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REVIEW

Organic nitrogen fertilization benefits selected soil fauna in global agroecosystems

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Abstract
Soil fauna plays an essential role in agricultural productivity as it mediates nutrient cycling and soil organic matter dynamics, alters soil physicochemical properties and supports plant growth. Nitrogen fertilization may have a positive or negative influence on soil fauna in a manner that alters ecosystem functioning, but these links have not yet been quantified. We present the results of a global meta-analysis of available literature data on the effects of N fertilization on taxonomic and ecological groups of soil fauna. Our results show that organic N fertilization increases the density of springtails, mites and earthworms, as well as the biomass of earthworms compared to when no fertilizer is applied. The meta-analysis for different nematode feeding groups and ecological categories of springtails and earthworms as well as different mite orders showed that organic fertilization has an overall positive effect on most groups as opposed to inorganic fertilization, which has neutral or negative effects on most groups, alone or in combination with organic fertilizers. Additional meta-analyses showed that the effects of N fertilization on soil fauna depend on the N application rate, on soil texture and on climatic conditions. Our findings suggest that the adoption of less intense farming practices such as organic fertilization combined with site-specific N fertilization regimes is a suitable strategy for protecting and enhancing functional communities of soil fauna.

Keywords Soil biodiversity · Impacts on soil fauna · Anthropogenic effects · Soil amendments · Agricultural intensification

Introduction

Soil fauna mediates numerous functions in the pedosphere, such as nutrient cycling, the formation and turnover of soil organic matter, degradation of pollutants, improvement of soil structure, biotic regulation and plant growth (Briones 2018). Microfauna (protozoa and nematodes) stimulate microbial mineralization of organic matter, thereby increasing the availability of nutrients to plants (Griffiths 1994). Microarthropods (i.e., mites, collembolans) stimulate organic matter decomposition and produce fecal pellets that promote microbial activity (Maaß et al. 2015). Ecosystem engineers (mainly earthworms) produce organo-mineral structures and a large variety of pores, which promotes denitrification, N-fixation, C and N mineralization as well as infiltration of water and air (Lavelle 1996). Consequently, soil fauna drive soil processes strongly affecting agricultural production (de Ruiter et al. 2005).

Concurrently, agricultural management practices can positively or negatively influence soil fauna and their contribution to agricultural productivity. Agricultural land use, particularly the shift from extensively (low input) to intensively (high input) managed agroecosystems, is often seen as one of the main drivers of global biodiversity decline (Newbold et al. 2015), and is considered to be the main pressure on soil biodiversity (Gardi et al. 2013). Several studies have shown the negative effects of intensive agriculture on the abundance, species richness and community composition of specific taxonomic groups of soil fauna (Parfitt et al. 2010; Tsiafouli et al. 2015; Andriuzzi et al. 2017; Fiera et al. 2020). On the other hand, other studies have shown examples of high yields and high biodiversity coexisting in the same agricultural systems as a result of sustainable intensification practices (Choudhary et al. 2018).

The choice of crops, the level of disturbance as well as the management of external inputs can directly or indirectly alter soil faunal populations (Brussaard et al. 2007).

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Particularly, N fertilizers applied to enhance aboveground primary productivity can alter soil biotic communities and change the food web structure and ecological functions (Bai et al. 2010). The effects of fertilization on soil faunal communities are determined by food availability, changes in soil physicochemical (Birkhofer et al. 2008) and microbiological properties (Yan et al. 2012), and by changes in the quality and quantity of plant residues and root exudates (Reeve et al. 2010).

The application of both organic and inorganic N fertilizers to cropland can have positive effects on soil fauna, due to enhanced resource availability, as well as negative effects resulting from the deterioration of soil physicochemical properties (Zhao et al. 2015). Inorganic fertilizers provide available nutrients for plant growth, which can lead to higher microbial activity and higher resource availability for soil fauna through plant and root residues (Wang et al. 2016). Organic fertilizers improve overall soil quality and nutrient cycling and foster microbial biomass, which leads to higher availability of food resources for soil fauna (Birkhofer et al. 2008). However, negative effects of fertilization on soil fauna have also been reported, particularly inorganic fertilization (Gardi et al. 2008), explained mostly by direct toxic or osmotic effects (Aslam et al. 2015), acidifying effects, the reduction of aggregate stability and therefore significant losses of organic C previously protected in microaggregates (Mikha and Rice 2004). The magnitude of the positive and the negative effects determine the net effect of N fertilization on the biomass, density and diversity of soil fauna (Zhao et al. 2015).

The responses of soil fauna to N fertilization are complex and may vary among groups of organisms due to their diverse feeding habits and life histories. For instance, the effects on the different ecological life forms on earthworms can be dissimilar. The effects may depend on type of fertilizer, and especially acidification, although earthworms prefer N-rich environments (Edwards and Lofty 1982). Other factors such as climate, type of fertilizer, soil properties, vegetation cover, or crop stage may determine the response of soil fauna to N fertilization. Multiple studies have reported different effects of fertilization on soil communities in various geographical locations. For example, the application of organic and inorganic fertilizers was linked to a reduced density of nematodes in tea plantations on a sandy loam soil in Southern China (Li et al. 2014), but to an increased density of nematodes in cereal crops in a similarly textured soil in Spain (Garcia-Alvarez et al. 2004). Furthermore, organic and inorganic fertilization of a grassland in Belgium resulted in higher earthworm density (Leroy et al. 2007), but a negative effect of organic fertilization on earthworm density was observed in a grassland in the UK (Briones et al. 2020). This high variability might be the result of a lack of consideration of factors contributing to the effects of N fertilization. For example, different types of fertilizer (organic and inorganic), fertilization regimes, soil factors (pH, organic matter, texture) and climatic factors, which can be better assessed at broader spatial scales.

In this meta-analysis, we examined the effects of N fertilization on the density of nematodes, springtails, mites and earthworms, and on the biomass of earthworms in agricultural landscapes. We included studies that compared the density or biomass of the selected organisms determined in fertilized versus unfertilized fields to assess the following treatments related to agricultural management: (1) organic and inorganic fertilizers as well as their combination; (2) increasing N application rates; (3) duration of the fertilization experiment; (4) influence of crop type. Furthermore, we assessed soil properties (texture, pH, organic matter) as well as climatic variables (climatic zone, mean annual precipitation) as abiotic moderators of N fertilization effects on soil fauna. We hypothesize that (1) organic fertilizer has a positive effect on soil fauna by providing food resources and improving soil structure; (2a) inorganic fertilizer has negative effects due to direct toxicity, and (2b) positive effects via improved plant production; (3) the effects of N fertilization on soil fauna depend on climate and soil properties.

Methods

Data collection

We aimed to include all available published studies that compared communities under inorganic or organic fertilization (i.e., N fertilization) with unfertilized controls. The literature was systematically reviewed in compliance with the Preferred Reporting Items for Systematic Reviews and Meta-analysis framework ("PRISMA", Fig. S1) (Moher et al. 2009). Peer-reviewed publications reporting results on the effects of N fertilization on soil fauna were searched using the Web of Science search engine, including all available databases with the following search term: "(earthworm OR acari OR mite OR springtail OR collembola OR nematode OR fauna) AND (fertilis* OR fertiliz* OR amendment*)".

