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Quantification of the global impact of agricultural practices on soil nematodes: A meta-analysis

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ABSTRACT

Agricultural practices significantly affect soil biodiversity and functions, altering biogeochemical cycles and potentially compromising food production. Increased employment of sustainable agricultural practices is of growing policy concern and requires a better understanding and quantification of how agriculture affects soil functioning. We conducted a worldwide meta-analysis by computing 4855 effect sizes from 103 publications to quantify the effect of agricultural practices on soil nematodes, known to be key biological indicators of soil health. Our meta-analysis summarized the effects of tillage, pesticides use, fertilization, manipulation of above-ground plant including cover crop, rotation and agricultural system shift (the conversion from the conventional to conservation or organic agriculture systems). We quantified how each agricultural practice alters nematode indices of ecological relevance including the absolute abundance of trophic groups, the taxonomic richness and diversity and the food web structure based on functional guilds. At the global level, organo-mineral fertilization, conservation system, cover crop and nematicides exhibited the greatest effect sizes (averaged all nematode indices) while herbicides, plant association, mineral fertilization and tillage had the lowest ones. At the level of trophic groups, the agricultural practices had varying impacts, e.g. crop rotation mainly reduced the abundance of the plant-feeding nematodes (−47%), cover crop mainly increased the abundance of omnivore-predators (+80%) while organic fertilization predominately promoted bacterial (+113%) and fungal feeders (+141%). Crop rotation reduced the absolute abundance of plant feeders by 47% when the rotation is longer than 2 years. At the community level, chemical inputs, monoculture and pesticide application reduced nematode abundance, the food web structure and favoured copiotrophic nematode communities. Biocides and nematicides reduced total abundance, Shannon diversity and the food web complexity of soil nematode (structure index). Using meta-regressions, our meta-analysis revealed that the effect of agricultural practices depends on the time since the last agricultural intervention (e.g. input of fertilizers, pesticide application) and on how long a practice has been adopted. This study will be a useful aid for decision maker to better manage soil nematode community and to identify gaps in current available literature. In providing the direction and magnitude of soil nematode responses to agricultural practices, the effect size produced by this study are critical in facilitating worldwide modelling of soil biodiversity under global change scenarios.

1. Introduction

We are currently experiencing a profound human-induced extinction of life on Earth (Dirzo et al., 2014; Ceballos et al., 2015; Young et al., 2016). One of its main causes is agriculture, which constitutes a major threat to soil biodiversity and function (Foley et al., 2005; Tsiafouli et al., 2015; Bender et al., 2016; Molotoks et al., 2018; Tibbett et al., 2020), with the potential to compromise sustainable food production to humankind (Azadi et al., 2011; Dobermann and Nelson, 2013; McKenzie et al., 2015). We still lack understanding of how soil biodiversity responds to agricultural practices at the global scale and to what extent agro-ecological practices can be beneficial for soil health. This is of

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growing policy concern and detrimental to moves towards an agriculture that preserves and promotes soil biota and function (Tsiafouli et al., 2015).

Nematodes are cosmopolite highly abundant invertebrates on Earth (van den Hoogen et al., 2019). In soils, these microscopic worms are a dominant component of the active community and occupy multiple positions in the soil food web (Yeates et al., 1993). Their fundamental roles in carbon flows (Sohlenius, 1980; Jiang et al., 2018), in biogeochemical cycling (Bardgett et al., 1999; Trap et al., 2016) and in changing the activity and composition of the soil microbial populations (Mamilov et al., 2000; Knox et al., 2004; Irshad et al., 2012) directly contribute to soil functioning. Their functional feature and pivotal role in the biogeochemical cycle makes nematodes key indicators of soil health and they have been used extensively in environmental monitoring for almost three decades (Bongers, 1990; Bongers and Ferris, 1999; Neher 2001; Shao et al., 2008; Reeves et al., 2014; Gao et al., 2020). This has been possible thanks to the relevant ecological indices (Maturity Index, Plant Parasite Index, Enrichment Index and Structure Index), developed by nematologists, directly related to the soil functioning (Bongers, 1990; Ferris et al., 2001).

Much work has been done on the effect of agricultural practices on soil nematodes. Not exhaustively, the response of nematodes to agricultural practices is well documented regarding the different types of agricultural systems (Freckman and Ettema, 1993; Neher, 1999b; Djigal et al., 2012; Henneron et al., 2015; Karimi et al., 2020), physical and chemical disturbance (Neher et al., 1995; Fiscus and Neher, 2002; Zhao and Neher, 2013), herbicides (Yeates et al., 1999; Zhang et al., 2002; Zhao et al., 2013) or fertilization (Villenave et al., 2003; Agyarko et al., 2005; Ferris and Bongers, 2006; Liu et al., 2016). Soil nematode communities have also been extensively compared between agricultural ecosystems and unmanaged ecosystems (Wasilewska, 1979; Neher, 1999a; Villenave et al., 2001; Ponge et al., 2013; Pothula et al., 2019). Briefly, conventional agriculture profoundly alters the composition, taxonomic richness and size of soil nematode populations (Liu et al., 2016) likely through reducing local plant diversity (De Deyn et al., 2004), disturbing surface soil by plowing (Zhang et al., 2019) and creating nutrient disorders through fertilization (Liu et al., 2016). While the slow-growing omnivore nematode species involved in pest regulation (Devi et al., 2018) seem the most susceptible to disappearance (Bongers and Bongers, 1998), plant-parasitic species, which cause significant damage to crops (Jones et al., 2013), are quickly selected by conventional practices (Bongers et al., 1997). In contrast, alternative cropping systems such as conservation agriculture and organic farming could offer more suitable conditions for free-living nematodes, possibly by enhancing soil water-holding capacity and organic matter content, known to greatly increase soil biota abundance (Schnurer et al., 1986; Briar et al., 2012; Henneron et al., 2015; Margenot et al., 2016, Van Den Hoogen et al., 2019).

These trends must be quantified at the global scale to evaluate to what extent agricultural practices constitute threats to soil biodiversity and health. Recent efforts have been done to synthetize the global response of soil nematodes to soil fertility management (Liu et al., 2016), herbicides (Zhao et al., 2013) or on land-use changes (Pothula et al., 2019; Li et al., 2020). However, a meta-analysis that quantifies and ranks the distinct effects of the main worldwide agricultural practices on nematode is still missing. Using a meta-analysis to quantify the effect of each agricultural practice on nematodes exhibits benefits over a qualitative narrative reviewing because (i) it provides the size of the effect, and allows ranking of these effect sizes, (ii) it offers the possibility to weight the studies according to their inherent variability (more weight for studies with narrower interval of confidence) (iii) it allows exploring the potential of co-variables (moderators) to explain the variance of the effect size. We believe that a quantitative understanding of the impact of the common worldwide agricultural practices on soil nematode communities is necessary to simulate potential trajectories of soil health, guiding the future of agriculture management.

