory, where soil is managed organically and is subject to different anthropic gradient. Advances in nematode ecology and realization of their trophic impacts are needed, considering their use as bioindicators in soil health assessments. Such advances are needed to provide required support to drive policy change in sustainable soil management and conservation practice.

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Availability of data and materials All relevant data are contained herein.

Author contribution EH Mayad and I Filali Alaoui conceived the study design. I Filali Alaoui, E. Mzough, A. Idhmida, A Braimi, H Benjlil, K Basaid, and EH Mayad contributed to soil sampling and nematodes extraction. I Filali Alaoui and EH Mayad carried out the nematological analysis. I Filali Alaoui, A. Hallouti, MA Hamza, JN Furze and EH Mayad performed data analysis and interpretation. Authors contributed equally in the writing of the manuscript.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests

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