Our selection criteria for including identified studies in the meta-analysis were: (1) studies that report abundance/biomass data measured in fertilized treatments vs. non-fertilized (control); (2) all the fertilization trials were done on the same site or the sites were adjacent to each other; (3) the control and treatment plots had similar soil properties (in order to isolate the effects of physicochemical characteristics of soil from other sources of variation); (4) the amendments used did not have high concentrations of high concentration of heavy metals or other potential toxicity to soil fauna (i.e., studies with untreated sewage sludge or other types of industrial residues were not selected); (5) control plots had no amendments or inorganic fertilizer applications added and (6) had the same vegetation cover and cropping system as fertilized plots. The full-text documents of all studies identified as potentially relevant (see Supplementary material for a complete list of references of studies included in the meta-analysis) were screened manually and processed further.

For each pairwise comparison (observation) within the study, we collected the means (abundance for all taxonomic groups; due to data availability, biomass data was only collected for earthworms) of the unfertilized treatment (control) and the fertilized treatment (experiment), as well as their replicate numbers (n) and standard deviation (SD) or standard error (SE). Additionally, we extracted information on experimental setup (field or laboratory); site location (longitude and latitude); mean annual precipitation; soil properties (soil textural class using the USDA textural soil classification (USDA 1987), pH, organic matter and N content); management practices (crop, fertilizer application rate, type of fertilizer, duration of the fertilization experiment); zoological sampling methods (depth of hand sorting and collection methods). When soil properties were reported per soil depth, the mean value was calculated and used in the analysis. When the data were presented as graphs, we manually digitized the figures to estimate means and SD or SE using WebPlotDigitizer Version 4.3 (Rohatgi 2020).

From all studies, individual data for each sampling date was extracted as well as the time period after fertilization (time of faunal measurement after fertilization) and treatment duration (the period of time during which the same fertilization regime was maintained). The time of measurement and treatment duration were analyzed as moderators to control for heterogeneity in the results and to allow comparison of studies of different durations (Curtis et al. 2013). This was done to avoid substantial loss of data (if only one data point was selected from each time series) and to analyze trends of the effect of fertilization over time. The resulting database covers 3826 observations from 132 publications (see Fig. S2 for a global distribution of the studies) published between 1979 and 2020.

Moderator variables

Ecological groups Soil fauna were categorized into ecological groups, i.e., nematodes were categorized by trophic groups, springtails by ecological categories (epi-, hemi- and euedaphic), mites by higher taxonomy and earthworms by ecological groups (epigeic, anecic, endogeic) as shown in Table S1. If studies only reported species-specific data, the ecological category of each species was determined based on global databases (i.e., Burkhardt et al. (2014), Drilobase Project (2021), Janssens (2007), Bottinelli et al. (2020)) or using secondary literature, or based on expert opinion. The density of each ecological group was calculated based on the single species density of the respective ecological group. If standard errors or standard deviations were reported for each species, the individual variances were used to calculate a pooled standard deviation. These analyses were performed for total animal group density or biomass; data paucity precluded analyses for ecological/functional groups.

Management practices Other influencing factors considered in the analyses include fertilization type (inorganic, organic or mixed), and time of faunal sampling after fertilization. Except for type of fertilizer and application rate, the analysis of influencing factors was only carried out for total animal group density or biomass, as data scarcity did not allow analysis at the functional or ecological group level. Some categorical and continuous variables extracted from the studies required grouping or categorization (Table 1) to increase within-group homogeneity (Koricheva et al. 2013). The N

Table 1 Moderators of nitrogen fertilization effects on soil fauna

Moderator	Subgroups/Range
Type of fertilizer	Organic
	Inorganic
	Organic + Inorganic
Nitrogen application rate	11–1620 $kgN\ ha^{-1}$
Time period after fertilization	0–22 years
Treatment duration	< 1 year
	1–5 years
	5–10 years
	> 10 years
Crop cover	Barley
	Cereals
	Grasses
	Legumes
	Maize
	Other perennials
	Other grain crops
	Rice
	Root crops
	Wheat
	Woody crops
Soil texture classes	Clay: Clay, clay loam
	Silt: Silt, silt loam
	Loam: Loam, loamy sand
	Sand: Sand, sandy loam
Soil pH	4–8.7
Soil organic matter	0.4–8.3%
Earthworm sampling methods	Digging
	Mustard extraction
	Formalin extraction
	Monolith/soil core
	Plastic traps

application rate was included as a continuous moderator. The treatment duration was categorized in four levels (Table 1) due to an insufficient number of observations within each individual length of experimental duration. Crops were grouped into broader classes based on the guidelines provided by FAO (FAO 2021). Furthermore, if experiments that studied the effects of organic fertilizers on soil fauna did not report the application rate as $kgN\ ha^{-1}$ or the N content of the fertilizer used, the N content of the specific fertilizer was estimated based on secondary literature. As the efficiency of different earthworm sampling methods may differ (Bartlett et al. 2010), the methods used were also included in the meta-analysis as moderator variables (Table 1).

Abiotic and soil-related factors Soil texture was grouped into four major classes either as reported in the studies or calculated from the particle size distribution using an online soil texture calculator (USDA 2016). Climate zones were determined based on the Koeppen classification system (Kottek et al. 2006), using the coordinates reported in each study or the name of the nearest city as reference for search in the global database. This system uses five main climate categories with further subdivisions according to seasonal distribution, amount of rainfall and temperature regimes. The mean annual precipitation, soil pH, and soil organic matter content were included as continuous moderators.

Meta-analysis

The magnitude of the effect of N fertilization on the density or biomass of soil fauna was calculated as the natural logarithm of the response ratio ($lnR = ln(E/C)$) where E and C are the means of experimental (fertilized) and control (unfertilized) treatments, respectively (Hedges et al. 1999). Inverse-variance weights were used for the estimation of the pooled-effect size, which is a common approach for meta-analysis (Borenstein et al. 2011). The analyses for general effects of fertilization on the different taxonomic groups as well as the moderator analyses were done in R 4.1.2 (R Core Team 2019). The *escalc* function was used to calculate the effect sizes and the *rma.mv* function (*metafor* package, Viechtbauer (2010)) to fit mixed effects models. To address the non-independence of the data, we implemented the correlated and hierarchical effects model described by Pustejovsky and Tipton (2022), which combines dependence structures arising from a multilevel data structure (i.e., observations within studies). Missing variances from individual studies were imputed with multiple imputation using chain equations of the *mice* package (Buuren and van Groothuis-Oudshoorn 2011). The estimated effect sizes and variances are pooled estimates of imputed datasets, applying Rubin's combination rules (Rubin 2004). When more than half of the values of standard deviation were missing from a given dataset, the weights were estimated based on the number of replicates (Lajeunesse et al. 2013). The mean effects of fertilization on different faunal groups were considered significant when the 95% confidence interval did not overlap with zero. The scatterplots show the effect sizes and regression line estimated by the model. Due to data scarcity, it was not possible to assess the significance of interactions among different abiotic factors.