The study aimed to quantify the impact of a set of agricultural practices on soil nematode communities using meta-analysis modeling. Our main hypotheses are (H1) agricultural practices affect soil nematode communities in different ways (e.g. tillage affects large nematodes, while managing plant diversity shapes plant-feeding nematode communities) (H2) shifting the type of agricultural system (e.g., conventional *versus* organic systems), has a more pronounced effect on the nematode community because it integrates the impact of several distinct practices. Our meta-analysis summarized the effects of tillage, pesticides use, fertilization, manipulation of above-ground plant including cover crop, rotation and agricultural system shift (the conversion from the conventional to conservation or organic agriculture systems). To evaluate the effect of agricultural practices on soil nematodes, we employed absolute abundance of nematodes in trophic groups (Yeates et al., 1993), taxonomic richness and diversity, and the widely used nematode ecological indices (Bongers, 1990; Ferris et al., 2001).

2. Methods

2.1. Literature search and data collection

This meta-analysis followed the PRISMA guidelines (Fig. 1) and recommendations from Vetter et al. (2013) and Gurevitch et al. (2018). We collected data from studies investigating the effect of agricultural practices on soil nematodes. Studies should include nematode data and evaluate the effects of at least one of the four main agricultural practices (manipulation of plant diversity, pesticide use, tillage, fertilization) or those of different types of agricultural systems ("system") on the nematode community, as defined in Table 1.

To reach this goal, we conducted a literature search, last updated in October 2019, using the Web of Science (Thomson Reuters) search engine. Studies of interest were identified based on the following search string: "nemat* AND (legum* OR "cover crop" OR cover-crop OR agro OR legum* OR fallow OR arable OR crop OR perennial OR agroecosystem OR rotation OR association OR agrofor* OR "plant diversity" OR diversity OR weeds OR cultiv* OR intensi* OR manag* OR unmanag* OR intercropping OR "agricultural practices" OR agri* OR "agrochemicals" OR "biological control" OR interculture OR Leguminous OR pesticide* OR nematicide OR solariz* OR biofumigation OR "chemical control" OR "catch crop" OR disinfect*OR carbofuran OR input* OR nutrient* OR ferti* OR amend* OR compost* OR residue* OR litter OR addition manur* OR addition* OR nitrogen OR phosphorus OR conservati* OR compaction OR tilla* OR working OR plough* OR plow*)". We used this search string to find articles based on the title or abstract of the article. We obtained a result of 3884 articles (Fig. 1). To complete our literature search, we allowed for discrete inclusions of relevant publications before the screening process (see Fig. 1). To facilitate article screening, we uploaded the literature search results to the reference management software EndNote (version X8, Clarivate Analytics).

2.2. Inclusion criteria

We first screened all the sampled articles (3925) based on their titles and abstracts and discarded articles considering only one plant-parasitic nematode species (e.g., *Meloidogyne* sp.), review articles, studies conducted in greenhouses, in unmanaged ecosystems (forests or savannah) and articles not on the soil system (e.g., fresh water). After this first step of the selection, 465 articles (Fig. 1) were screened according to inclusion criteria:

(1) Data should be available in the articles either in table or in graphical forms. In the case of graphics, the programme GetData Graph Digitizer (version 2.26 http://getdata-graph-digitizer.com/), was used to extract data from figures.
(2) Nematode data should be a measurement of the abundance of nematode trophic groups, that is bacterial feeding (BF), fungal

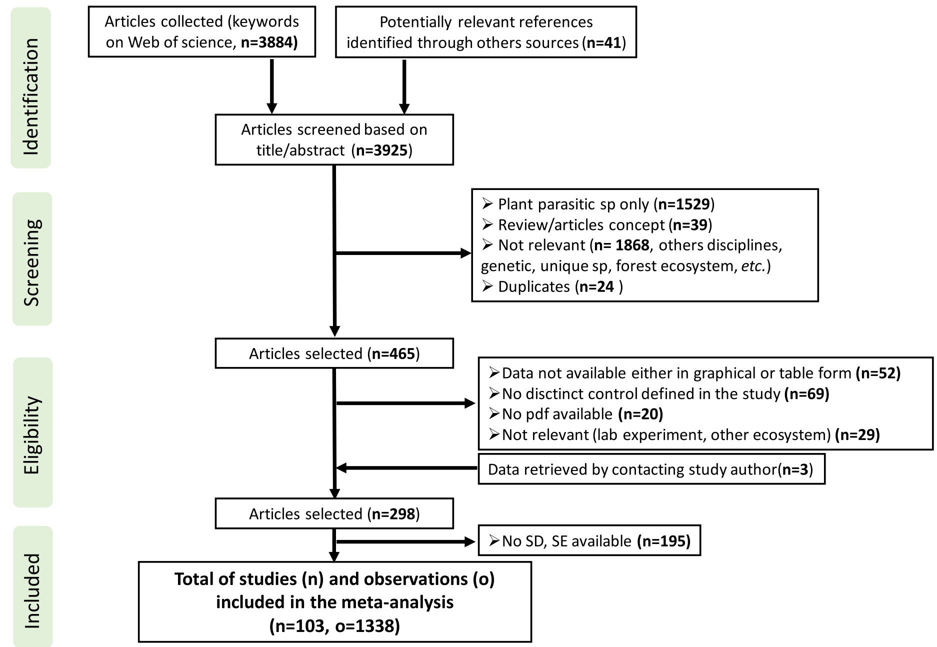

Fig. 1. The PRISMA Flow Diagram. "n" = number of papers; "o" = number of observations.

feeding (FF), omnivores and predators (OP) and plant feeding nematodes (PF), and/or nematode diversity and/or nematode indices as described in previous studies (Bongers, 1990; 1999; Ferris et al., 2001; G. W. Yeates et al., 1993). Diversity indices were taxonomic richness (S) and Shannon diversity (H′). Nematode indices were the maturity index (MI), plant-parasitic index (PPI), structure index (SI), enrichment index (EI), and nematode channel ratio (NCR). Studies had to report at least one of the abovementioned nematode parameters to be included in our synthesis.

(3) Studies needed to evaluate the effects of at least one of the four main agricultural practices: managing plant diversity (rotation, cover crop and association), pesticide input (herbicide, biocides and nematicide), tillage, organic and mineral fertilization (Table 1). Plant diversity management included rotation, i.e. succession of different crops over time, association, i.e. field combining plants of different species such as intercropping, cover crop, i.e. soil covered by living plants (Table 1). We discarded any experimental data reporting multiple treatments combined into one, e.g., treatment (fertilization + tillage) *versus* control (no fertilization and no tillage) to avoid confounding effects. The effect of pesticide application, fertilization, tillage and plant diversity management (Table 1) had to be clearly distinct and identifiable with a control and an associated treatment. The effect of agricultural systems, that is the conversion of conventional agriculture to conservation or organic agriculture, include several distinct practices (Table 1) and had to be defined as such by the authors. Conservation agriculture is based on no-tillage and cover crop; pesticides are use only when necessary. Conventional systems use pesticide, mineral fertilizers and tillage. Organic agriculture does not use synthetic pesticide and mineral fertilizers. Tillage is used for weed management.

