



Impact of land use type and organic farming on the abundance, diversity, community composition and functional properties of soil nematode communities in vegetable farming

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ABSTRACT

The excessive application of chemical fertilizers in intensively managed agricultural fields worldwide has resulted in soil degradation and biodiversity loss. This has contributed to a growing interest in sustainable management, such as organic farming. Until now, studies addressing the impact of conventional and organic management on soil biodiversity and functioning have mainly focused on arable farming and only a few reports are available on vegetable production. Vegetable farming is of particular interest, since management intensity is usually very high and there is an increasing demand for vegetable products. Soil nematodes are useful indicators of management intensity on soil ecosystem functioning because they occupy several trophic levels in soil micro-food webs and play a crucial role in nutrient cycling, pest suppression, and the regulation of microbial communities. In this study, we assessed the impact of management intensity and farming system on the community structure and functional guilds of soil nematodes, comparing 20 conventional vegetable fields, 20 organic vegetable fields, and 20 extensive grasslands in Switzerland, analyzing over 30'000 nematode individuals and detecting 98 different nematode genera. We found significant differences in the community structure and functional composition across three farming systems. Extensive grasslands contained the highest nematode abundance, followed by organic vegetable fields, and conventional vegetable fields, indicating a decline due to land-use intensification. Organic farming led to a significant increase in the abundance of herbivores (+82%), bacterivores (+206%) and omnivores (+135%) in comparison with conventional farming. Organic management also enhanced composite (+195%) and herbivores (+451%) footprints, suggesting greater carbon and energy enrichment in soil food web through these functional groups. Community composition of soil nematodes varied significantly across the three farming systems, with each farming system fostering specific indicator taxa. In conclusion, our results show that farming system has a major impact on soil nematode communities with increasing nematode populations under organic vegetable farming. Although organic vegetable production may benefit from enhanced soil fertility due to increased population densities of microbe feeding and omnivorous nematodes, the threat from plant parasitic nematodes to vegetable production requires attention and control strategies should be developed further.

1. Introduction

Soil nematodes are of particular interest in soil food webs as they are the most abundant group of multicellular organisms in the soil (van den

Hoogen et al., 2019). They occupy several trophic levels in the soil food web and can be classified into herbivores (plant parasitic nematodes), bacterivores, fungivores, omnivores and predators (Yeates, 2003). Additionally, they form complex networks with other soil biota, and

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play a crucial role in decomposition of soil organic matter, mineralization of plant nutrients and nutrient cycling (Ingham et al., 1985). For instance, nematodes regulate soil microbial communities and enhance microbial colonization through grazing on soil microbes (Villenave et al., 2004; Knox et al., 2010). Being predators and prey, nematodes also provide information about the abundance and activity of other soil organisms, and thus have been used as indicators to study soil food web conditions (Bongers and Ferris, 1999; Neher, 2001; Zhang et al., 2017), soil biodiversity and ecosystem functioning (Neher, 2001; Ferris and Tuomisto, 2015; Zhang et al., 2017).

Vegetable farming has become a major source of income for farmers worldwide. Globally, vegetable fields account for approximately 7% of the total croplands, and this percentage is usually higher in developed countries (Li and Wang, 2007). Compared to crop fields, vegetable fields are characterized by higher N application rates, more intensive production and management practices such as frequent irrigation and tillage as well as multiple planting-harvest cycles during the year (Rashti et al., 2015). For example, fertilizer inputs in vegetable production were up to 600 kg N * ha⁻¹*yr⁻¹ (Zhong et al., 2016) in comparison to 300 kg/ha of nitrogen per year in cereal cropping systems (Meng et al., 2005). Intensive agriculture has been shown to reduce soil biodiversity (Wardle et al., 1999; Postma-Blaauw et al., 2010; Tsiafouli et al., 2015), which is of utmost importance for ecosystem functioning (Bardgett and van der Putten, 2014; Wagg et al., 2014; Wall et al., 2015). Therefore, it is important to investigate how intensive farming practices may affect soil nematode communities.

Organic farming systems are typically thought to be more sustainable than conventional systems (Mäder et al. 2002; Hartmann et al., 2015; Reganold and Wachter, 2016), and organically managed farmlands have been growing to approximately 4.4 × 10⁷ ha worldwide and are expected to increase further (Bonanomi et al., 2016). This increasing trend is also true for organic vegetable farming in the Switzerland. Two global meta-analyses have shown that organic farming has a positive effect on soil biota (Bengtsson et al., 2010; Lori et al., 2017), whereas a comprehensive understanding about whether and how organic management influences soil nematode community structure and associated functions is still lacking.

Although the effects of organic farming on soil nematode have been assessed in grasslands (e.g., Yeates et al., 1997; Mulder et al., 2003), arable fields (Atandi et al., 2017; orchards (e.g., Coll et al., 2011) and vegetable fields (e.g., Ferris et al., 1996; Neher, 1999; Wu et al., 2005; Tsiafouli et al., 2006; Birkhofer et al., 2008; Benkovic-Lacic et al., 2016; Ilieva-Makulec et al., 2016), most studies are based on field experiments under homogeneous soil conditions at one particular location (e.g., Neher, 1999; Berkelmans et al., 2003; Briar et al., 2007; Quist et al., 2016). The effect of organic farming on soil nematodes may vary with soil texture (Yeates et al., 1997; van Diepeningen et al., 2006), crop species and land-use history (Quist et al., 2016; Sánchez-Moreno et al., 2018). Thus, the effects of organic farming on soil nematode community may be dependent upon spatial scale because nematode abundance and community composition can be related to edaphic and climatic variations across scales (Nielsen et al., 2014). Finally, previous studies assessing the effect of organic farming on soil nematodes often focused on single vegetable types such as tomato (Ferris et al., 1996), green peppers (Wu et al., 2005), and asparagus (Tsiafouli et al., 2006), and the comparative effect of organic farming on soil nematode communities across different vegetable types is largely unknown. Given the critical role of soil nematode in ecosystem functioning combined with increasing demands for organic vegetables, it is necessary to compare multiple field sites to obtain a robust assessment and a general understanding of how organic vegetable farming system influences soil nematodes. The wide-scale adoption of organic farming in Switzerland, particularly the Canton of Zurich with the second most licensees for organic products in 2020, provides a unique opportunity to elucidate how soil nematode communities and associated ecological processes respond to organic farming compared to conventional farming at a

larger spatial scale.