Results

Overall effects of N fertilization on soil fauna

Overall, organic N fertilization significantly increases the total density of springtails, mites and earthworms, as well as earthworm biomass (Fig. 1). The application of inorganic fertilizers alone or in combination with organic fertilizers has no significant effect on the total density of nematodes, springtails and mites, or on the earthworm biomass. The application of inorganic fertilizers has a significant negative effect on the total earthworm density. For different nematode feeding groups, organic fertilizers significantly increase the density of bacterivorous, fungivorous and omnivorous nematodes. Inorganic fertilizers have a significant negative effect on omnivorous nematodes. The application of organic and inorganic fertilizers does not affect any nematode feeding group. We observed a positive response of hemiedaphic and epedaphic springtails to organic fertilization, and there is a significant positive effect of inorganic fertilizers on prostigmatid mites. Organic fertilization has a significant positive effect on the biomass of epigeic, endogeic and anecic earthworms. Inorganic fertilizers alone or in combination with organic fertilizers have no significant effect on the different springtail ecological categories, on oribatid, mesostigmatid and astigmatid mites and on the density and biomass of the different ecological categories of earthworms. The effects of N fertilization on earthworms assessed by different sampling methods (Fig. S3) showed significant positive effects on earthworms when formalin and mustard were used as sampling methods, and a significant negative effect when hand sorting was used.

Influence of fertilization intensity

Nitrogen application rate The effects of N fertilization on the nematode density significantly increase with the N application rate when a combination of organic and inorganic fertilizers is applied (Fig. 2). When organic or inorganic fertilizers are applied separately, the effects of fertilization on nematode density do not vary with the application rate. The effects of N fertilization on springtail, mite and earthworm density do not vary with the application rate, regardless of

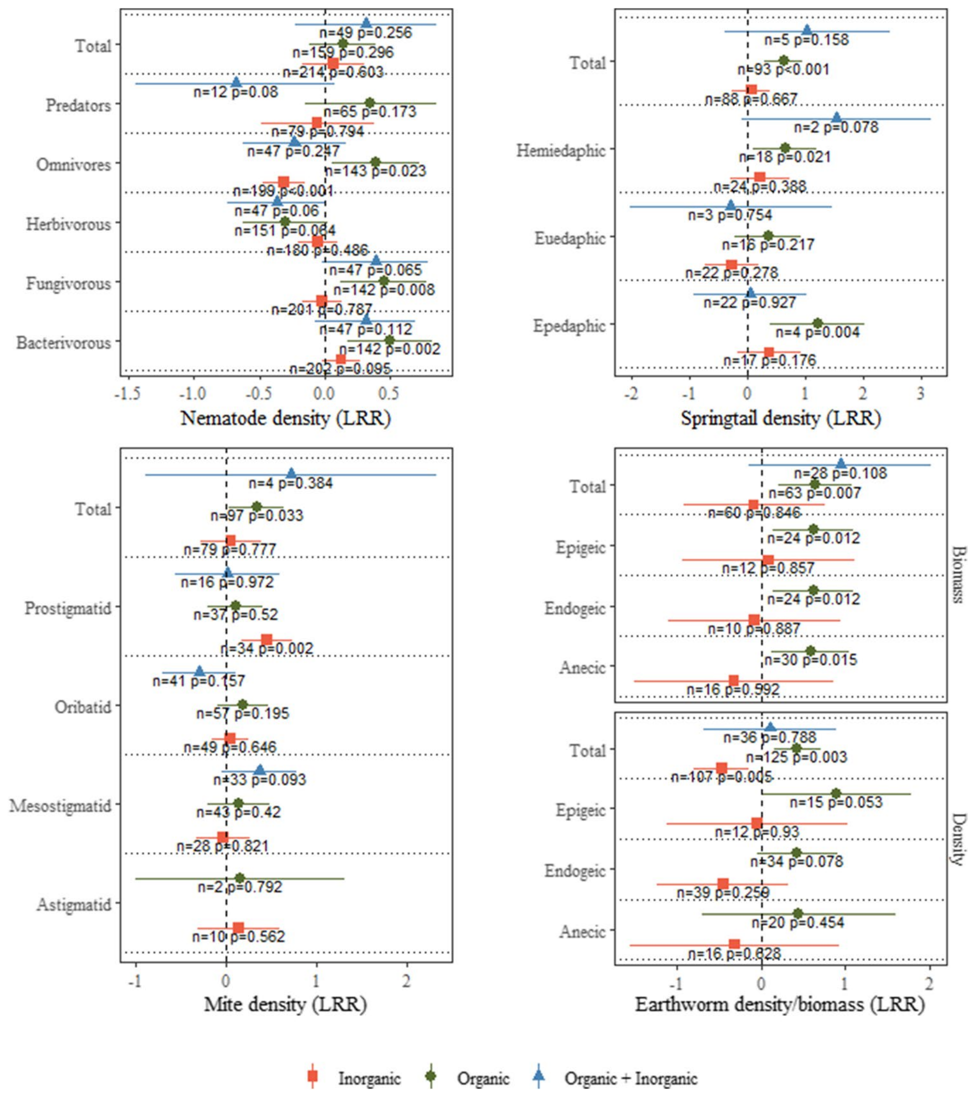

Fig. 1 Effect of different types of N fertilization on nematode trophic groups, springtail ecological categories, mite suborders and earthworm ecological categories as well as total densities as log-response ratio (LRR) compared to (unfertilized) controls. Mean effects, 95% confidence intervals, sample sizes and p-values (in parentheses) for each ecological/functional group and fertilizer type are shown

the type of fertilizer used. The effects of organic N fertilization on earthworm biomass increase when higher application rates are used. However, the effects on earthworm biomass of inorganic fertilizers alone or in combination with organic fertilizers do not vary with the N application rate.

Time after fertilization The effects of N fertilization on nematode, springtail, mite and earthworm density do not vary with time after fertilization (Fig. S4), when these effects are assessed separately for different types of fertilizer. However, the effect of a combined use of organic and inorganic fertilizer on earthworm biomass decreases significantly when more time has passed after fertilization.

Treatment duration The effects of N fertilization on soil fauna vary with the treatment duration (Fig. 3). In short-term experiments (less than a year), increases of the nematode density, although marginally significant ($p = 0.051$) when a combination of organic and inorganic fertilizers is applied, and on springtail and mite density when inorganic fertilizers are applied. In experiments of intermediate duration (1–5 years), significant negative effects of combinations of organic and inorganic fertilizers on nematode density are observed. In long-term experiments (> 10 years), significant effects are observed on nematode density for the combined application of organic and inorganic fertilizers.

Crop type The effects of N fertilization on soil fauna differ between crop types (Fig. 4). Fertilization significantly reduces nematode density when inorganic fertilizers are applied to legumes other than soybean. A positive effect on earthworm density is observed when organic fertilizers are applied to wheat. Positive effects on earthworm biomass are observed when organic and inorganic fertilizers are applied in combination to grasses.