(4) The samples should be collected from the topsoil layer (soil depth between 0 and 30 cm maximum).

(5) Studies needed to report means ($\bar{X}$), standard deviations (SD) or standard errors (SE) and sample size (n, number of true replications) of nematode variables in control and treatment groups. When SD, SE or sample size were missing, articles were discarded as these data are required to compute the effect size (Vetter et al., 2013; Gurevitch et al., 2018). A total of 103 articles, i.e. 30% of articles (Fig. 1), met these inclusion criteria and were used in the meta-analysis, corresponding to a total of 1338 unique observations (control + treatment, Fig. 2). The list of these articles is given in Supplementary Table 2.

2.3. Data check & homogenization

Collected data were first subjected to a double check to avoid potential errors made by manual entering. Outliers were checked (due to potential data entry error) by ranking all "effect sizes". We also checked if the same data from one study were reported in different publications and none duplicated data were found (Supplementary Materials). Due to different units and ways of reporting data between articles, data were converted and homogenized into the same units. When only the relative abundance of each trophic group together with the total nematode abundance was reported, we back-calculated the absolute abundance of nematode groups (number of individuals per kg of dry soil). For articles reporting the abundance of nematodes per volume of soil, we converted the value into a number of individuals per kg of dry soil using a bulk density of 1.3 g cm^3 and a soil water content of 15% (Heuscher et al., 2005; Dorigo et al., 2012). The majority of the studies gathered omnivore and predator taxa within a single trophic group. Therefore, we pooled the absolute abundances of omnivores and predators into one group (omnivore-predators) when studies presented distinct abundances for these taxa. If only the standard error (SE) was reported, we calculated the standard deviation (SD) as follows: $SD = SE.\sqrt{n}$ (Altman and Bland, 2005).

2.4. Collecting associated metadata

For each study, we extracted generic metadata corresponding to the GPS location; mean annual temperature (MAT); mean annual precipitation (MAP); soil pH; total soil organic carbon (SOC); soil texture as a percentage of sand, silt and clay or as a qualitative description provided in the article (sandy, loamy, clay); soil sampling depth; time since the experiment started (experiment duration); time since treatment (e.g., time since fertilizer or pesticide application); and soil total nematode abundance in the control. When GPS coordinates were not reported, we

Table 1
Description of agricultural practices and their respective modalities tested in the meta-analysis.

Practice types	Practices	Controls	Treatments	Description (effect of)
Fertilization	Inorganic[a]	No fertilization	Input of mineral fertilizers	Mineral fertilization
	Organic[b]	No fertilization	Input of organic fertilizers	Organic fertilization
	Combined	No fertilization	Input of mineral + organic fertilizers	Fertilization including mineral and organic fertilizers
Plant diversity	Rotation[c]	Monoculture	Rotation of 2 years or more	Rotation
	Association[d]	Monospecific crop	≥2 plant species	Plant richness
	Cover crop[e]	Bare soil	Presence of crop	Plant presence versus bare soil
Pesticides	Herbicides	No pesticide	Input of herbicide	Herbicide
	Biocides[f]	No pesticide	Input of biocide (except nematicide)	Biocide but no nematicide
	Nematicides[g]	No pesticide	Input of nematicide (alone or with biocide)	Nematicide, alone or with biocide
Tillage	Conventional[h]	No-till	Deep tillage (>10 cm)	Conventional tillage
	Conservation[i]	No-till	Surface tillage (<10 cm)	Conservation tillage
	All type	No-till	Tillage	Tillage
System	Conservation[j]	Conventional system[k]	Conservation agriculture	Conversion from conventional to conservation agriculture
	Organic[l]	Conventional system	Organic agriculture	Conversion from conventional to organic agriculture
	All types	Conventional system	Alternative system	Conversion from conventional to organic or conservation systems

[a] Concerns N (sodium nitrate or ammnonium nitrate), NP (ammonium phosphate), NK, P alone, NPK or urea.
[b] Concerns cattle manure, pig manure, poultry droppings, composts, residue (straw or soybean meal) and vermicomposts, biochars, biosolids, sludge.
[c] The frequency and the rotation duration are co-variables. The presence of legumes in the rotation is possible.
[d] In associations, this can be an annual or perennial species. The presence of legumes is possible.
[e] Perennial or annual crop.
[f] Bactericide, fungicide, insecticide, fumigation or broad-spectrum pesticide or cocktails.
[g] Usually fosthiazate, 1,3-Dichloropropene, terbufos or carbofuran.
[h] Deep tillage with soil turning, using mechanization (usually rotary harrow) or not.
[i] Superficial soil working without soil turning.
[j] Conservation agriculture is usually based on no-tillage and cover crop; pesticides are use only when necessary.
[k] Conventional systems use pesticide, mineral fertilizers and tillage.
[l] Organic agriculture does not use synthetic pesticide and mineral fertilizers. Tillage is use for weed management.

extracted GPS coordinates based on the name of the location given in the article. Climate data (MAP & MAT) were extracted using WorldClim global climate datasets (10 km resolution) derived from the geographic location (Fick and Hijmans, 2017). Additionally, we collected metadata corresponding to specific agricultural practices as follows: the presence of legumes for plant diversity that is known to affect the soil nematode communities (Blanchart et al., 2006; Bagayoko et al., 2000; DuPont et al., 2009), the dose of organic carbon (C), mineral and organic nitrogen (N), total potassium (K) and mineral phosphorus (P) for fertilization (in kg/ha).

2.5. Effect size calculation

To determine the effect of agricultural practices (as defined in Table 1) on each nematode community index, we computed the effect size using the natural-log response ratio (lnRR; Hedges et al., 1999; Lajeunesse, 2011). This ratio quantifies the natural-log proportional change in the means of a treatment and control group (Hedges et al., 1999). We employed "escalc" in the Metafor package (Viechtbauer, 2010) implemented in R (R Core Team, 2019) to calculate the effect sizes (equation (1)) and their respective variance (equation (2)) as follows:

$$\mathrm{lnRR} = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) \tag{1}$$

$$\mathrm{var(RR)} = \frac{(SD_t)^2}{n_t \overline{X}_t^{\,2}} + \frac{(SD_c)^2}{n_c \overline{X}_c^{\,2}} \tag{2}$$

where $\overline{X}$, SD and n represent the mean, standard deviation and sample size, respectively, of the control (c) or the treatment group (t). To express the effect size as a percentage, we used equation (3):

$$\mathrm{lnRR\ \ (expressed\ \ in\ \ percentage)} = (e^{lnRR} - 1) \times 100 \tag{3}$$

In total, we computed 4855 effect size (Table S1).