The objective of our study was to assess the impact of farming systems (organic and conventional farming) on soil quality in vegetable fields, focusing on the soil nematode community as an indicator of the soil food-web. We compared nematode communities in vegetable fields with extensively managed grasslands that do not receive any fertilizer and plant protection products. These grasslands are cut at least once per year and autumn grazing is allowed. Due to the agricultural intensification under conventional farming, organic farming and extensive grasslands represent a gradient of management intensity, representing high-, moderate- and low-intensive management, respectively. We specifically addressed the following questions: (1) to what extent does management intensity affect the abundance, diversity, community composition and functional guilds of soil nematodes? (2) What accounts for the difference in soil nematode assemblages among conventional vegetable farming, organic vegetable farming and extensive grassland? (3) Are there any nematode taxa that can be used as indicators of a specific management system?

2. Materials and methods

2.1. Experimental design and sampling

A farmer network consisting of 60 fields was established with 20 conventional vegetable fields and 20 organic vegetable fields in the Canton of Zurich. As a standard reference, 20 extensive grassland fields in close location were also selected. The conventional vegetable fields received pesticides and synthetic fertilizers and were managed according to guidelines of the federal office of agriculture. The organic vegetable fields were managed according to the guidelines of the Swiss organic farmers association (<https://bio-suisse.ch/>), including no application of synthetic pesticides or synthetic fertilizers. Grasslands were managed according to the Swiss regulations for extensively managed meadows (Zingg et al. 2019), which do not receive any fertilizer input and are mown at least once per year. In Switzerland, extensively managed meadows are considered as biodiversity promotion areas (BPA) and farmers are financially compensated by the federal government with biodiversity contributions for the adapted use of their land. Agri-environmental schemes such as the Swiss BPA were introduced in many European countries in the 1990 s (Kleijn and Sutherland, 2003) to alleviate the loss of biodiversity due to agricultural intensification. Swiss farmers must manage at least 7% of their agricultural land as BPA. The three farming systems are characterized in the Table S1 (field size, management regime duration and vegetable types at or before sampling). The soils of the fields are classified as Cambisol, which is the predominant soil type in this region (World Reference Base for Soil Resources, FAO).

The soil samples were collected in the period from 13 to 20 December 2016. At each field, we collected 10 soil cores (3 cm diameter and 10 cm deep) with a stainless steel auger. These cores were immediately homogenized and placed into a sealing plastic bag. Subsamples for soil analyses, pesticide analysis and molecular analyses were dried at room temperature, or stored at 4 °C or −20 °C (Riedo et al., 2021). In addition, a soil composite sample of approximately 20 kg of soil and consisting of ten individual soil samples was collected at each site with a shovel for nematode assessment and for the purpose of a greenhouse experiment of another study. In the laboratory, the composite sample for each site was passed through a 5 mm sieve, and visible living plant materials, visible macro-fauna (e.g., earthworms), and stones were removed. The sieved soil samples were stored in a plastic bag at 4 °C until further processing.

2.2. Soil analyses

The gravimetric soil moisture was determined with ten grams of field-moist soil samples at 105 °C for 24 h. Soil texture was determined

using hydrometer method. Briefly, the mixture of 10 g 2 mm sieved and dried soils, 150 ml water and 40 ml hydrogen peroxide were gently shaken periodically and allowed to settle for at least 12 h. Soil texture is based on the mineral content of sedimentation (the sum of clay, silt and sand = 100%). Soil clay and silt content were assessed in water suspension aliquots by sedimentation analysis, whereas sand content was estimated by the subtraction of clay and silt content from 100%. Soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were extracted by 1 M KCl (soil: solution ratio of 1:10) and were determined with a San++ Automated Wet Chemistry Analyzer-Continuous Flow Analyzer (CFA, Skalar, Holand). Soil total carbon (TOC) and nitrogen (TN) were analyzed by combustion of the samples on pure oxygen and selective determination of resulting gaseous products using TruSpec CN Analyzer (LECO, MI, USA). Soil organic carbon (SOC) content was analyzed by potassium-dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$) oxidation method. Soil pH was determined with a glass electrode in 1:2.5 (weight: volume) soil: water solution. Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were measured by the chloroform fumigation method (Vance et al., 1987; Joergensen, 1996; Joergensen and Mueller, 1996). Chloroform fumigation was performed in triplicate on 20 g of soil samples. Soils were incubated for 24 h and were extracted with 80 ml of a 0.5 M K_2SO_4 solution. Microbial activity was estimated from basal respiration, which was quantified by measuring the carbon dioxide released in the process of microbial respiration during 10 days of incubation (Fernandes et al., 2005).

