Soil Free-living Nematode Composition Near the Vineyard Rhizosphere in a Basaltic Soil

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Abstract

The soil free-living nematode community composition was compared for five agro-management systems in a basaltic soil. The sites differed in their long-term management and were designated as organic farming (OM), conventional (MI), natural pasture (NP), foliage farming (FF) and open field (OF). The effect of five diverse land use types in vineyard growth in basaltic soils on soil free-living nematodes' density, diversity, and functionality was examined in the plant rhizosphere. We found 22 families, 42 genera of which only 14 were present in all soil samples collected from the five sampling sites (3 bacterivores, 4 fungivores, 3 omnivores-predators and 4 plant parasites). The organic and conventional managements were found to influence the soil free-living nematode community and its trophic composition. The higher abundance of bacterivores included the Cephalobidae and Panagrolaimidae families. The fungivores included the Anguinidae and Aphelenchidae families. Ominvores-predators included the Aprocelaimidae and Qudsianematidae, and the plant parasite nematodes were among the main pests in the below-ground rhizosphere biome. Promoting the bacterial community could be a beneficial and promising way for a considerable increase in organic management.

Keywords: soil nematodes, community structure, basaltic soil, vineyard

1. Introduction

In the last 20 years, the planting of vineyards has increased dramatically all over the world. It was estimated to be 7.3 mha in 2021, with a world market of 34.3 bn EUR (Roca, 2022). Viticultural areas use a broad spectrum of soils, although experts suggest that the soil should be well drained and loamy, containing a mix of sand, silt, and clay. However, grapes also tolerate poor alkaline soils. Regarding climate, grapevines can grow in a wide range of climates, from mild tropical to arid or cold. However, grape quality is substantially affected by soil type and origin. Volcanic origin soils contain a wide range of minerals, have low water retention and organic content, and have great potential for viticultural use (Maltman, 2018; Szabo, 2016; Wilson et al., 2016). In Israel, the Golan Heights volcanic soils are basaltic clay soils found at an altitude of 400 to 1,200 meters above sea level. These soils are in demand by many vineries that consider the basaltic soils, temperature, and altitude as conditions suitable for the growth of high-quality grapes.

The capacity of soil to function as a vital living ecosystem that fulfills all its nutrient supply functions is a fundamental requirement for the plants grown within it. These functions are dependent on the soil biota that maintains diverse soil organisms with high activity, retains and decomposes organic matter, which can meet the plant's nutrient demands.

Soil quality is predominantly assessed by its physical structure and chemical nutrient levels, followed by its biological components (Jing et al., 2015; Paz-Ferreiro and Fu, 2013). The composition and function of the biotic components of the soil food web are determined by resources supplied by organic matter. In agricultural systems, organic and mineral amendments can be supplied from other sources. The applied organic substrates are degraded by bacteria and fungi, that can potentially be used as indicators representing the nature of the organic matter. However, according to Ferris and Bongers (2006), available methods do not reliably indicate the soil microbial

community composition, whereas the nematodes that regulate the microbial community and enhance plant nutrition are a good indicator of substrate quality and nutrient release along the decomposition process (Christensen et al., 1992; Griffiths, 1994; Neher, 2001). Nematodes constitute a numerically important component of the soil biotic community, and their community composition follows the changes in food source availability depending on their trophic functions, which include bacterivores, fungivores, plant parasites, omnivores, and predators (Ferris and Bongers, 2006; Georgieva et al., 2005; Yeates, 2003; Yeates et al., 1993). Earlier studies have elucidated nematodes' ability to reflect changes in soil physico-chemical properties and function based on the nematode community structure (Neher et al., 1997). In agricultural management, the use of diversity indices that combine between taxa richness and evenness may contribute to elucidating the frequency of less abundant trophic groups (Ludwig and Reynolds, 1988; Neher et al., 1997). According to Wardle and Yeates (1993), the most dominant interaction in the soil food web is determined by bacteria and fungi predation and competition, that may be limited by resource quality. In agro-ecosystems, where soil bacteria and fungi are closely linked with input of organic matter, the nematode community and its trophic components are positively correlated with the amount and turnover of organic matter. Since nematodes occupy an important position in the detritus food web, they can be used as indicators for determining the effects of the different agro-managements on the soil detritus food web (Steinberger et al., 2001; Steinberger and Sarig, 1993). Application of organic materials from different sources to the soil will trigger changes in soil physical and chemical components, and in the bacterial and fungal communities, which will influence the trophic composition of the soil nematode community. Alteration between the different vineyard farming practices affects soil properties, some of which can have negative impacts on soil quality (Coll et al., 2012). Recent studies conducted in vineyard soil have elucidated the importance of the use of nematodes in soil quality determination as playing a key role in soil organic matter decomposition. Use of soil free-living nematodes, that have been presented as good bioindicators of vineyard soil quality, is based on trophic group diversity and characteristics of demographic groups such as colonizers and persisters (Bongers, 1990; Yeates et al., 1993).