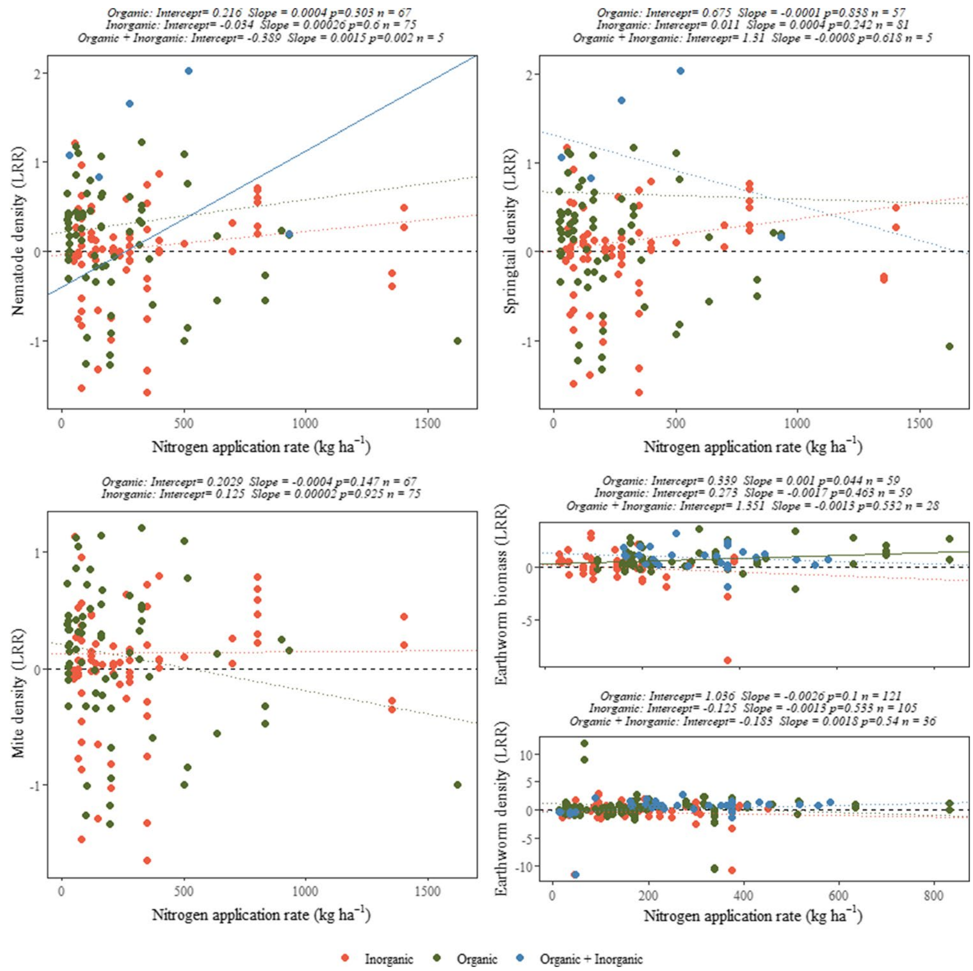

Fig. 2 Effect of N application rates ($kgN\ ha^{-1}$) on the density of nematodes, springtails, mites and earthworms, as well as earthworm biomass as log-response ratio (LRR) compared to (unfertilized) controls for different fertilizer types. Mean effects (points) and linear regression line (dotted: non significant, continuous: significant) are shown for different fertilizer types

Influence of soil properties

Texture The effects of N fertilization on soil fauna estimated separately for different soil textures (Fig. 5) show that organic fertilization significantly increases the nematode density in sandy soils, but significantly reduces the nematode density in loamy soils. Positive effects of organic fertilizers on springtail density are observed in sandy soils.

Soil chemical properties The effect of N fertilization on the density of the studied faunal groups does not vary significantly among soils with different pH values (Fig. 6) or organic matter content (Fig. 7), when these effects are assessed separately for different types of fertilizer.

Influence of climatic variables

Climatic zone The separate estimates of N fertilization effects in the different climatic zones of the individual studies (Fig. 8) show that in sites with continental climates (D), dry winters and warm summers (Dwb), organic and inorganic fertilization led to a significant increase in springtail density. In sites, with no dry season and warm (Dfb) summers, inorganic fertilization led to a significant increase in the nematode density.

In sites with temperate climates (C) with dry winters and hot summers (Cwa), inorganic fertilization led to a significant increase of the springtail density and a significant reduction of earthworm biomass, whereas organic fertilization led to a significant increase of earthworm density. In sites with Mediterranean cold summer climates (Csc), organic fertilization led to a significant reduction of springtail density In sites with no dry season and warm summers (Cfb), organic fertilization led to an increase of springtail density and earthworm biomass. In sites with humid suptropical climate with hot summers (Cfa), inorganic fertilization led to a significant reduction of springtail density.

In sites with hot semiarid climates (BSh), inorganic fertilization led to a significant reduction of nematode density. In sites with tropical climate with monsoon (Am), inorganic fertilization led to a significant increase of springtail density.

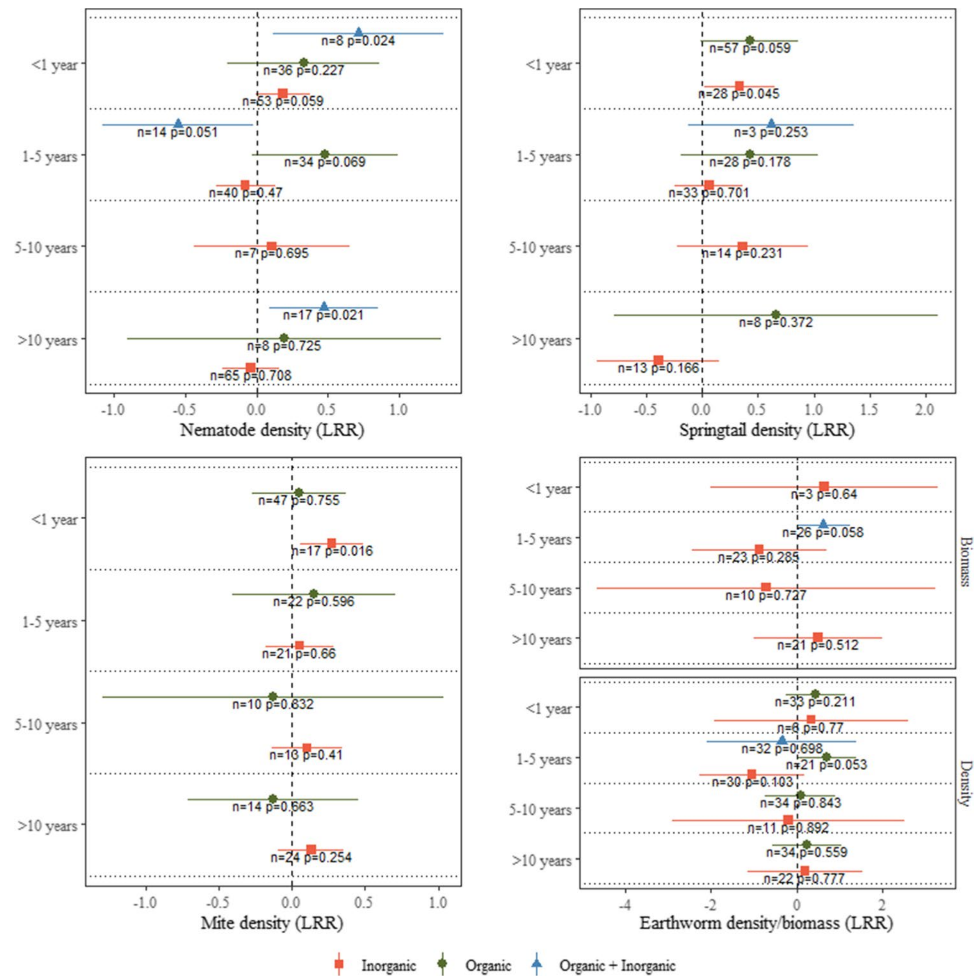

Fig. 3 Effect of treatment duration on the density of nematodes, springtails, mites, as well as earthworm density and biomass as log-response ratio (LRR) compared to (unfertilized) controls for different fertilizer types. Mean effects, 95% confidence intervals, sample sizes and p-values (in parentheses) for each treatment duration and fertilizer type are shown

Mean annual precipitation The effect of the different N fertilizers on the density nematodes, springtails and mites is not significantly modulated by the mean annual rainfall (Fig. S5). However, there is a significant reduction on the effects of combined organic and inorganic fertilization on earthworm density in sites with higher mean annual precipitation.