2.6. Statistical modelling

To calculate the combined effect size and its corresponding variance, we used a multilevel meta-analysis model (mixed model) run with the "rma.mv" function from the Metafor package (Viechtbauer, 2010). The model was fed calculated effect sizes and sampling variances (as described above) and fitted via restricted maximum-likelihood estimation. As we obtained multiple effect size values per study (e.g., several sampling dates), we used a mixed model with "study identification" (study ID) as a random factor to take into account the dependencies among estimates from the same study. To estimate the overall effect of agricultural practices on nematode variables under investigation, we first ran a random-effects model without any moderator variables. This model was run for i) every type of agricultural practice and its respective subgroups and ii) each type of agricultural system (as defined in Table 1). The responses of the nematode community parameters were statistically significant if the 95% confidence intervals of the agricultural effects did not overlap zero. The average response ratios were tested for heterogeneity using the QE statistic (Hedges and Pigott, 2004; Viechtbauer, 2010). When the QE was significant (P-value < 0.05), moderators have been added in the models to explain this heterogeneity. When the QE was not significant, we did not perform further models with moderators (corresponding to 15% of the models, Table S2).

To further determine whether the collected metadata (moderators) explained the heterogeneity of effect sizes, we used a mixed model with moderator variables as a fixed factor and 'study ID' as a random factor. This second mixed-model was run separately for each moderator variable under study (Table 2). Levels of significance for meta-regressions were adjusted and corrected with the truncated product method for combining P-values (Zaykin et al., 2002). Publication bias was first evaluated by conducting a visual inspection of the funnel plot (x-axis: observed effect sizes; y-axis: standard error) to identify asymmetrical distributions and heterogeneity. Asymmetry of effect sizes was tested using the variance of effect size "VI" as a moderator in the meta-analysis model that was run with the "rma.mv" function (Egger's test; Jennions et al., 2013). Overall, 65% of our effect sizes were not significant,

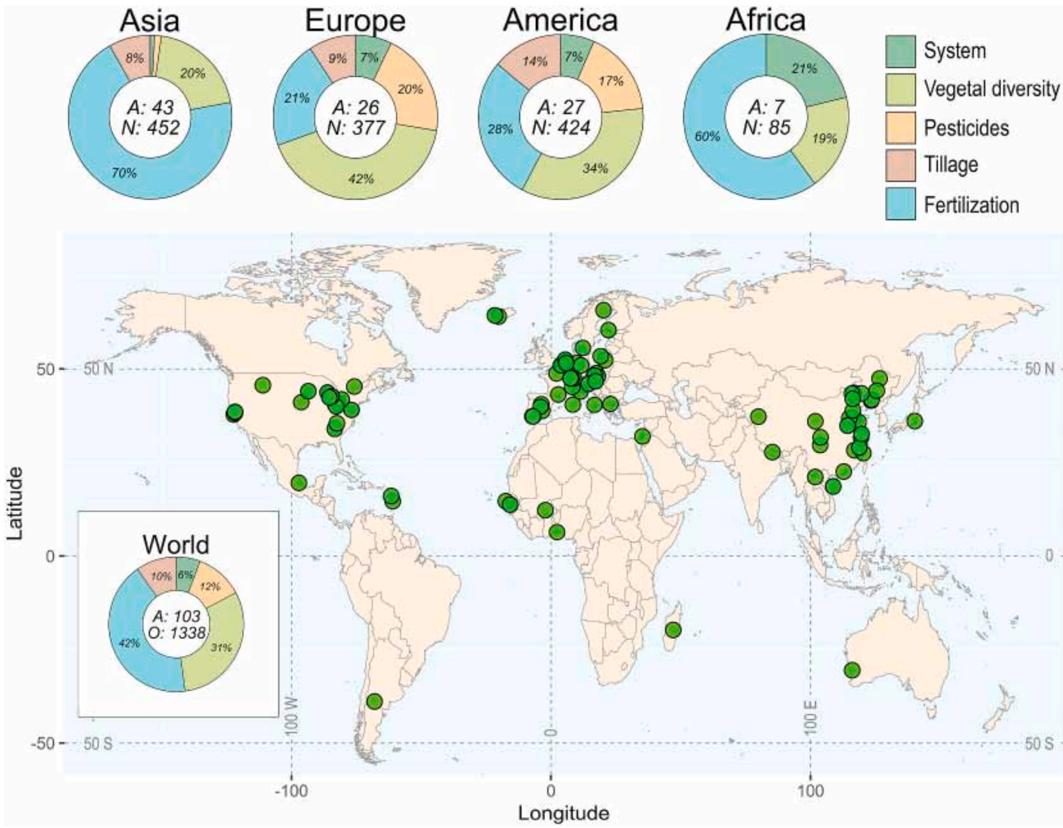

Fig. 2. Donut charts illustrating the percentages of observations per agricultural practice within each region and a worldwide map showing the distribution of studies (green circles) per continent and agricultural practices. In the centre of the donut, "A" and "N" indicate the total number of articles and observations, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

indicating that publication bias (e.g., a statistically significant result is more likely to be published) was unlikely in our meta-analysis. This approach was completed using Rosenberg's fail-safe number (Rosenberg, 2005), which yielded the number of studies with an effect size of zero that would need to be included to overturn the result. The Rosenberg's fail-safe number for each model was on average 6256 (657 times the number of observations), indicating that our results are robust. We, however, found 3 models (1.7% of the total number of models) presenting effect size distribution asymmetry and a Rosenberg's fail-safe number corresponding to less than 3 times the number of observations collected in this meta-analysis (pesticide biocide-MI model, Rosenberg's number = 20; pesticide nematicide-SI model, Rosenberg's number = 14; agricultural system conventional-MI model, Rosenberg's number = 161). The effect sizes of these models were not interpreted.

3. Results

Compiling a total of 1338 observations, we quantified the effects of the main agricultural practices on the soil nematode communities at the global scale (Fig. 2). The majority of the observations were collected from America (32%), Europe (28%) and Asia (34%), while Africa (6%) was poorly represented (Fig. 2).

3.1. Fertilization

We combined 64 studies (561 observations, 42% of total observations) on mineral, organic or mineral + organic combination. We showed that, overall, the supply of mineral fertilizers did not significantly affect the absolute abundance of soil nematodes not the absolute abundance of the trophic groups but it marginally reduced taxonomic richness, diversity and food web stability (S: 7.2%, H': 3.7% and MI: 7.7%, respectively; Fig. 3A). The enrichment index (EI) was the only nematode parameter that significantly increased following inorganic fertilization (+14.4%; Fig. 3A). The sampling time after fertilization and the amount of fertilizers (in kg/ha) significantly explained the effect size of inorganic fertilization on the nematode community (Table 2, Supplementary Table 1). For instance, taxonomic richness was more affected by inorganic fertilizers when high inorganic N amounts were applied ($R^2 = 0.35$, P-value < 0.001; Fig. 4A).