2.3. Quantification of bacterial and fungal abundance

Soil DNA was extracted with two replicates of 0.5 g of soil using NucleoSpin soil kit (MACHEREY-NAGEL GmbH & Co. KG, Germany) following the manufacturer's instructions. Two technical replicates were combined to obtain 100 μL DNA. DNA concentrations were determined by the NanoDrop 1000 spectrophotometer (Thermo Fisher Scientific, USA). Once the yield and quality were determined, DNA samples were standardized using nucleus free water to obtain 100 μL at a concentration of 5 ng/ μL . PCR was performed using the reagent mix 5X PRIMER HotMasterMix (Quantabio, Beverly, MA, USA), the iCycler Thermal Cycler (Bio-Rad Laboratories, CA, USA) and Gel Electrophoresis using 1% Agarose LE gel (Promega Corporation, WI, USA). The abundance of bacterial 16S rRNA gene was estimated using quantitative PCR with 338F-518R primers (Ovreås et al., 1997). Thermal cycling conditions for bacterial 16S rRNA were, initial denaturation at 95 °C for 15 min, followed by 40 cycles of 95 °C for 30 s, 60 °C for 30 s, 72 °C for 45 s; and melt curve at 65–95 °C. The fungal ITS gene was quantified using the primer set ITS1F-ITS2R (Gardes and Bruns, 1993; McGuire et al., 2013). The thermal cycling conditions were, initial denaturation at 95°C for 15 min, followed by 30 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 45 s; and melt curve at 65–95 °C. Standard curves were obtained using serial dilutions of linearized plasmids containing cloned genes amplified from bacterial and fungal strains. Standard curves linear over four orders of magnitude and r^2 values of 0.99 or higher were selected. The efficiency of the reaction was between 63% and 112% (based on the slopes of the standard curves). All samples and standards were run with three replicates. The specificity of the amplified products was assessed with melting curve analysis.

2.4. Nematode extraction and identification

Nematodes were extracted from 150 g of field-moist composite soils for each field using the modified sucrose centrifugation-flotation method (Jenkins, 1964). To reduce the variation of due to soil heterogeneity, we used three technical replicates for each soil sample when extracting and identifying nematode. The total number of nematodes was counted under low magnification (50 $\times$), and population size was expressed in terms of individuals per 100 g of dry weight soil. Subsequently, 200 specimens per sample were randomly selected and identified to the genus level when possible using the higher magnifications

(400 $\times$ or 1000 $\times$) of an inverted compound microscope for better reproducibility. If the specimen of a sample was less than 200, all the individuals were identified. The length and width of each specimen were measured with an ocular micrometer. Identified nematode taxa were then arranged into the trophic groups, namely bacterivores, fungivores, herbivores (plant parasitic nematodes), omnivores and predators, based on morphology of the stoma and oesophagus (Yeates et al., 1993; Bongers and Bongers, 1998; Yang et al., 2014, 2017). The groups were ordered according to the colonization-persistence gradient (c-p values) (Bongers, 1990; Bongers and Bongers, 1998; see Supplemental Text 1) and assigned to functional guilds by combining trophic groups with c-p values.

Nematodes biomass was estimated as $w = (L^3/a_2)/1.6 \times 10^6$, where the w is the fresh weight (μg) of each specimen, L is the nematode length (μm), and a represents the length to maximum body diameter ratio of nematodes (Zhang et al., 2012). The nematodes metabolic footprints (NMFs) provide metrics for the effect size of ecosystem functions and services provided by component organisms of the soil food web (Ferris, 2010). The NMFs are based on the calculation of the lifetime amount of carbon used by nematode taxa in growth and egg production and in carbon losses with respiration following the formula: $\text{NMF} = \sum (N_i(0.1w^{\text{wt}}/mt) + 0.273(w^{0.75}))$, where W_t and mt stand for the body weight and colonizer-persister (cp) values of genus t , respectively (Zhong et al., 2017). The enrichment and structure footprint is the metabolic footprint of lower (c-p value of 1–2) and higher (c-p value of 3–5) trophic levels, respectively (Neher et al., 2004; Ferris, 2010). NMF can be computed either for specific trophic group (herbivores-, bacterivores-, fungivores-, omnivores- and carnivores-footprint) or for the functional groups (enrichment-, basal- and structural- footprint) of whole nematode community.

The composite metabolic footprint (CMF, μg^2) was calculated as $\text{CMF} = \frac{(F_s + F_e)}{2}$, where F_s and F_e represent the sum of standardized C labile by structured and enrichment indicator taxa, respectively, with a high CMF to suggest nematode assemblage store high amount of soil carbon (Ferris, 2010). Nematode specified ecological indices, such as plant parasite index (PPI), maturity indices (MI), basal index (BI), channel index (CI), enrichment index (EI) and structure index (SI) were also calculated (Yang et al., 2014). The NMFs and ecological indices were obtained by submitting soil nematode array to NINJA-Nematode Indicator Joint Analysis (beta) (Sieriebriennikov et al., 2014), which is also provided in <http://plpnemweb.ucdavis.edu/nemaplex>. Further details about the different indices used to characterize nematode communities are given in the Supplemental Text 1.

2.5. Statistical analyses

Effects of farming system on variables including total nematode abundance, abundance per trophic group, nematode diversity indices, maturity indices, food web indices and metabolic footprints of soil nematodes were analyzed using one-way ANOVA with farming system as the fixed factor in R (R Core Team, 2018). Before analysis, the normality and the homogeneity of the residuals for data were examined by Shapiro-Wilk test or by Kolmogorov-Smirnov test in the 'stats' package. When the assumption of ANOVA of a given variable was violated, the effect of farming system on this variable was examined with non-parametric Kruskal-Wallis test. When the effect of farming system on a given variable was significant, difference between treatments was further compared with a post-hoc test by the Tukey's Honestly Significant Difference (HSD) test or the Wilcoxon Signed Rank test at $\alpha = 0.05$ level. A Pearson correlation analysis was used to evaluate relationships between abiotic soil characteristics and nematode abundance as well as between microbial properties and nematode abundance. Community composition of soil nematodes across the three farming systems were compared with Bray-Curtis similarity using the canonical analysis of principal coordinates (CAP) and per-mutational