Discussion

Organic N fertilization generally has an overall positive effect on the total density of springtails, mites and earthworms, as well as on earthworm biomass. The overall response to organic N fertilization is likely to reflect the positive effects on, i.e., food sources (Nahar et al. 2006; Hu and Cao 2008), improved habitat conditions (Kautz et al. 2006), higher plant biomass (López-Fando et al. 1999), additional organic matter (Griffiths et al. 2010) and N content (Xie et al. 2015). In the case of inorganic fertilization, the negative fertilization effects may be due to, i.e., ammonium toxicity (Edwards and Lofty 1982; Ma et al. 1990). The responses to fertilization are (1) dissimilar for different feeding groups and ecological categories; (2) the size and direction depend on the type and intensity of the fertilization regime and (3) are modulated by site-specific factors, such as climate and soil characteristics. It is unfortunate that, due to data sparsity, we were not able to investigate interactive effects among moderators.

The responses to N fertilization vary among ecological groups

Organic N fertilization consistently increases the density of bacterivorous nematodes, which could be explained by the sensitivity of the enrichment opportunists (colonizer-persister group cp1 (Bongers 1990)) to fertilization (Hu and Qi 2010; Azpilicueta et al. 2014) as well as to an increase in bacterial populations (Bulluck and Ristaino 2002; Bittman et al. 2005). Positive effects on fungivorous nematodes could be explained by the higher C:N ratio and complexity of the organic material used for fertilization (Ferris and Matute 2003). This positive effect may be transient, as fertilization effects on nematodes tend to decrease with time, albeit not

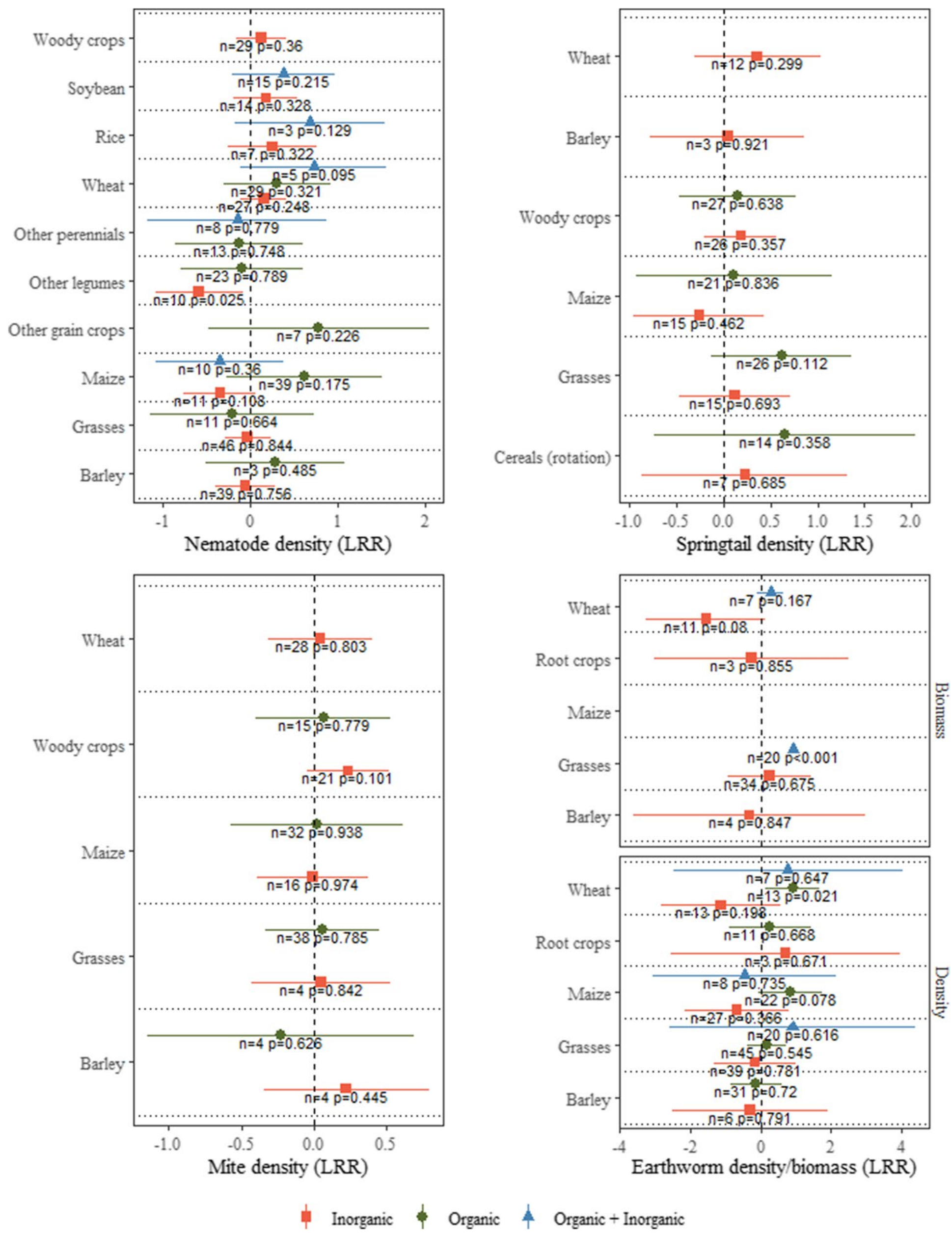

Fig. 4 Effect of crop type on the effect of N fertilization on the density of nematodes, springtails, and mites, as well as earthworm density and biomass as log-response ratio (LRR) compared to (unfertilized) controls for different fertilizer types. Mean effects, 95% confidence intervals, sample sizes and p-values (in parentheses) for each crop and fertilizer type are shown

significantly when the effects of different types of fertilizer are studied separately, corresponding with a potential microbial growth pulse after fertilization. The increase of microbial populations and their positive effect on bacterivorous nematodes may result in a trophic (bottom-up) cascade that contributes with the higher density of omnivorous nematodes observed in our meta-analysis (Neilson et al. 2020).

Based on the results for different ecological groups of springtails and mites, we hypothesize a potential shift in the trophic structure of the community as a result of N fertilization, in line with individual studies (i.e., Cole et al. (2005)). Higher density of predatory mites (families within the Prostigmatid suborders) could be expected in fertilized plots related to a higher density of prey (Berch et al. 2006). Surface active epedaphic springtails as well as hemiedaphic springtails are positively affected by organic fertilization. This positive response could be caused by the organic material applied to the soil surface which provides an important nutritional source for these groups of springtails, as well as by an increase in bacterial and fungal populations observed in the individual studies (Kanal 2004).