In contrast, the application of organic fertilizers strongly enhanced the total abundance of nematodes (+69.8%), originating from the increase abundance of all trophic group, although not significant for plant-feeding nematodes (Fig. 3A). The amount of organic fertilizer significantly changed the effect of organic fertilization on nematode parameters, such as omnivore-predator abundance (Supplementary Table 1). Organic fertilization also promoted taxonomic diversity (+8.7%), but induced a significant decrease in the maturity index (−6.5%). Similar patterns were observed when inorganic and organic fertilizers were applied together (Fig. 3A). However, mixed fertilization induced lower NCR and SI values (−10.2% and −22.0%, respectively; Fig. 3E).

3.2. Plant diversity

A total of 414 observations focusing on plant diversity-based agricultural practices (rotation, association, cover crop) were included in our study, corresponding to 31% of the total observations. A key result from our statistical analysis was a significant reduction in the absolute abundance of plant feeders (PF, −47.2%) without impacting the total abundance or the abundance of other trophic groups (Fig. 3B) when a rotation of more than 2 years was applied. This negative effect of rotation on the abundance of plant feeders increased with the duration of the experiment (Fig. 4B). Rotation also promoted taxonomic richness

Table 2
Results of the meta-regressions for each agricultural practice. The symbols (+) or (−) indicate the positive or negative direction of the effect of an agricultural practice on soil nematode (reminder of Fig. 2 results). The symbols ▲ or ▼indicate if the moderator amplifies or reduces the observed effect of an agricultural practice on soil nematode parameters. The reading must be horizontal. For instance, inorganic fertilization negatively affected (−) nematode taxonomic richness (S) and this negative effect is amplified (▲) when mean annual precipitation (MAP) increases.

Practices	Moderators[a]								
	Climate		*Soil*			*Nematode*	*Experimental protocol*		
	Mean Annual Temperature	Mean Annual Precipitation	pH	Carbon	Texture	Total abundance in the control	Duration	Time since last agricultural activity	Soil depth
Fertilization									
Inorganic fertilization		S*(−)▲				MI***(−)▼	MI***(−)▲	MI***(−)▲	H'***(−)▲
						S***(−)▼		EI**(+)▲	
						EI***(+)▼			
Organic fertilization		H'***(+)▲		FF*** (+)▲	H'*** (+)▲	TN***(+)▲	TN*** (+)▲	TN***(+)▼	MI*** (−)▲
		FF***(+)▲		H*(+)▲	MI*(−)▲	BF***(+)▲		BF***(+)▼	
		TN***(+)▲		BF*(+)▲		FF***(+)▲		FF***(+)▼	
						OP**(+)▲		H'***(+)▼	
						MI***(−)▲		OP**(+)▼	
Combined	BF*(+)▼	BF***(+)▼			SI*(−)▲	TN***(+)▲	TN**(+)▲	SI**(−)▼	
		FF***(+)▲					SI**(−)▼		
Plant diversity									
Rotation			EI* (+)▲	PF*** (−)▲	PF*** (−)▲		PF***(−)▲		
Association		MI***(−)▼					MI***(−)▼		
Cover crop		PF***(+)▲				PF*(+)▲		BF***(+)▲	
Pesticides						H'*(−)▼		PPI**(+)▼	
Tillage						MI***(−)▲			
						OP***(−)▼			
System		OP***(+)▲				TN***(+)▲	EI***(+)▲		
						BF***(+)▲			
						EI**(+)▼			

Significant thresholds: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
[a] Mean annual temperature (MAT) and precipitation (MAP); Total nematode density (TN); bacterial-feeder density (BF); fungal-feeder density (FB); omni-predator density (OP); plant-feeder density (PF); taxonomic richness (S); plant parasite index (PPI); maturity index (MI); structure index (SI); Shannon diversity index (H′).