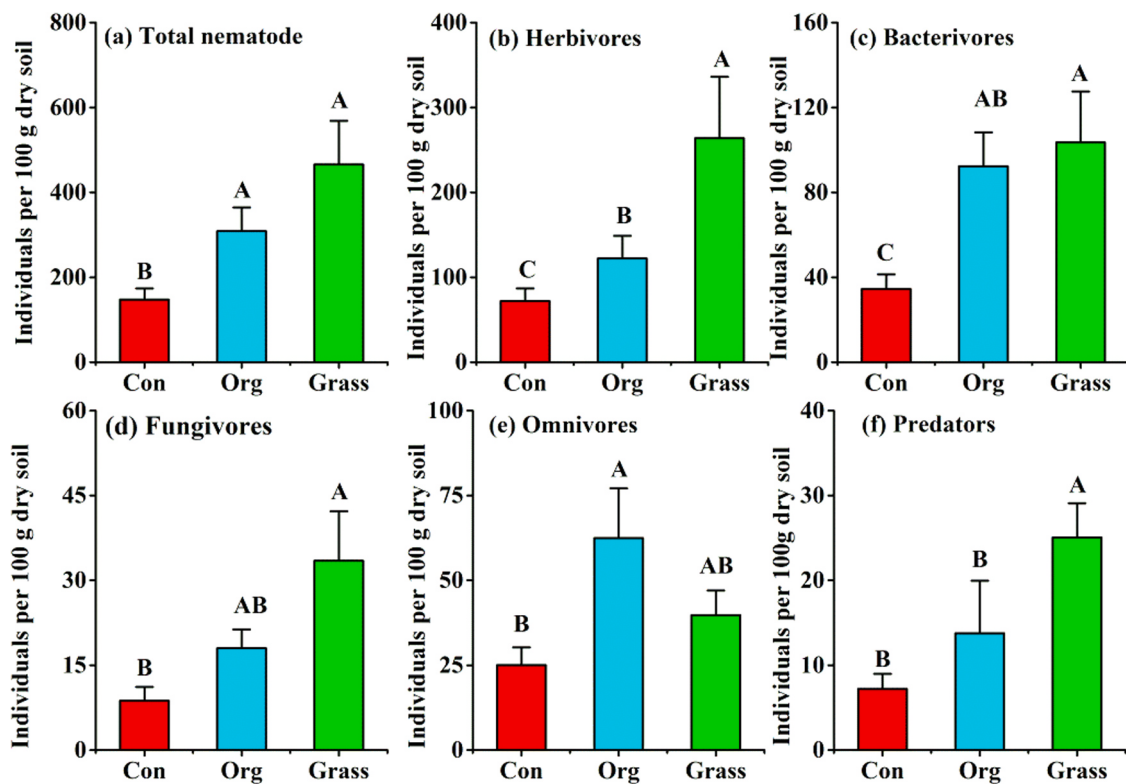


Fig. 1. Abundance of total nematodes and individual trophic groups (individual number of nematodes/100 g dry soil) in the topsoil of conventional vegetable fields (Con), organic vegetable fields (Org) and extensively managed grasslands (Grass) in Switzerland. Different uppercase letter indicates no statistically significant ($P < 0.05$) difference between the management intensity groups.

multivariate analysis of variance (PERMANOVA) with 999 permutations using the 'vegan' packages in R. Finally, we identified potential habitat specialists or indicator taxa for conventional vegetable fields, organic vegetable fields and grasslands, using the indicator species analysis. The indicator species approach identifies a given taxa that tends to be present mostly in a single habitat type and most of the samples from that habitat based on the relative frequency and average abundance, and thus implies the nematode taxa preference for a given environmental condition. Specifically, the clusters were categorized by farming system (conventional vegetable farming, organic vegetable farming and extensive grasslands,) in the analysis. Indicator species for each cluster were identified using the 'multipatt' function in the 'indicspecies' package in R (Roberts, 2007). For each of the three farming systems, taxa with a p -value ≤ 0.05 and IndVal > 0.30 were selected as potential indicator species. IndVal analysis was performed on soil nematode dataset.

3. Results

3.1. Abundance and drivers

Farming system exerted significant effects on nematode abundance,

with the highest abundance occurring in grasslands, followed by organic vegetable fields and the lowest numbers occurring in conventional vegetable fields (Fig. 1; Table S2). Vegetable production, regardless of conventional or organic vegetable production, reduced predator abundance in comparison with grasslands ($P < 0.005$). Conventional vegetable production reduced the abundance of herbivores, bacterivores and fungivores in comparison with grasslands (Wilcoxon Rank Sum Test: Herbivores ($P < 0.0006$); Bacterivores ($P = 0.003$); Fungivores ($P = 0.003$)) and organic vegetable production (Wilcoxon Rank Sum Test: Herbivores ($P = 0.03$); Bacterivores ($P = 0.003$); Fungivores ($P = 0.05$)). Omnivore abundance was higher in organically managed fields compared to conventionally managed fields (Wilcoxon Rank Sum Test: $P = 0.02$). Nematode abundance was positively correlated to gravimetric soil moisture, SOC, TN, $\text{NH}_4^+\text{-N}$, MBC and MBN, and the correlation coefficients varied depending on the trophic group of soil nematode examined (Table S3; Fig. S1). However, there were weak correlations between microbial feeding nematodes and microflora (Fig. S2).

Table 1

Genera richness (S), Margalef richness (SR), Shannon-Weaver index (H'), Simpson dominance index (λ), Pielou index (J') of soil nematode communities in soils of conventional vegetable fields, organic vegetable fields as well as grasslands in Switzerland.

Variable	Conventional vegetable	Organic vegetable	Extensive grassland	χ^2	P
S	22.0 $\pm$ 2.1c	28.0 $\pm$ 1.6 b	34.3 $\pm$ 1.5 a	11.57 *	< 0.0001
SR	4.00 $\pm$ 0.29b	5.00 $\pm$ 0.25ab	6.00 $\pm$ 0.26 a	5.788 *	0.005
H'	2.4780 b	2.7780 ab	2.9360 a	7.9859	0.018
λ	0.0800 a	0.0935 a	0.1205a	3.9461	0.139
J'	0.8320 a	0.8415 a	0.8540 a	0.7149	0.700

Note: *, F-value of one-way ANOVA. Different lowercase letters among different columns indicate significant difference between treatments based on the TukeyHSD Tests or the Wilcoxon Rank Sum Tests.