The positive effects of organic fertilization on earthworm density and biomass, in line with the findings of individual studies (Parfitt et al. 2005; Curry et al. 2008), and may be explained by indirect effects of higher N accumulation in crops and higher crop productivity, resulting in more available organic matter (e.g., via microbial growth or root exudates) and improved habitats for earthworms (Drakopoulos et al. 2018). With regard

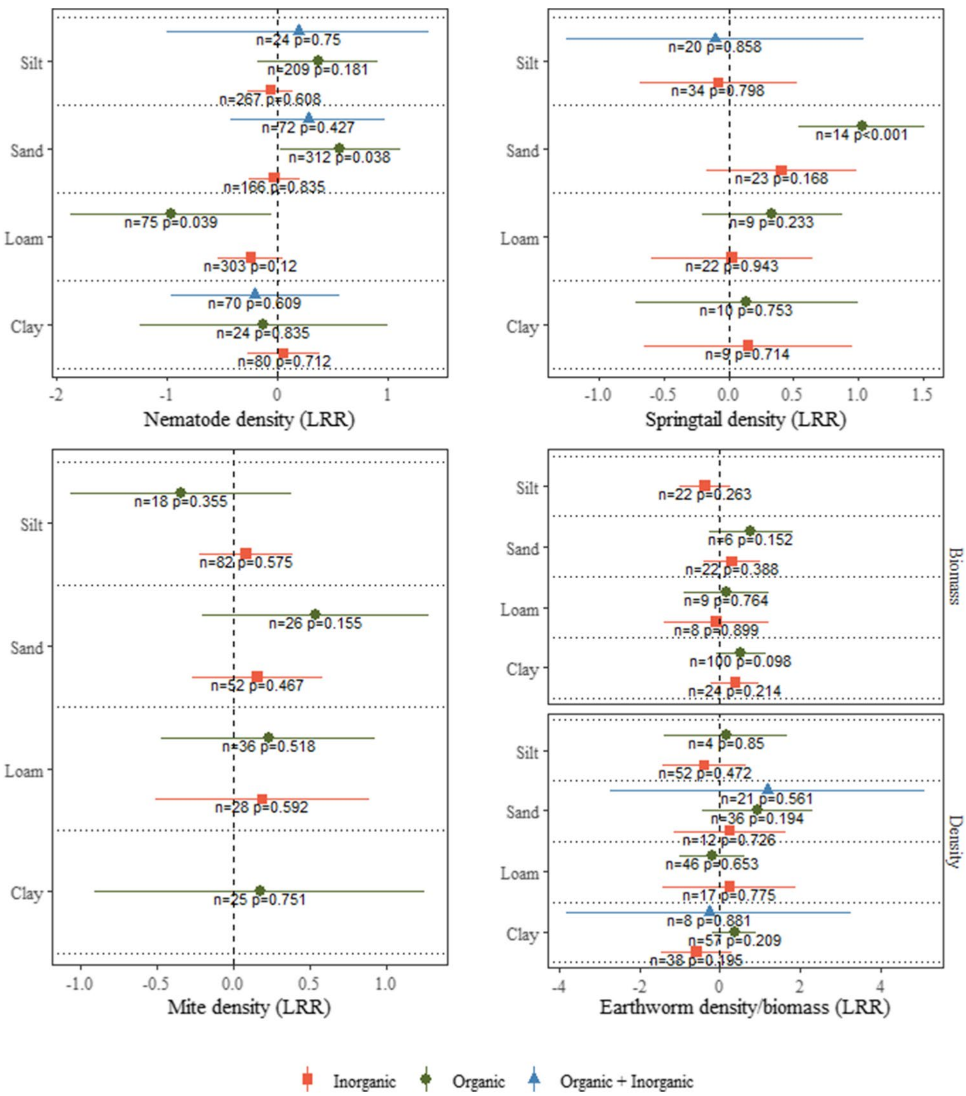

Fig. 5 Effect of different types of N fertilization in soils of different textures on the density of nematodes, springtails, and mites, as well as earthworm density and biomass as log-response ratio (LRR) compared to (unfertilized) control. Mean effects, 95% confidence intervals, sample sizes and p-values (in parentheses) for each soil texture and fertilizer type are shown

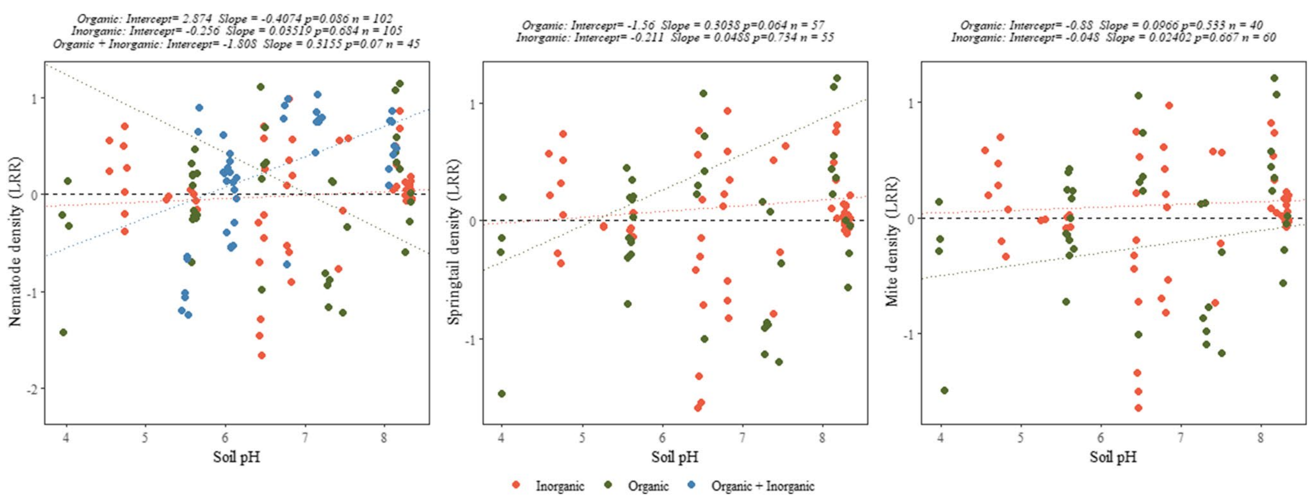

Fig. 6 Effect of different types of N fertilization in soils with different pH on density of nematodes, springtails and mites as well as earthworm biomass as log-response ratio (LRR) compared to (unfertilized) controls. Mean effects (points) and regression line (dotted: non significant, continuous: significant) are shown for different fertilizer types