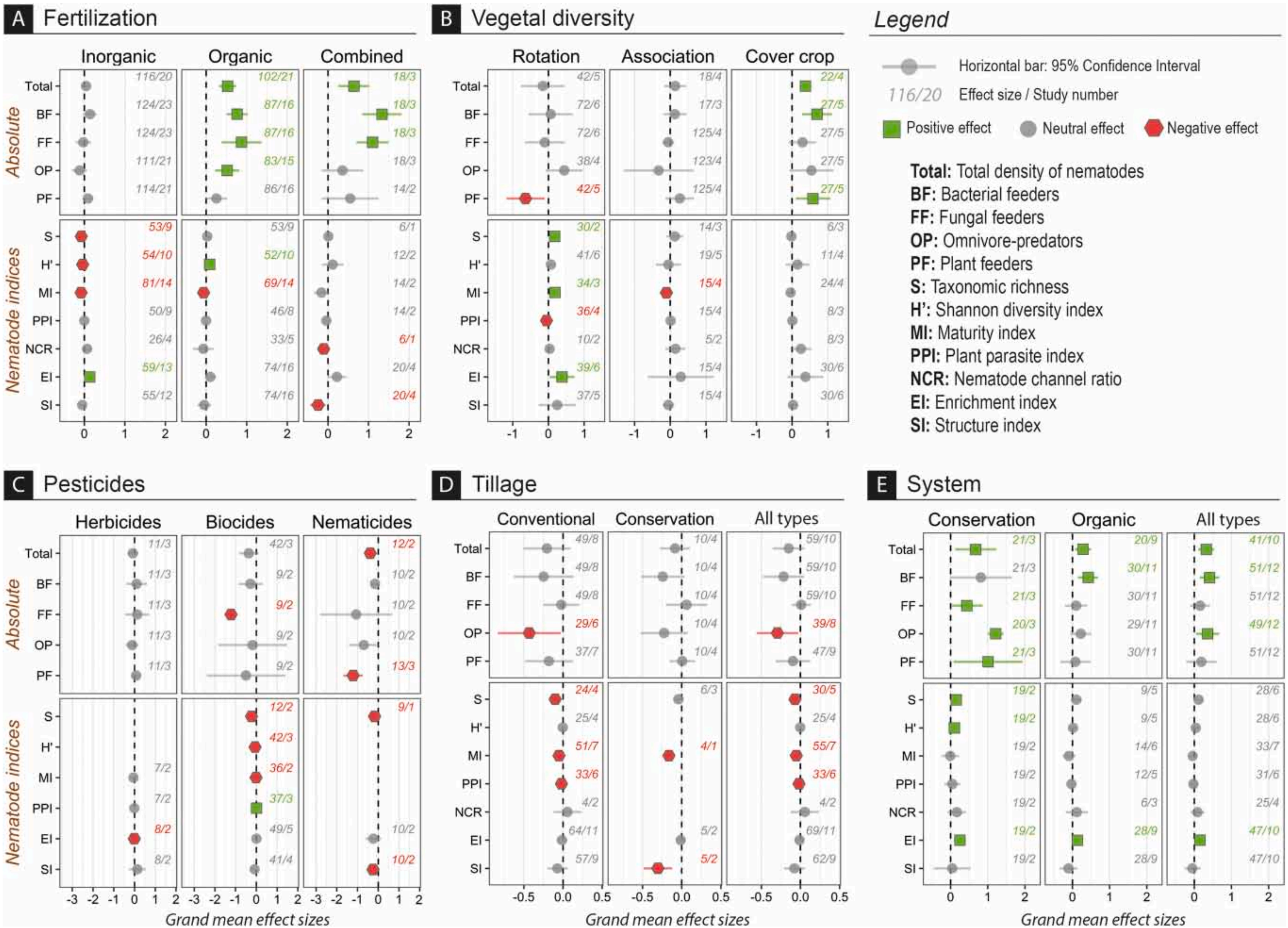

Fig. 3. Summary effect sizes over all studies of each nematode parameter in response to (A) fertilization, (B) plant diversity, (C) pesticides, (D) tillage, and (E) system conversion. The total number of observations and studies for one summary effect size are indicated on the left and right side of the slash symbol, respectively. Values are the mean ± 95% confidence intervals. Red hexagons and green squares indicate significant negative and positive effects, respectively, at the 5% threshold. Grey circles are not significantly different from zero." (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

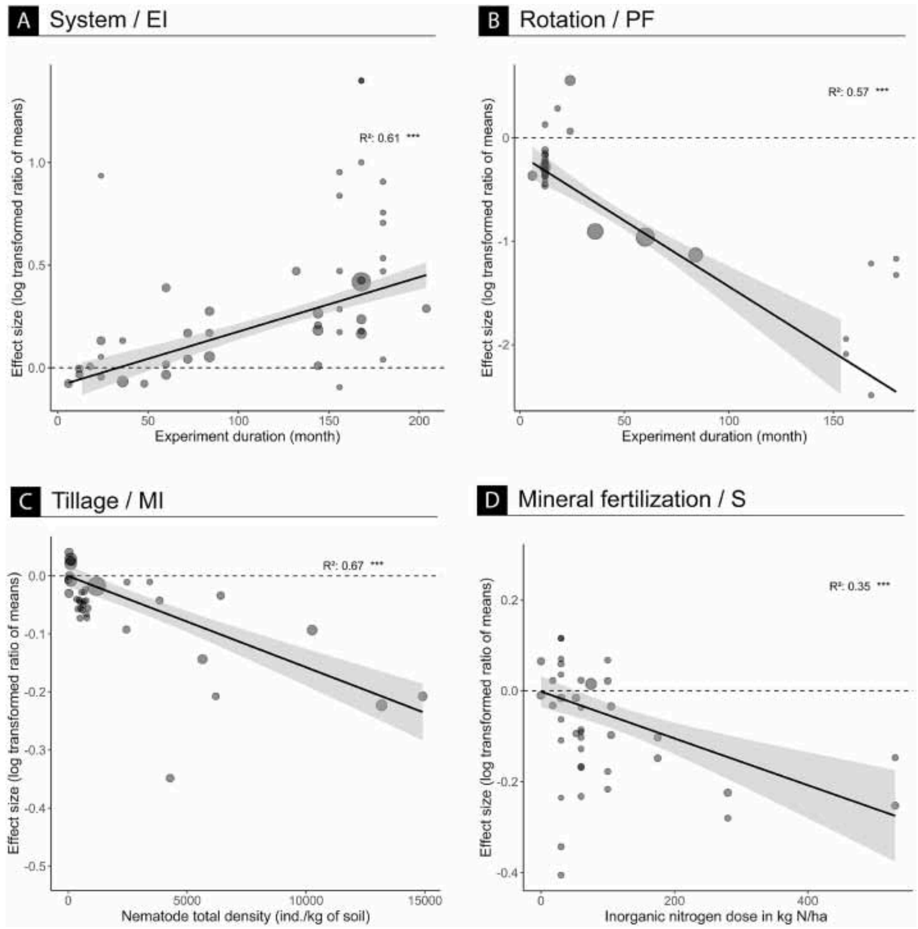

Fig. 4. Selection of meta-regressions for a set of moderators and nematode parameters within specific practices (EI = enrichment index, PF = abundance of plant feeders, MI = maturity index, S = taxonomic richness). Linear meta-regressions are shown as black solid lines and grey area represents 95% CIs. The area of the points is drawn proportional to the inverse sampling variances. Significant thresholds $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

(+19.3%), the maturity index (+20.3%), enrichment index (+47.0%) and abundance of omnivore-predators (+55.8%, although not significant), while slightly reducing the plant parasitic index (−5.2%). Meta-regressions revealed that this effect of rotation on the soil nematode community was modulated by the climate and soil context (Table 2). For instance, the negative effect of rotation on the abundance of plant-feeding nematodes was more pronounced in soils with higher soil carbon content. We also found positive effects of cover crop on the total nematode abundance (+45.3%), bacterial-feeders (BF, +101.0%) and PF (+79.6%) abundances. In contrast, no effect of plant association on nematode parameters was found, except a slight decrease in community maturity (−10.3%; Fig. 3B), but this effect appeared transitory and decreased with the experiment duration (Table 2). Additionally, the introduction of legumes (*Fabaceae*) to the cropping system was not found to be a significant moderator (Table 2).

3.3. Pesticides

Few studies investigating the impact of pesticides on nematodes and that met our criteria were included in the meta-analysis: corresponding to 160 observations from 12 studies. We showed no significant global effects of herbicides on the different soil nematode community parameters (except a slight decreasing effect on EI -5%; Fig. 3C). In contrast, biocides or nematicides had similar deleterious effects on soil nematodes (Fig. 3C). Biocides significantly reduced the absolute abundance of nematodes, especially fungal feeders (−52.6%), as well as nematode richness and diversity (S: 7.5%, H': 6.5%), but slightly increased the plant parasite index (+0.7%). The use of nematicides also affected nematodes at the community level by decreasing the total abundance of nematodes (−32.1%), plant feeders (−70.2%), taxonomic richness (−16.6%) and the food web structure (−22.6%, but Rosenberger's number = 14, indicating possible publication bias for these effect sizes).