The present study aimed to determine the interaction between the soil free-living nematode community structure, from both a taxonomic and a functional aspect, and how it is affected by five long-term managements in a basaltic soil in Northern Israel and to compare the soil free-living nematode community in terms of density, diversity, and functionality between the five agro-managements in the vineyard rhizosphere. The rhizosphere is recognized as a hotspot for biota activity, functioning as a precursor to soil organic matter and affecting community composition and diversity.

We hypothesized the following: (1) Organic and foliar managements that increase organic matter will stimulate bacterivores and fungivores more than conventional, open field and natural pasture; (2) In undisturbed sites, there will be a decrease in predation pressure; (3) Guilds of nematodes (bacterivores and fungivores - e.g., Cephalobidae, Aphelenchidae, Aphelenchididae, respectively) will be responsive to changes in the abundance of their food.

2. Materials and Methods

2.1 Study Site and Sampling

The soil samples were collected from five different sites, northern Golan Heights (33°04'10"N 35°46'11"E) next to Mount Shifon at 820 m above sea level. This area has a humid Mediterranean climate, with cold winters (6-8°C range in January) and hot summers (24-26°C in August). The average multiannual rainfall is 760 mm y⁻¹ (Israel Meteorological Service gov.il), and the topography of the area is slopes with a moderate gradient. A tall volcanic mound, Shifon Mountain, which creates a mountainous morphology, stands out on the surface, which is covered with a thick layer of basalt, tuff, and scoria (Dan et al., 1972). The soil is a Mediterranean reddish-brown basalt, on the slopes of the volcanic cone (Yaalon et al., 1974).

Five replicates of soil samples were collected by using a randomized sampling technique at a depth of the upper soil layer (0-10 cm) adjacent to the trunk of the vine plants rhizosphere, under five different plants, in December 2021. Each soil sample was placed in an individual plastic bag, placed in an insulation container, transported to the laboratory and stored at 4 C.

After sampling, the soils were kept with their existing moisture to minimize changes in nematode populations. Subsamples were taken from each sample for estimation of nematode populations and different soil parameters. Soil moisture was determined gravimetrically by drying samples at 105°C for 48 h and expressed as a percentage of dry weight.

Soil was sampled from five sites: 1. Merom Golan *Organic Vineyard* (MO) (33°03'50.9"N 35°45'10.6"E). This is a certified organic vineyard planted in 2014. Fertilization is based on compost, applied once every 2 years; 2. Merom-Golan Intensive – *Conventional Vineyard* (MI) (33°03'29.5"N 35°44'57.4"E). This is an intensive vineyard that was planted in 2017. Fertilization is applied according to leaf analysis and compost is applied, on

demand. Heliun (a strong long-lasting herbicide) was applied a year ago. 3. *Natural pasture* (NP) (33°03'44.4"N 35°45'06.9"E); 4. *Foliar fertilization* (FF). This vineyard was planted in 2014 (33°04'45.8"N 35°46'21.8"E). Fertilization is based on foliar application of mainly N, K and micro-Mg, Zn and compost application, without herbicide application. 5. *Open field* (OF), (33°04'45.6"N 35°46'22.5"E). Each sample included 3 replications.