Table 2

Maturity index of free-living nematode (MI), maturity index of free-living nematode with a c-p value of 2–5 (MI_{2–5}), maturity index of combined plant parasitic nematode and free-living nematode (sigma maturity index: Σ MI), plant parasite index (PPI), basal index (BI), channel index (CI), enrichment index (EI), structure index (SI), decomposition and nutrient mineralization pathway represented by Fungivore/(Fungivore+Bacterivore), and primary production weighted by (Fungivore+Bacterivore)/Herbivore in soils of conventional vegetable fields, organic vegetable fields as well as grasslands in Switzerland.

Variable	Conventional vegetable	Organic vegetable	Extensive grassland	χ^2	df	p
MI	3.03 ± 0.11 a	2.98 ± 0.12ab	2.66 ± 0.12 b	3.218*	2	0.047
MI _{2–5}	3.39 ± 0.10 a	3.22 ± 0.11 a	3.42 ± 0.07 a	1.312*	2	0.277
Σ MI	2.78 a	2.78 a	2.70 a	2.2804	2	0.3197
PPI	2.71 a	2.63 a	2.75 a	3.1319	2	0.2089
PPI/MI	0.84 b	0.92 ab	1.01 a	3.801	2	0.026
BI	16.07 a	11.59 ab	5.62 b	13.796	2	0.001
CI	19.23 a	20.00 a	11.01 a	1.9064	2	0.3855
EI	49.90 b	48.05 b	85.59 a	23.143	2	<0.0001
SI	87.59 ab	81.16 b	91.22 a	8.4291	2	0.0148
Fu/(Ba+Fu)	0.17 ± 0.03ab	0.14 ± 0.02 a	0.26 ± 0.03 a	5.474*	2	0.007
(Ba+Fu)/Herb	0.67 a	0.86 a	0.46 a	3.6998	2	0.1573

Note: *, F-value of one-way ANOVA. Different lowercase letters among different columns indicate significant difference between treatments based on the TukeyHSD Test or Wilcoxon Rank Sum Tests.

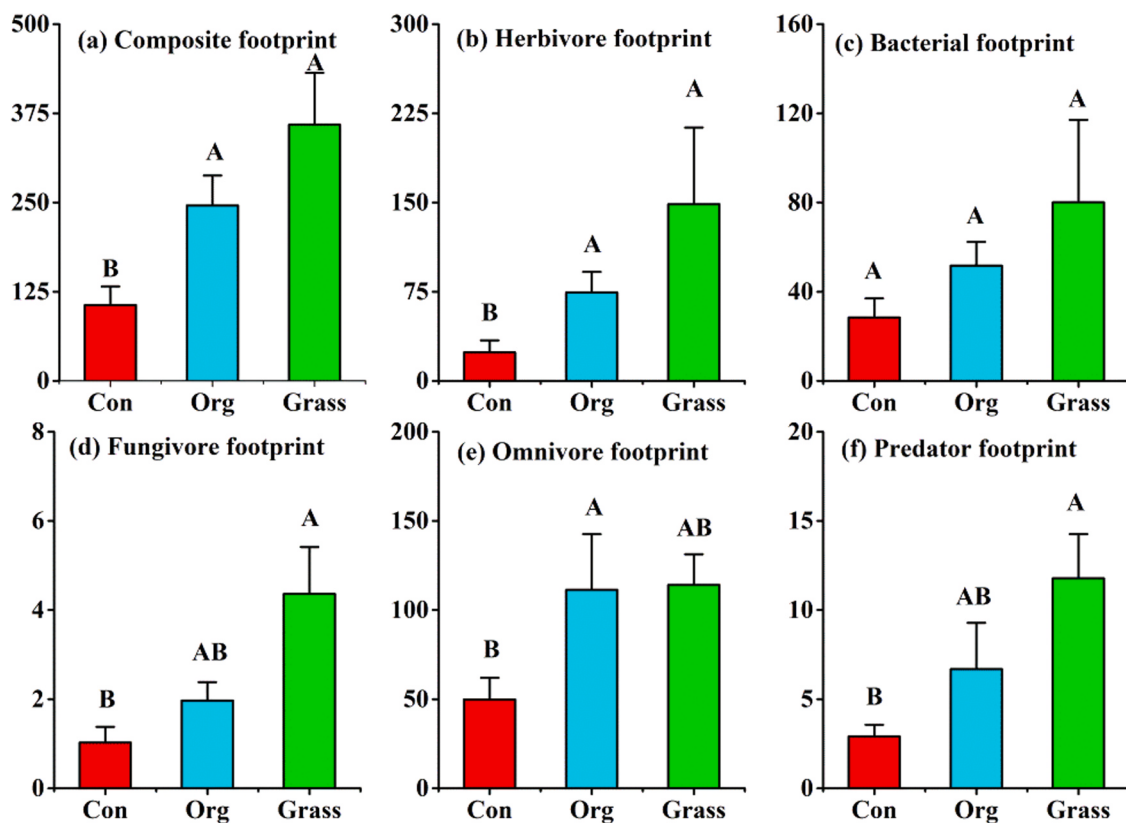


Fig. 2. Metabolic footprints of soil nematodes in the topsoil of conventional vegetable fields (Con), organic vegetable fields (Org) and extensively managed grasslands (Grass). Different uppercase letter indicates no statistically significant ($P < 0.05$) difference between the farming system groups.

3.2. Taxa richness, diversity and soil food web indices

The taxa richness (S), Margalef's richness (SR) and Shannon-Weaver diversity index (H') strongly responded to farming system (Table 1). The S , SR and H' in grasslands were consistently the highest, followed by organic vegetable fields, and the lowest occurring in conventional vegetable fields. By contrast, the Simpson dominance index (λ) and the Pielou evenness index (J') showed a comparable level among conventional vegetable fields, organic vegetable fields and grasslands (Table 1).

Neither maturity indices (including Σ MI, MI_{2–5}, PPI) nor the CI of soil nematode community responded to farming system ($P > 0.05$, Table 2). Other variables examined varied greatly among farming systems (Table 2). The BI and the EI in vegetable fields were significant

lower than those of grasslands, whereas the opposite is true for the maturity index of free-living nematode community (MI). Organic vegetable management did not change the ecological indices and the condition of soil food web in comparison with conventional vegetable management. The PPI/MI and the SI in organic vegetable fields were significant lower than grasslands, whereas there was no significant difference for these variables between conventional vegetable fields and grasslands and between two contrasting management vegetable fields (Table 2).