3.4. Tillage

Through the compilation of 134 observations (Fig. 2), we showed that tillage affected soil nematodes to a lesser extent than 2 other type of practices: managing plant diversity and fertilization. Notably, the absolute abundance of omnivore-predators was significantly reduced by conventional tillage (−14.4%; Fig. 3D), especially when the initial nematode abundance was high (Table 2; Fig. 4C). The maturity and structure of the nematode community were reduced by tillage (−15.1% and −26.2%, respectively) while BF and fungal-feeder nematodes (FF) were not significantly impacted by tillage (Fig. 3D). The effects of conventional and conservation tillage on soil nematode were similar except for the abundance of omnivore-predators and SI (Fig. 3D).

3.5. Impact of types of agricultural systems

We recorded 80 observations among 12 studies that met the data criteria (mean +SD or SE) and investigated the effects of conservation and organic agriculture on soil nematodes compared to conventional systems (Fig. 2). Converting conventional to organic agriculture or conservation agriculture was found to have a profound effect on soil nematodes (Fig. 3A). Conservation or organic agricultural systems improved nematode abundance, irrespective of trophic groups.

Conservation agriculture significantly improved the total abundance of nematodes (+96%) and the absolute abundance of fungal feeders (+54.9%), omnivore-predators (+237.2%) and plant feeders (+174.4%; Fig. 3A). The positive effect of conservation agriculture on the abundance of omnivore-predators was more pronounced in regions with high mean annual precipitation (Table 2). Bacterial feeders were also more abundant under conservation agriculture than under conventional agriculture (+126%). Beyond this increase in abundance, conservation agriculture also improved taxonomic richness (+16.3%), Shannon diversity (+10.2%) and the enrichment index (+28.4%). Similar patterns were found for organic agricultural systems, which induced higher absolute abundance in total nematodes (+33%) and bacterial feeders (+52.8%) but with no effect on nematode diversity and richness.

4. Discussion

Overall, conventional practices (e.g., nematicides or mineral fertilization) had the highest negative impacts on nematode communities by reducing abundance, trophic structure and taxonomic richness. Agroecological practices based, for instance, on promoted plant diversity and organic fertilization, had positive effects by increasing the functional and taxonomic diversity of soil nematodes. Our approach succeeded to quantify the distinct effect of practices on nematodes and showed that tillage and herbicides had less pronounced effects in comparison to biocides, managing plant diversity and fertilization (Fig. 3). Our meta-analysis also revealed that the magnitude and direction of the effect of agricultural practices were modulated by the local abiotic and biotic contexts (mean annual precipitation and nematode abundance). The nematode abundance, known to vary greatly at both local (Cluzeau et al., 2012; Villenave et al., 2013) and global scales (van den Hoogen et al., 2019), was a significant moderator explaining the effect sizes of agricultural practices on several nematode parameters (Table 2). Knowing the worldwide abundance of soil nematodes is thus relevant to better predict the local effects of agricultural practices on nematode community.

4.1. Fertilization

Among all agricultural practices, fertilization resulted in the greatest effects on nematode community parameters. Mineral fertilization reduced the richness and diversity of soil nematodes by favouring bacterial cp1 and fungal cp2 feeding taxa as described by lower maturity index and higher enrichment index (Ferris et al., 2001). Most favoured taxa have high reproductive rates, high colonization rates, form *dauer larvae* (for cp1 nematodes) and exhibit greater resistance to perturbations (Bongers, 1990; Ferris et al., 2001). This decrease in taxonomic richness has been ascribed to either production of nematicidal compounds following fertilization or during degradation of organic fertilizers, the introduction or enhancement of antagonistic microorganisms or to less favourable soil physico-chemical conditions (mostly pH) for large size nematodes (see review Oka, 2010).

As observed by Liu et al. (2016), nematode abundance, taxonomic richness and food-web structure were greater in soils amended with organic fertilizers. These data provided evidence that amending the soil with organic fertilizers enhanced the total abundance by almost 70% without increasing plant feeders. The amount of organic fertilizers changed the effect of organic fertilization on nematode parameters, such as omnivore-predator abundance. It is noteworthy that the term organic fertilization used in this study does not capture the biochemical heterogeneity and resulting effects on nematode communities parameters identified across difference sources (Leroy et al., 2009; Lashermes et al., 2010; Liu et al., 2016), e.g., specific products such as chitin wastes or slurry have been shown to have nematicidal action (Akhtar and Malik, 2000; Thoden et al., 2011). They showed that C-rich materials such as straw-based crop residues greatly improved soil nematode abundance, richness and the structure index while N-rich organic fertilizers such as animal manures and sludge were more effective in controlling plant-feeding nematodes than straw-based crop residues.

4.2. Plant diversity

Increased plant diversity has been shown to be associated with pest suppression, reduced chemical inputs, and the closing of biogeochemical cycles (Altieri, 1999; Kennedy et al., 2002; Tilman et al., 2002; Letourneau et al., 2011; Isbell et al., 2017). Increasing plant diversification within cropping systems through rotation, association or cover crops is thus recognized as a relevant way to promote well-functioning agroecosystem (Altieri, 1999; Barot et al., 2011; Prieto et al., 2015). In soil nematology, plant diversification is known to significantly affect populations of plant parasitic nematodes (De Deyn et al., 2004; Brinkman et al., 2005; Cortois et al., 2017). Our synthesis highlighted that increasing plant diversity, regardless of plant functional groups, is a significant factor affecting not only plant feeders, but also total nematode abundance, bacterial feeders, taxonomic richness and maturity index. Rotation appears to be a relevant practice to increase the taxonomic and functional diversity of soil nematodes. The practice of cover crops, mostly used for weed management, reduced nutrient loss and soil erosion, favours the soil nematode community, in line with other studies on soil biota (Teasdale, 1996; Moonen and Barberi, 2008). Using a meta-analysis, Kim et al. (2020) showed that cover cropping enhanced the soil microbial abundance, activity and diversity compared to those of bare fallow. This pattern has also been found by Daryanto et al. (2018). This response has been mostly ascribed to the input of above- and belowground plant biomass and root exudates by cover cropping (Vukicevich et al., 2016). Thus, promoting vegetal richness may increase the quantity of available carbon (Yeates, 2007), fueling the soil microbial community and large populations of bacterial- and fungal-feeding nematodes. These positive results must be tempered by the potentially higher risk of damage caused by plant feeders according to the host status of the plants used in the crop system (Villenave et al., 2018). Indeed, we observed a higher abundance of plant feeders with cover crops (Fig. 3B). However, plant diversity, in both space and time, has also been shown to promote interspecific competition between plant feeder taxa, reducing damage to crops (Viketoft, 2008; Kepler et al., 2020), and likely to be involved in the suppressive potential of soils (Grabau et al., 2020). As a consequence, a decrease in taxonomic richness (or diversity) of the nematode community can thus induce a higher risk of plant-parasitic nematode population development (Wardle, 1995; van Capelle et al., 2012; Zhang et al., 2012).