2.2 Soil Free-living Nematode Community Analysis

Soil free-living nematodes were extracted using a modified Baermann funnel procedure (Cairns, 1960) with 200 g of soil. The extracted nematodes were counted under a binocular to determine the total nematode amount per 100 g dry soil. The nematodes were transferred to a 1.5 mL tube and centrifuged for 10 min at 10,000 rpm to reduce the amount of remaining water. The obtained pellets were placed at -20 °C until DNA extraction. Nematode DNA was extracted from the pellets using PureLink Genomic DNA Mini Kit (Invertogen, Thermo Fisher Scientific Inc., Waltham). The eluted DNA was stored at -20 °C until PCR amplification. DNA wase amplified by PCR using SimpliAmptm thermal cycler (Thermofischer Scientific), by mixing 12.5 µL PCRBIO HS Taq Mix Red, 9.5 µL ultrapure water. μL extracted DNA. 1 иL CS1-NF1 (ACACTGACGACATGGTTCTACAGGTGGTGCATGGCCGTTCTTAGTT) and CS2-18sr2b 1 μL (TACGGTAGCAGAGACTTGGTCTTACAAAGGGCAGGGACGTAAT). The thermal cycling program was set to: 98 °C for 30 sec, 20 cycles of 98 °C for 10 sec, 58 °C for 30 sec, 72 °C for 1.5 min, and after the cycles 72 °C for 10 min. Sequencing (Miseq) was performed at the Hylabs Laboratory Ltd. (Rehovot, Israel) (www.hylabs.co.il) sequencing facility using an Illumina sequencing platform (Illumina Inc., San Diego, CA, USA).

Data Availability Statement: The genetic data generated for this study can be found in NCBI under accession number PRJNA908721.

2.2.1 Ecological Indices and Statistical Analysis

The characteristics of the nematode communities were described by means of indices. The classification of trophic groups was assigned to: (1) bacterivores; (2) fungivores; (3) plant parasites; and (4) omnivores-predators (Liang et al., 2000; Steinberger and Sarig, 1993; Yeates et al., 1993). The nematode community was analyzed by the following approaches: (1) absolute abundance of individuals expressed per 100 g^{-1} dry soil; (2) trophic structure; (3) FB (Fungivoress/Bacterivores, or - FF/BF) reflects the structure of the microflora community. Bacteria-based food webs (lower values) exhibit higher decomposition rates than fungi-based webs (Twinn et al., 1974); (4) Wasilewska Index (WI) = ratio of (fungivores+bacterivores) to plant parasites [(FF+BF)/PP], which represent substantial changes in the trophic structure of the community, indicates the dominant pathway of mineralization (Wasilewska, 1994, 1991); (5) Shannon Index (H²), a species diversity measure which gives more weight to rare species, H'+Pi(ln Pi), where Pi is the proportion of each trophic group in the total population (Pielou, 1975); (6) trophic diversity, TD= $1/\Sigma$ P2 i, where Pi is the proportion of the individuals in the i-th trophic group (Higgins and Thiel, 1988; Neher, 2001) and describes the trophic group distribution; (7) genus dominance, $\lambda = P2i$ (Neher, 2001; Simpson, 1949); (8) modified maturity index (Σ MI), is the c-p value assigned by (Bongers, 1990) of the i-th taxon and pi is the proportion of the i-th taxon in the nematode community. The c-p values describe the nematode life strategies and range from 1 (for colonizers and individuals tolerant to disturbance) to 5 (for persisters and individuals sensitive to disturbance), including plant parasites (Yeates et al., 1994). ΣMI incorporates ecological characteristics of families based on a colonizer-to-persister scale of 1–5, where lower Σ MI values indicate more disturbed environments; (9) evenness J' = H'/ln (S), where S is the number of taxa (Simpson, 1949) and is highest when all species in a sample have the same abundance.

2.3 Statistical Analysis

The data were subjected to statistical analysis of variance using the SAS model (ANOVA and Duncan's multiple range test, T-test, genera indicator analysis and Pearson correlation coefficients) to evaluate differences between the treatments, by using the statistical package Statistica 4.3. Differences obtained at levels of p<0.05 were considered significant.

The Indicator Species Analysis was run in R using the "multipatt" function from the "indicspecies" package. This function calculates the indicator value for each genus in relation to each type of land management. For those genera that were found to be significantly different ($p \le 0.05$), we provide bar plots created in R using gplot of their relative abundance across the different land managements.

3. Results

3.1 Soil Nematode Community

3.1.1 Total Number of Nematodes

The mean total number of soil free-living nematodes ranged between 108 individuals 100^{-1} g dry soil in samples collected from the conventional management to 776 individuals 100^{-1} g dry soil (Fig. 1) in the foliar fertilization treatment. No significant differences were obtained in the total number of nematodes between the natural pasture (NP) and open field (OF) that represent control sites. The total number of nematodes in the organic (OM) management site (339.8 individuals 100^{-1} g dry soil) was almost two-fold lower compared to the FF management site (775.5 individuals 100^{-1} g dry soil).