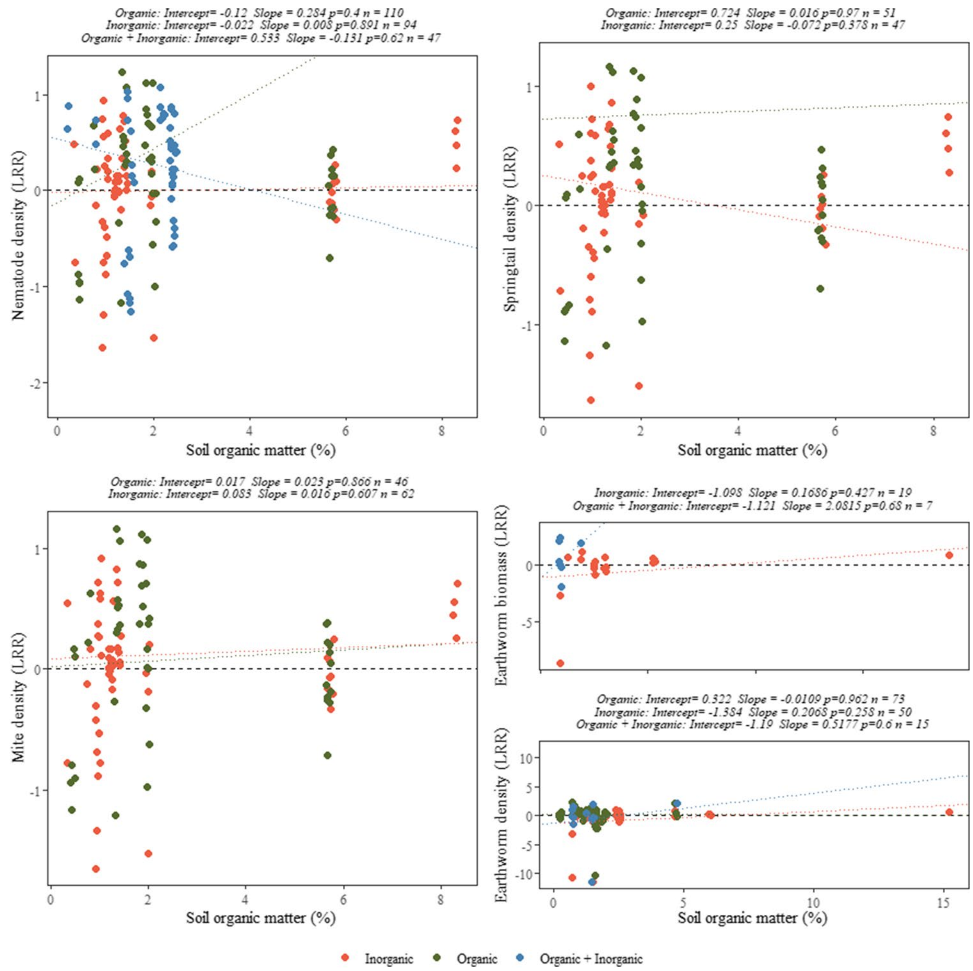

Fig. 7 Effect of different types of N fertilization in soils with different organic matter content on the density of nematodes, springtails and mites as well as earthworm biomass as log-response ratio (LRR) compared to (unfertilized) controls. Mean effects (points) and regression line (dotted: non significant, continuous: significant) are shown for different fertilizer types

to the ecological groups, we observed positive effects on the biomass of epigeic and endogeic earthworms, but no effect on their density. This seems to indicate effects more on individual growth than on population development, consistent with the explanation above concerning indirect effects due to nutrient resources and the generally short experiment duration of the studies. However, an alternative explanation could simply be the different sampling methods used in the studies selected for meta-analysis (Fig. S3), as often smaller and likely more abundant individuals may not be efficiently sampled (Schmidt 2001). Most of the studies included in the meta-analysis used digging and hand sorting; however, those studies which used mustard and formalin extractions (as more efficient methods; Schmidt (2001)) showed positive effects of N fertilization on earthworm density.

An overall positive effect especially of organic fertilizers on several taxonomic groups of soil fauna was observed. Bacterivorous, fungivorous and omnivorous nematodes become more prevalent under fertilization with organic than inorganic sources, which is consistent with previous findings of individual studies, i.e., Arancon et al. (2003); Garcia-Alvarez et al. (2004); Hu and Cao (2008); Hu and Qi (2011). Mites also responded positively to organic N fertilization, which is likely due to increased microbial biomass in fertilized treatments. The organic fertilizers may increase earthworm density and biomass by increasing food supply for earthworms, which is particularly true for species that feed directly upon surface organic matter (Edwards and Lofty 1982). Additionally, there may be indirect effects related to an improvement of the soil physicochemical properties (Kamau et al. 2019), i.e., greater structural stability (van Eekeren et al. 2009) which may result in enhanced habitat conditions.

In agreement with the findings of some individual studies, i.e., Jiang et al. (2013); Wang et al. (2006); Chen et al. (2015), inorganic fertilizers have no significant effect on the density of nematodes, springtails, mites and earthworms, as well as a negative effect on earthworm density. The application of inorganic fertilizers may have an indirect effect on soil microarthropods as it leads to higher plant biomass and root residues, which increase the microbial populations that act as food sources (Moore et al. 2003). However, the lack of an observable effect could suggest that for springtails and mites inhabiting the topmost soil layers, inorganic fertilization may not be as beneficial as direct organic fertilization, in terms