4.3. Pesticides

Previous studies reported either negative (Das et al., 2010; Zhang et al., 2010) or positive (Ishibashi et al., 1983; Zhang et al., 2002) effects of herbicides on soil nematodes. Here, we found low effects globally (effect sizes below 0.5; 65%) of herbicides on the soil nematode parameters. Zhao et al. (2013) also observed low effect sizes of herbicides on the abundance of total nematodes and distribution within trophic groups. Still, we hypothesized that the use of herbicides may affect soil nematodes mostly by altering plant composition and thus resource availability (indirect effect) rather than by direct toxic effects. A recent study also showed few changes in the microbial community structure after herbicide application and suggested that microbial cells can metabolize herbicide compounds (Kepler et al., 2020). Zhao et al. (2013) concluded that herbicides may cause the soil food web to become dominated by bacteria. Indeed, we observed a slight increase in the enrichment index (EI) suggesting higher proportion of fast-growing bacterial-feeding nematodes adapted to bacterial-rich environments. This effect was explained by the deleterious effects of herbicides on surface fungi and fungivores that are more directly exposed. Here, we did not test the contrasting responses of predators and omnivores showed by Zhao et al. (2013) because most often, studies grouped together predators and omnivores. This is a serious limitation since it is highly probable that the responses of predatory and omnivores nematodes differ to practices other than herbicides. Finally, in contrast to Zhao et al. (2013), we did not observe a significant effect of herbicides on plant parasitic nematodes nor PPI. However, given the small sample size for herbicide application, caution must be taken. In contrast to herbicides, biocides or nematicides had significant deleterious effects on soil nematodes. In agreement with previous observations (Yeates et al., 1991; Sipes and Schmitt, 1998; Neher and Olson, 1999; Wada et al., 2008; Carrascoca et al., 2015), the meta-analysis revealed that broad-spectrum biocides and nematicides do not target specific nematode taxa, and deleterious effects of these compounds at the nematode community level are observed. Thus, managing plant-parasitic nematode species with the use of biocides potentially leads to strong side effects on soil functioning, underlying the need to identify effective nematicides without non-targeted impacts (Grabau et al., 2020).

4.4. Tillage

By disturbing the soil structure and residue supply, tillage can greatly impact nematodes (Zhang et al., 2019). Tillage had constant negative effects on soil nematodes but exhibited lower effect sizes in comparison to other practices. By comparing the soil fauna, van Capelle et al. (2012) observed that tillage had little impact on nematodes, in comparison to larger organisms, suggesting that smaller organisms are probably more affected by soil chemical properties (organic matter quantity and quality) than by physical disturbances. The notable significant effect of tillage was found on omnivore-predators. These nematodes, many of which belong to the dorylaimids (Yeates et al., 1993), are known to be the most sensitive to physical or chemical disturbances (Bongers, 1990; Ferris et al., 2001). In consequence, tillage decreases the maturity and structure of the nematode community (measured with MI and SI). Tillage, by physically perturbing the soil, supports a less stable nematode community and a food web based on opportunist taxa. Indeed, bacterial- and fungal-feeding nematodes were not significantly impacted by tillage, likely due to their high dispersal rates, their ability to rapidly colonize perturbed environments (Ettema and Bongers, 1993; Bongers, 1999; Ferris and Matute, 2003; Villenave et al., 2018).

4.5. Impact of types of agricultural systems

Agricultural system shifts have been shown to profoundly affect soil biota and functions (Henneron et al., 2015; Rivers et al., 2016), including nematodes (Neher, 1999b; van Diepeningen et al., 2006). The conversion from a conventional system to an alternative (organic or conservation) system results in a change in a set of practices in space and time, i.e., tillage, rotation, pesticides, fertilization. This set of practices and the frequency of their applications are potentially responsible for the very pronounced effect of different types of agricultural systems on soil nematode communities. Our results showed that conservation and organic practices deeply modify the nematode indexes with possible consequences on soil organic matter decomposition and nutrient recycling knowing the roles of nematodes in soil functions (Bongers and Bongers, 1998; Trap et al., 2016; Wilschut and Geisen, 2020). Interestingly, the enrichment index (EI) increased with increasing total duration of agricultural system establishment (Fig. 4D), suggesting that the soil functions and fertility shifts continue over time after the system conversion.

5. Limits and perspectives

In this study, we conducted a meta-analysis that meets the required statistical criteria (Vetter et al., 2013; Gurevitch et al., 2018). As mentioned in the material and method section, an important number of studies could not be included in our meta-analysis due to the lack of reporting SE, SD or sample size. We encourage the soil nematology research community to adopt the standardised practices and stress the importance of fully reporting the SD or SE and sample size (n) of their study to help further use of the data. Also, a large number of studies did not compute the nematode indices nor provide the full raw data of community taxonomic composition. Publishing the taxonomic composition of each nematode community would be highly useful for the nematologist community for further analyzes. We also underline that our findings are dependent on the current limits of soil nematology, in particular (i) the possible lack of consideration of rare taxa due to the low number of individuals identified per soil sample, (ii) the low resolution of the taxonomic assignment (genus or family) which can lead to underestimating taxonomic richness, or (iii) the low consideration of the functional traits that may better capture the ecological strategies of nematodes (Vonk et al., 2013; Liu et al., 2015). Our global pattern was mainly influenced by the three geological areas (Asia, Europe and America) and thus may not represent fully the worldwide pattern, corroborating limitations for global soil nematode samples distribution as already pointed out by van den Hoogen et al. (2019) and Guerra et al. (2020). Consequently, the number of studies for certain practices and types of agricultural systems may appear to be relatively low compared to the total studies published on these issues.

6. Conclusion

By collating worldwide data on soil nematode communities in croplands, this meta-analysis provides a quantitative assessment of the effect of agricultural practices on soil nematode community abundance, trophic groups and food web structure. Overall, our results demonstrate that some practices significantly affect soil nematode communities, either negatively or positively (e.g., manipulating plant diversity or organic fertilization), and others have less effect (e.g., tillage or herbicide application). We believe that this work (i) will be a useful aid for decision maker to better manage soil nematode community, (ii) identify gaps in current available data and (iii) could help the community to formulate new hypothesis. Importantly, this quantification of the variation in soil biological activity with agricultural practices could be of particular interest to represent soil life levels in models monitoring soil biodiversity worldwide under global change scenarios.

Code availability

The R code used in this study is freely available as supplementary material.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108383.

Author contributions

J.T. and C.V. conceived the idea. J.P., C.V., C.C. and J.T. designed the research. J.P. collected the data. J.P. and J.T. assembled the database. J. P., C.V., C.C. and J.T. revised the database. J.P. performed the data analyses. All authors wrote and edited the manuscript.

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