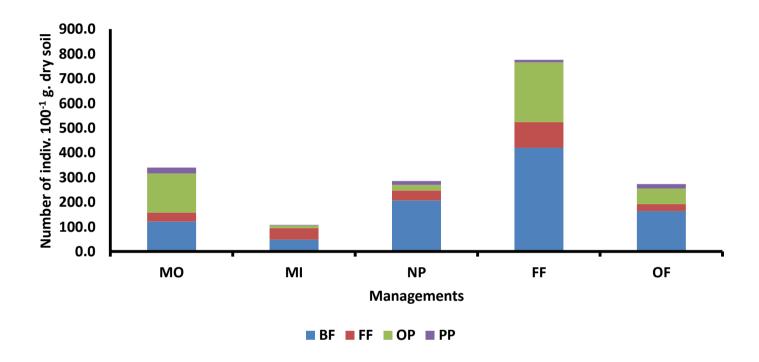


Figure 1. Total nematode abundance of the different samples, with different trophic groups in different colors MO – organic vineyard; MI – conventional vineyard; NP – natural pasture; FF – foliar fertilization; OF – Open field.

The mean percentage of bacterivores (BF) from the five sampling sites were NP > OF > FF > MI > MO, where the two control NP and OF sites showed 72 and 60% bacterivores out of the total population, followed by about 50% in the soil obtained from the foliage management. Lower values for bacterivores and fungivores were obtained in the MO (organic farming). However, the highest percentage of omnivore–predator and plant parasites were present in the MO compared to the other managements.

3.1.2 Ecological Parameters

A total of nine ecological indices (Table 1) were used to assess management differences between the sites. A relatively high variability in data was obtained, with a significant difference in the bacterivores between MI and NP (p< 0.0053), and no significant differences in FF, OP, and PP between the treatments. Moreover, as result, no significant difference was found in H' (Shannon Index). Of all the indices, only the dominance (λ) that measures the information energy elucidating that only one of a few representative individuals in the genera found in high numbers will have more dominance. In this case, the λ showed significant difference between MO and MI (p< 0.007). Only two genera showed a specific signal (Fig. 2): the Aphelenchoides in representing the MI treatment

with a p=0.034, and the Acrobeloides in the MO treatment, where the p=0.079 indicated a difference compared to the other four treatments.

Running a multilevel pattern analysis at a significance level (alpha) of p=0.05 on the total 42 genera, indicated that the only two genera were selected, where there were two associate genera in the first group, compared to the other groups, where no (zero) associate genera were found. Group number one (MI treatment) was represented by Aphelenchoides p=0.0278, and for the MO treatment, p=0.0329.

In both above cases the two genera determined the differences between the treatments.

Table 1. Mean for selected ecological indices of nematode community structure in soil samples collected from the five managements (MO – organic vineyard; MI – conventional vineyard; NP – natural pasture; FF – foliar fertilization; OF – Open Field).

	МО	MI	NP	FF	OF
BF	35.7	44.6	72.5	54.2	59.8
FF	10.6	42.4	14.2	13.3	10.3
OP	46.7	10.4	7.9	31.2	23.2
PP	7	2.7	5.4	1.3	6.6
FF/BF	0.2	1	0.2	0.4	0.4
WI	10.2	33.9	33	82	23.8
Н'	1.7	1.5	1.5	1.5	1.3
TD	0.5	0.4	0.6	0.6	0.6
λ	0.2	0.3	0.4	0.4	0.5
ΣΜΙ	3	1.9	1.6	2.2	2
J'	0.7	0.5	0.5	0.5	0.4

BF – bacteriovores- relative abundance (as percentage); FF – fungivores relative abundance (as percentage); OP – omnivores and predators' relative abundance (as percentage); PP – plant parasites relative abundance (as percentage); FF/BF – fungivores and bacterivores ratio; WI – Wasilewska Index; H' – Shannon Index; TD – trophic diversity index; λ – Simpson Index; ΣMI – sigma maturity index and J' – Evenness of nematode assemblages.

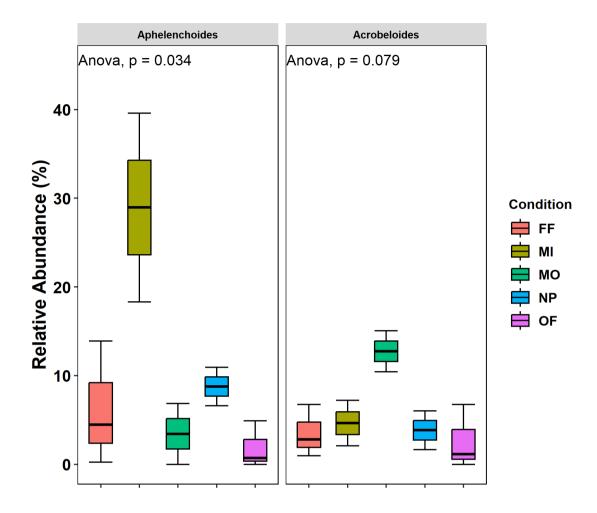


Figure 2. Relative abundance of the two genera Aphelnchoides and Acrobeloides showed specific signals: one in the MO and another in the MI treatment