3.3. Metabolic footprints

The composite footprint, herbivore footprint, bacterivore footprint,

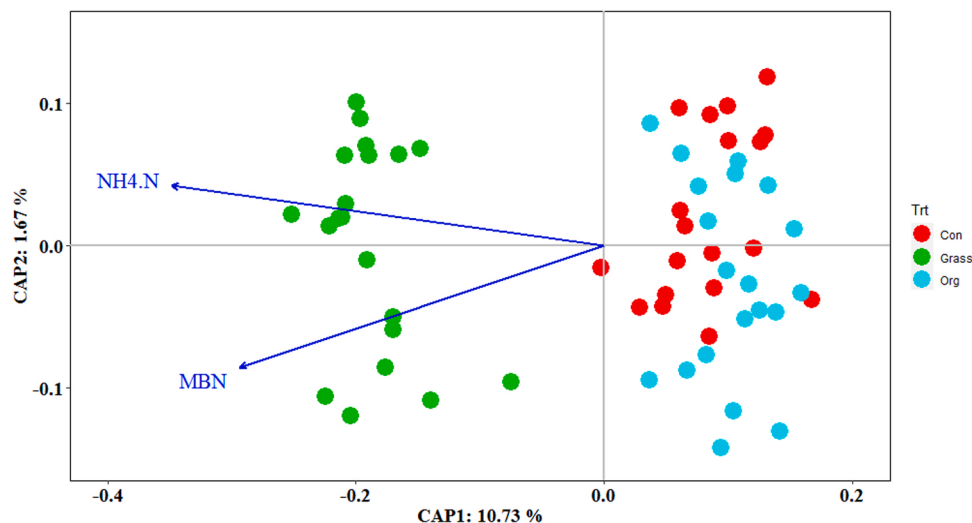


Fig. 3. Canonical analyses of principal coordinates (CAP) of the Bray-Curtis similarity matrix of soil nematode assemblage showing the clustering of soil nematode communities in topsoil of the three farming system groups: conventional vegetable fields (Con), organic vegetable fields (Org) and extensively managed grasslands (Grass).

fungivore footprint, omnivore footprint, predator footprint and enrichment footprint strongly varied among the farming systems, whereas the structure footprint showed a comparable level among conventional vegetable fields, organic vegetable fields and grasslands (Fig. 2; Table S4). The composite footprint (Wilcoxon Rank Sum Tests: $P = 0.0002$), herbivore footprint (Wilcoxon Rank Sum Tests: $P < 0.0002$), fungivore footprint (Wilcoxon Rank Sum Tests: $P < 0.0001$), omnivore footprint (Wilcoxon Rank Sum Tests: $P = 0.02$) and predator footprint (Wilcoxon Rank Sum Tests: $P = 0.002$) and structure footprint (Wilcoxon Rank Sum Tests: $P = 0.005$) of nematodes in conventional vegetable fields were significantly lower than those in extensively managed grasslands. In vegetable fields, organic management significantly increased composite footprint (Wilcoxon Rank Sum Tests: $P = 0.006$) and herbivore footprint (Wilcoxon Rank Sum Tests: $P = 0.001$) in comparison with conventional management (Fig. 2a and b; Table S4) (Fig. 3).

3.4. Community composition and indicator taxa

Over 100 genera were extracted from soil samples, including 35 genera of plant parasites, 29 genera of bacterivores, 10 genera of fungivores, 14 genera of omnivores and 12 genera of predators (Table S5). There were significant differences in soil nematode communities across conventional vegetable fields, organic vegetable fields and grasslands (PERMANOVA: $df = 2$, $F = 4.97$, $P = 0.001$; Fig. S3), and soil nematode community composition was linked to soil $\text{NH}_4^+\text{-N}$ (adjusted $R^2 = 0.11$, $F = 8.1522$, $P = 0.001$) and MBN (adjusted $R^2 = 0.12$, $F = 2.0489$, $P = 0.003$). Indicator species analysis revealed that each farming system fostered specific soil nematode taxa (Table 2). The *Heterodera*, *Tylenchus*, *Boleodorus*, *Paralongidorus*, *Tylencholaimus* and *Mylonchulus* were common to organic vegetable fields and extensively managed grasslands. The *Chiloplacus*, *Filenchus*, *Plectus*, *Rhabditis*, *Microdorylaimus*, *Mesodorylaimus*, *Dorylaimellus*, *Psilenchus*, *Heterocephalobus*, *Rotylenchus*, *Paratylenchus*, *Pararotylenchus* were specific to vegetable fields. The *Hemicriconemoides*, *Scutylenchus*, *Protorhabditis*, *Aphelenchus*, *Mesorhabditis*, *Prismatolaimus*, *Pungentus*, *Tylenchorhynchus*, *Dorylaimus*, *Pelioditis*, *Monhystrella*, *Nothotylenchus*, *Pelodera*, *Anatonchus*, *Oxydirus*, *Trichodorus*, *Criconema*, *Paratiripyla*, *Tylencholaimellus*, *Diphtherophora*, *Longidorus*, *Diploscapter*, *Labronema*, *Teratocephalus* and *Loofia* were more common in grasslands, whereas the *Eucephalobus* was specific to organic vegetable fields.

4. Discussion

Although the effect of organic management on soil nematode communities has been explored in previous studies, most of these studies were performed with field-trials (e.g., Neher, 1999; Berkelmans et al., 2003; Quist et al., 2016). The strength of field-trials is that farming treatments are assessed under a standardized management at one location and with a specific soil type. However, management effects on nematode communities may differ in actual farmlands and thus the results obtained at a single site cannot be generalized.