The Wasilevska Index (WI) was significantly (p<0.05) higher in the FF management compared to the other managements, except for the conventional (MI) samples. This shows the significant low number of plant parasites in FF compared to MO managements. Moreover, the H' (Shannon Index) showed a significant difference between the MO (organic management) and OF (open field – natural system), without any significant difference relative to the other managements. No significant differences between the managements were observed in trophic diversity (TD). The Σ MI values in the MO management reached a maximum value which was significantly higher compared to the other managements, indicating a higher disturbance in the MO management compared to the other management relative to the other managements, with the lowest value in the OF site.

3.1.3 Nematode Taxa

A total of six orders, 22 families, 42 genera and 89 species were detected in total from all soil samples collected from the five different managements. Eleven families were found to be dominant: Plectidae, Aporcelaimidae, Panagrolaimidae, Cephalobidae, Tylenchina, Qudsianematidae, Monhysteridae, Aphelenchoididae, Mononchidae, Anguinidae, and Aphelenchidae (Table 2).

A total of 25, 23, 27, 29 and 31 genera were present in the MO, MI, NP, FF and OF soil samples, respectively, from the total of 42 genera (Table 2). Eleven of the genera belonged to seven families of bacterivores, six genera belonged to 3 families of fungivores, six families represented by 8 genera belonged to omnivores-predators and six families are represented by 17 genera belonging to plant parasites. The bacterivore genera present in all samples included *Acrobloides, Panagrolaimuns* and *Plectus*. Out of the 6 fungivore genera, four were present in all managements: *Ditylechus, Aphelenchus, Paraphelenchus*, and *Aphelenchoides*. The omnivore-predator genera

present in all soil samples included *Aporceliamellus*, *Allodorylaimuns* and *Thonus*. Five out of a total of 17 genera of plant parasites were present in all soil samples: *Anguina*, *Mothotylenchidae*, *Aglenchus*, *Basiria*, and *Tylenchus*.

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Pratylenchus + + -	Nothotylenchidae	2	Nothotylenchidae	++	++	++	+	+
	Pratylenchidae	2	Hirschmanniella	+	+			
Tylenchidae 2 Aglenchus + + + +			Pratylenchus	+			+	+
	Tylenchidae	2	Aglenchus	+	+	+	+	+

Table 2. Generic composition, feeding group composition and relative abundance (RA) of nematodes in each management

Atetylenchus	+		+		+
Basiria	+	+	+	+	+
Cephalenchus				+	
Coslenchus					+
Discotylenchus		+			
Filenchus	+		+		+
Irantylenchus	+	+		+	
Malenchus					+
Tylenchus	+	+	+	+	+
Paratylenchus	+	+	+		

+++ ->10%, ++ ->1%, + ->0%. MO – organic vineyard; MI – conventional vineyard; NP – natural pasture; FF – foliar fertilization; OF – Open field.

4. Discussion

Agricultural practices have undergone enormous changes in recent years, attempting to afford solutions to increasing demands for higher primary production, soil health maintenance, use of organic amendment, and more natural and favorable practices that should go hand-in-hand with global requests. In order to do so, attempts are made to develop novel approaches to developing and improving organic amendments. The effect of organic amendments from different sources has been reported to improve biological, microbiological, and biochemical soil characteristics such as water and nutrient holding capacity.

In the present study, the response of the soil free-living nematode community, its density, functional composition, and additional attributes that are known to be good environmental indicators were used to reveal the differences between long-term forms of managements (organic, conventional, natural pasture, foliage, and open field). Studies conducted by Werner and Dindal (1990) on the contribution of conversion to organic agriculture to soil biota has shown that soil nematodes were the most abundant in organic plots. Our results demonstrate that organic farming contributes to improving the density of microbial feeding that tends to improve nutrient resource availability. As one of the primary grazers of the saprophytic community, nematodes increase nutrient availability to primary producers (Matlack, 2001). The changes in nematode community features reflect the changes in the below-ground soil milieu, including the below-ground plant rhizosphere biosphere (Bongers and Ferris, 1999; Fitoussi et al., 2016; Neher et al., 2005). Nematode feeding group indices show the impact of the different managements on accessibility and immediate utilization of food sources (bacteria and fungi) (Yeates et al., 1993). Although the determined nematode indices cannot help in understanding or differentiating between management performances in all cases, we should prolong the use the nematode community food web structure as proposed by Martin et al. (2022). This will increase our understanding of scale row-crop agriculture.

Manipulating managements in vineyards to reduce disease and improve yields is a popular and accepted practice. Various studies have tried to link cover crops and the soil nematode community – both beneficial and pathogenic – in order to enhance the control over parasitic nematodes. Our results indicated differences in soil food web function between managements. Shifting between the three main feeding groups (bacterivores, fungivores, and omnivores-predators) were found to be according to resource availability. Soil organic matter and organic residues support fungal development, which in turn is followed by fungivore abundance and a high presence of omnivores and predators. These findings are similar to those reported by Ferris (Ferris, 2010; Ferris and Bongers, 2006) and Ugarte et al. (2013). Nematode indices which were developed based on the various functional guilds (Ferris and Bongers, 2006) were inconsistent when comparing the managements, except the Wasilevska Index which showed a sharp increase in foliage management, thus elucidating the management effect on plant parasites.

Plant endoparasitic or ectoparasitic nematodes present in grapevine have a strong effect on plant growth and virus transmission, which are widespread worldwide, without any exception of geographical region or soil texture (Aballay et al., 2009). Plant parasitic nematode families followed by their genera were found to vary between the five managements. In the Pratylechidae family, the genus *Pratylenchus* was present in organic-related management (MO, FF) and in the open field (OF) that can be attributed to development of primary production over time (Coll et al., 2012). It is known as a root lesion and pin nematode pathogen of grapevine, as reported by Zasada et al. (2012) and Howland et al. (2014). The Nothotylenchidae family, represented by the genus *Nothatylenchidae*,

was present in relatively high numbers in all managements. The Nothotylenchidae (Thorne, 1941) is a redescription of Tylenchorhynchus (Elmiligy, 1955) and is known to be a pathogen present in the vicinity of clover roots (*Trifolium alexandrinum* L.), guava (*Pisidium guave* L.), squash (*Cucurbit moscbata* Duch.), turnip (*Brassica rapa* L.), as well as near grapevine according to the results of the present study. They can also predispose roots to invasion by other plant pathogens. The main damage of plant pathogen nematodes is in a disturbance of nutrient and water uptake, thus decreasing the yield.

Soil free-living plant-parasitic nematodes are very commonly found in vineyards (Schlüter et al., 2022; Zasada et al., 2012). Permanent grass cover, different types of managements, soil aggregate and pore size distribution affect the community structure, diversity, and abundance (Ferris et al., 2001; Neher, 2001; van den Hoogen et al., 2019). Long-term organic intercrops (grass cover) negatively influence diversity, while positively affecting omnivores-predators that are sensitive to disturbances in habitat constrains related to resource availability. Studies of plant parasitic nematodes have shown that competition with arbuscular mycorrhizal and endophytic fungi and predator nematodes can control their community size.

The present study has important implications for understanding the effect of different management types on the soil free-living nematode community composition (Siddiqui and Mahmood, 1999). This study emphasizes the importance of the bacterial and fungal community that can be used as a front line against pathogens such as nematodes. As the plant rhizosphere determines the habitat structure, the different managements contribute to the physical soil pore structure, moisture availability and resource distribution. The new and different habitat structure promoted by the different agromanagements stimulates new conglomerates of the soil biota composition. This supports our findings that organic managements suppress most parasitic nematodes, similar to the finding reported by McSorley (2011). These results provide a new perspective on a time axis, where a deeper study to link grapevine plant phenology, soil biota dynamics with emphasis on soil nematode community and its functionality, and physico-chemical components, are needed to evaluate and avoid the impact of these pests on vineyard productivity.

Author Contributions

Conceptualization, Y.S. and N.R.; methodology, Y.S.; software, T.D.; validation, C.S., and N.R.; formal analysis, Y.S. and I.A.; investigation, C.S. and I.A.; resources, Y.S.; data curation, T.D.; writing—original draft preparation, Y.S.; writing—review and editing, I.A.; visualization, Y.S.; supervision, Y.S.; funding acquisition, Y.S. and N.R. All authors read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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