Environmental problems that may be associated with the increase in vegetable production with its intensive management practices is a concern, particularly negative impacts on biodiversity, leaching of nutrients into drinking water, or emissions of greenhouse gases. However, we still have a limited understanding of how soil biota such as nematode respond to vegetable production practices at the farm scale where soil type and nutrient availability are of higher heterogeneity. The present study reports the impact of vegetable management practices on soil nematode communities across many fields at a regional scale analyzing a total of 60 fields. Our results suggest that organic management alters overall community characteristics of soil nematodes. The abundances of herbivores, bacterivores and omnivores were greatly enhanced by organic management in comparison with conventional management (Fig. 1b, c & e). Organic management also enhanced composite footprint and herbivore footprint (Fig. 2a & b), indicating that organic farming supports higher herbivore abundance and herbivorous nematode individuals of higher biomass. Moreover, organic farming in vegetable fields resulted in notable shifts in soil nematode community despite of no obvious change in soil food-web index represented by BI, CI, EI and SI, decomposition and nutrient mineralization pathway represented by the $\text{Fu}/(\text{Fu}+\text{Ba})$ and primary production represented by $\text{Herb}/(\text{Fu}+\text{Ba})$ between conventional vegetable fields and organic vegetable fields (Table 2). This indicates that there are no significant change in soil ecological processes and functions provided by the nematode communities in organic and conventionally managed fields in Switzerland. However, variation among fields was large and further studies need to verify our observation.

The observed higher abundance and biomass of total nematodes in soils under organic farming compared to conventional farming in our study is consistent with an earlier field experiment where organic management supported higher nematode abundance and biomass compared to conventional management in vegetable fields (Ferris et al.,

1996; Overstreet et al., 2010). We also found that the total nematode abundance in vegetable fields was lower than that in grasslands (Fig. 1a; Table S2). This result supports a previous report showing that the land transformation from grassland to agricultural use reduces soil biota (Postma-Blaauw et al., 2010; Overstreet et al., 2010). Soil biota in extensive grasslands is generally subjected to fewer disturbances, such as tillage and/or pesticides application compared to arable fields, particularly vegetable fields. Moreover, higher plant diversity and litter coverage in grasslands usually retain higher soil moisture, and thus favour soil nematode colonization and reproduction. Overall, our results suggest a negative impact of land-use intensification on soil nematode abundance. Compared to the conventional farming systems, organic farming systems contained increased population densities of micro-bivorous and omnivorous nematodes. However, the threat of plant-parasitic nematodes to vegetable production, especially in organic vegetable production should be given attention, and integrated management strategies should be further developed and implemented (Briar et al., 2007; 2016).

In agreement with previous studies (Ferris et al., 1996; Coll et al., 2011; Hallmann et al., 2007; Sánchez-Moreno et al., 2018), we found a higher abundance of herbivores, bacterivores and omnivores in organic vegetable fields, compared to conventional vegetable fields (Fig. 1b, c & e; Table S2). Previous studies proposed that the intensive application of mineral fertilizer in conventional farming systems reduced bacteria-feeding nematodes (Bulluck et al., 2002) due to direct toxicity of nitrogen solutions (Fiorentini and Portelli, 2004). Besides, intensive agriculture may alter the biotic interactions and patterns of resource availability in ecosystems (Matson et al., 1997). Such disturbance would further affect nematode abundance by changing the growth and reproductive capacity of nematodes directly and indirectly. As hypothesized, we found that the correlations among edaphic properties, microbial attributes and nematode abundance depended on the trophic group of nematode examined. Interestingly, nematode abundance was found to be positively correlated with $\text{NH}_4^{+}\text{-N}$ in the present study (Fig. S1). Note that further work is needed to confirm our observations because we only sampled once and the sampling was conducting at the end of the growing season. Moreover, we sampled to a soil layer in depth of 10 cm while other studies sampled to a depth of 30 cm. This may also affect the nematodes detected.

The EI indicates the prevalence of opportunistic species, whereas the metabolic footprint measures the carbon utilization of component taxa (Ferris, 2010). Previous studies report that crop residue retention increases EI and SI (Ferris, 2010; Ito et al., 2015; Zhong et al., 2017). We hypothesized that greater levels for these variables in soils would be observed in organic vegetable fields due to increased residue inputs in organic management compared to conventional management. Against expectation, we found the EI and SI in soils under organic management were comparable to those under conventional management. However, the composite metabolic footprint and herbivore footprint in soils under organic management was greatly enhanced in comparison to conventional management, implying vegetable fields under organic management supported herbivores with larger body size and higher biomass.

The observed comparable level in Shannon-Weaver index between organic management and conventional management in the present study is in disagreement with earlier studies demonstrating that the application of organic manure resulted in a decline in Shannon-Weaver index possibly due to the predominance of r-selected species (Ferris et al., 1996; Bulluck et al., 2002). One possible reason is that there are greater differences in mulch treatment which has been found to reduce the total number of nematode genera in organic vegetable fields (Porazinska et al., 1999) across studies. Another likely explanation is that the effect of organic farming on the richness of nematodes might be time-dependent. A previous study found that organic vegetable farms were more diverse in terms of genera of herbivores than conventional farms at the vegetative and/or reproductive stage (Pascual et al., 2017). However, in the present study, farmers could not allow us to sample

Table 3

Specific genera and common genera of soil nematodes for conventional vegetable fields, organic vegetable fields and grasslands based on indicator species analysis using soil nematode community composition of 60 samples.

Management intensity group	Indicator	IndVal	p-value
Grasslands	<i>Hemicriconemoides</i>	1.000	0.001
Grasslands	<i>Scutylenchus</i>	0.922	0.001
Grasslands	<i>Rotylenchulus</i>	0.921	0.001
Grasslands	<i>Protorhabditis</i>	0.91	0.001
Grasslands	<i>Aphelenchus</i>	0.841	0.001
Grasslands	<i>Mesorhabditis</i>	0.837	0.001
Grasslands	<i>Prismatolaimus</i>	0.818	0.001
Grasslands	<i>Pungentus</i>	0.802	0.001
Grasslands	<i>Tylenchorhynchus</i>	0.755	0.028
Grasslands	<i>Dorylaimus</i>	0.74	0.002
Grasslands	<i>Pellioiditis</i>	0.703	0.013
Grasslands	<i>Monhystrella</i>	0.702	0.001
Grasslands	<i>Nothotylenchus</i>	0.684	0.001
Grasslands	<i>Pelodera</i>	0.676	0.001
Grasslands	<i>Anatonchus</i>	0.666	0.004
Grasslands	<i>Oxydiris</i>	0.655	0.001
Grasslands	<i>Trichodorus</i>	0.632	0.001
Grasslands	<i>Criconema</i>	0.622	0.001
Grasslands	<i>Paratrypa</i>	0.592	0.002
Grasslands	<i>Tylencholaimellus</i>	0.582	0.005
Grasslands	<i>Diphtherophora</i>	0.503	0.031
Grasslands	<i>Longidorus</i>	0.502	0.019
Grasslands	<i>Diploscapter</i>	0.49	0.032
Grasslands	<i>Labronema</i>	0.468	0.032
Grasslands	<i>Teratocephalus</i>	0.459	0.028
Grasslands	<i>Loofia</i>	0.447	0.029
Organic vegetable fields	<i>Eucephalobus</i>	0.712	0.002
Vegetable fields	<i>Chiloplacus</i>	0.848	0.001
Vegetable fields	<i>Filenchus</i>	0.837	0.001
Vegetable fields	<i>Plectus</i>	0.835	0.001
Vegetable fields	<i>Rhabditis</i>	0.806	0.001
Vegetable fields	<i>Microdorylaimus</i>	0.755	0.001
Vegetable fields	<i>Mesodorylaimus</i>	0.742	0.001
Vegetable fields	<i>Dorylaimellus</i>	0.738	0.001
Vegetable fields	<i>Psilenchus</i>	0.735	0.001
Vegetable fields	<i>Rotylenchus</i>	0.713	0.037
Vegetable fields	<i>Heterocephalobus</i>	0.676	0.029
Vegetable fields	<i>Paratylenchus</i>	0.57	0.022
Vegetable fields	<i>Pararotylenchus</i>	0.524	0.041
Grasslands & Organic vegetable fields	<i>Heterodera</i>	0.87	0.001
Grasslands & Organic vegetable fields	<i>Tylenchus</i>	0.807	0.007
Grasslands & Organic vegetable fields	<i>Boleodorus</i>	0.785	0.008
Grasslands & Organic vegetable fields	<i>Paralongidorus</i>	0.637	0.02
Grasslands & Organic vegetable fields	<i>Tylencholaimus</i>	0.632	0.026
Grasslands & Organic vegetable fields	<i>Myonchulus</i>	0.626	0.014

when their fields had fully grown vegetables, and thus herbivores can be difficult to detect due to unfavorable climatic factors and limited food at the harvest of vegetables.

Previous study suggested that shifts in community composition of soil organism are usually accompanied by changes in the functioning of soil food webs (Morriën et al., 2017). The ratio of fungi to bacteria (F/B) indicates soil microbial shifts, whereas the $\text{Fu}/(\text{Fu}+\text{Ba})$, reflects the decomposition and nutrient mineralization pathway due to microbial feeders for a given ecosystem. Small ratios are associated with faster decomposition and nutrient turnover. We observed no difference in the ratio of fungivore to bacterivore. This finding is in line with previous studies suggesting no difference in $\text{Fu}/(\text{Fu}+\text{Ba})$ ratio between conventional and organic fields (Neher, 1999). It is possible that the effects of organic farming on the $\text{Fu}/(\text{Fu}+\text{Ba})$ depend on the ecosystem type.

The PPI, MI, and PPI/MI are valuable indicators used to evaluate agricultural ecosystems conditions (Freckman and Ettema, 1993; Ferris et al., 1996; Neher and Campbell, 1996; Bongers et al., 1997). In the present study, PPI was unaffected by the management intensity whereas MI and PPI/MI ratio were significantly affected. Previous studies also reported mixed results with some studies reporting higher values for both variables under organic farming than conventional farming (Sánchez-Moreno et al., 2018) whereas another study reporting that

organic farming increased the PPI, but did not affect the MI and PPI/MI (Neher, 1999). One likely reason may be that the effect of organic management on MI varies with depending on crop type. However, other factors, such as soil type, plough depth, cover crop type, and the management history might also contribute to the divergent effects of organic farming on nematode assemblage (van Diepeningen et al., 2006). For example, land transformation from grasslands to arable fields under intensive management results in a reduced the MI of soil nematode community (Bongers and Ferris, 1999; Postma-Blaauw et al., 2010), whereas the conversion from grasslands to vegetable fields did not change MI (Stirling et al., 2010). It is possible that the effect of organic farming on PPI varies depending on sampling time (Neher, 1999). Anyhow, our results suggest that PPI/MI can be a useful indicator of soil ecological quality of vegetable farming.

We found that the three farming systems fostered specific nematode assemblages (Table 3). In line with other studies (Hallmann et al. 2007; Briar et al. 2016; Pascual et al., 2017), the *Rotylenchus* was found associated with vegetable in both organic and conventional farms. Regarding the *Eucephalobus*, previous study suggested it was sensitive to the direct effect of tillage (Fiscus and Neher, 2002), and there is a noticeable difference in tillage between organic and conventional vegetable fields. Therefore, it is reasonable to be regarded as indicator taxa for organic farming system. The occurrence of nematodes specific to a given management likely indicates habitat filtering and community assembly due to eco-physiological preferences. Since the observed effects of management intensity on soil nematode community are based on one sampling event, and thus more sampling events during the vegetable growing season may be needed to explore the seasonal consistency of our findings. Nonetheless, the results were obtained from 60 field sites with different soil properties and management practice. Therefore, observed patterns can be generalized at least for this time because data are independent of a given location or a specific management regime.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107488.

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