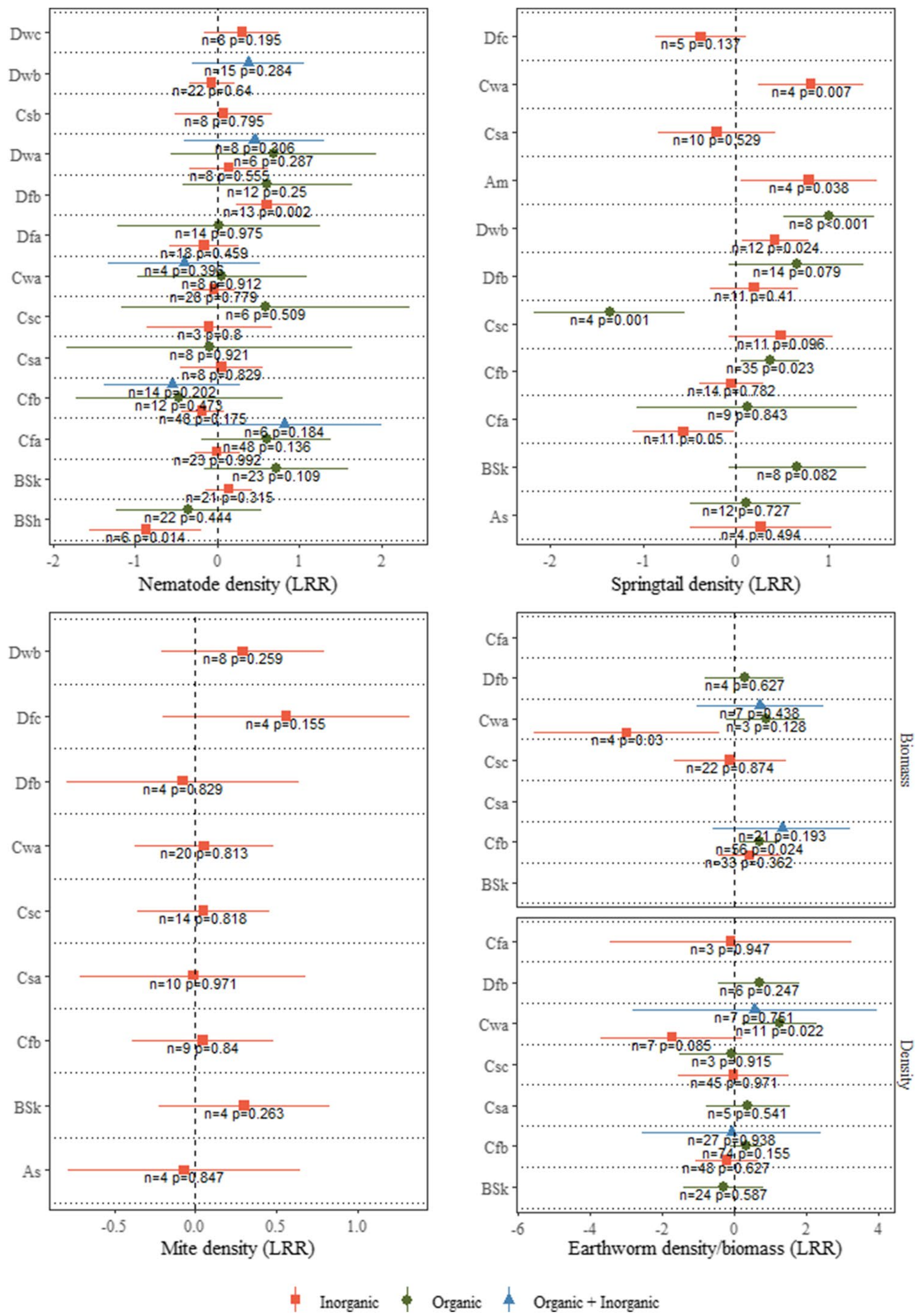

Fig. 8 Effect of N fertilization in sites with different mean annual precipitation on density of nematodes, springtails, and mites (only for inorganic fertilizers due to data sparsity), as well as earthworm biomass as log-response ratio (LRR) compared to (unfertilized) controls. Mean effects (points) and regression line (dotted: non significant, continuous: significant) are shown for different fertilizer types

of quality or accessibility (Kautz et al. 2006), or that the positive and negative effects are counterbalanced, which leads to a neutral overall effect.

The effects of N fertilization on selected soil fauna vary with fertilization intensity and duration of the fertilization regime

In addition to the nature of the fertilizer, i.e., organic or inorganic, higher organic N application rates lead to greater positive effects on nematodes and earthworms, but not on springtails or mites. This agrees with individual studies, i.e., Domek-Chruscicka and Seniczak (2005), who observed that higher doses of fertilizer did not have a positive effect on mite density but, in contrast, increased the density of springtails. It is also noteworthy that the highest N application rates documented in the studies concerned organic N inputs, which may have driven the increase of density or biomass of soil fauna.

The positive effects of combined organic and inorganic N fertilization on earthworm biomass decrease over time.

Eisenhauer et al. (2012) highlight the time lag between changes in plant productivity and the response of soil fauna, explained by the buffering effects of soil organic matter pools. Furthermore, the interrelation of biotic and abiotic properties is highly dynamic, and suffers continuous changes during a cropping season, especially under annual crops (Kanal 2004). However, our meta-analysis shows that the effect of fertilization on nematodes, springtails and mites does not vary significantly with time after fertilizer application, which may be due to data scarcity, as only a few studies reported data on the effects of fertilization on springtails and mites during an entire growing season.

The positive effects of combined organic and inorganic N fertilization on total nematode density are observed only in experiments lasting less than one year. A plausible explanation for this is that resource pulse inputs lead to fast bacterial growth, which then leads to higher bacterivorous nematode density (Ferris et al. 2001). Significant effects of organic fertilization on earthworm density are observed in experiments of 1–5 years of duration, which highlights the potential importance of the legacy effects of fertilization on earthworms (Leroy et al. 2007; Miller et al. 2019), mostly related to higher N availability, crop yield and enhanced N turnover.

The negative effects of inorganic fertilization in legumes other than soybean could be explained by the decline of bacterial feeding populations as a result of chemical fertilization, combined with the effects of crop rotation, which often determines their dominance in the nematode trophic structure throughout the cropping season (Garcia-Alvarez et al. 2004). We also noted positive effects of combined organic and inorganic N fertilization on earthworm biomass in soils sown to grasses, possibly explained by a higher amount of palatable substances associated with these plants, greater availability of decaying roots and rhizospheric microorganisms (Binet et al. 1997).

Soil properties and climatic variables modulate the effects of N fertilization on soil fauna

Concerning soil texture, the positive effect of organic N fertilization on nematode and springtail density is particularly high in sandy soils, probably because of high initial levels of nematode and springtail populations in sandy soils (Yeates and Bongers 1999), which then receive a stronger boost from N fertilizers. Furthermore, in soils with higher sand content, communities are dominated by bacterivores (van den Hoogen et al. 2019), which have a greater response to fertilization. By contrast, we observed negative effects of organic N fertilization on nematodes in loamy soils.

The effects of N fertilization on nematode density can be modulated by climatic factors. This may be explained by the findings of individual studies that reveal seasonal trends in the dynamics of the nematode community (Jiang et al. 2013), which could be understood as changes related to environmental conditions. In hot semiarid climates, we observed a negative effect of inorganic fertilization on nematode density, which may be explained by exacerbated negative effects of fertilization during dry seasons (Song et al. 2016) or by species-specific annual phenologies. The effect of N fertilization on the density of springtails also changes depending on climatic conditions. Kanal (2004) observed that the population size of springtails, particularly euedaphic species, increases proportional to the amount of rainfall and decline in dry seasons (Kautz et al. 2006). We observed positive effects of organic or inorganic fertilization on springtails in sites with continental, temperate, semiarid and tropical climates, which shows a consistent positive response of springtails in different latitudes and regardless of their vulnerability to drought (Petersen 2011).

Several factors related to agricultural management such as tillage, the application of plant protection products and herbicides, the presence of toxic compounds on the soil surface, soil salinity, site characteristics as well as seasonal variations of faunal density may have influenced the effect of N fertilization on soil fauna and therefore increased the heterogeneity of the results of our meta-analyses. For example, the disturbances on soil structure caused by tillage could potentially offset any amendment effect. These factors are unfortunately too underrepresented to be able to be included in the meta-analyses. Further research could broaden the present meta-analysis by analyzing the effects of agricultural practices on soil fauna with a higher taxonomic resolution (i.e., measurement of species-specific effects), as well as management practices occurring simultaneously (i.e., fertilization and tillage) on soil fauna, considering that in agricultural fields these practices often occur simultaneously or are scheduled within very short time in the cropping calendar.

Conclusion

The size and direction of the effects of N fertilization on soil fauna vary among different taxonomic and ecological groups, and depend mostly on the type of fertilizer used. Despite the heterogeneity of the responses, we noted that organic fertilization has a positive effect on most taxonomic groups of soil fauna, and could potentially protect soil fauna and improve the overall health of agricultural landscapes. Site-specific factors also determine the overall effect of fertilization on soil fauna. We identified varying responses of soil fauna to N fertilization, with significant increases or reductions of faunal density limited to certain taxa and some unresponsive taxonomic groups. The feeding habits, habitat preferences, the predominant life history strategy and interactions of the soil fauna with abiotic factors coupled with a complex soil-plant structure may explain the different responses of different ecologic and taxonomic groups to N fertilization. The positive observed effects on predators and omnivores can be due to bottom-up effects of increased microbial populations. Climatic conditions may affect soil temperature and moisture and cause inconsistent responses to fertilization. The interrelation of biotic and abiotic properties is highly dynamic, and suffers continuous changes during a cropping season, especially under annual crops which could also influence the response of soil fauna to fertilization. However, the observed effects of N fertilization on some faunal groups could be a transient response to resource pulses, which may indicate a lack of stability and resilience of soil fauna in the studied agroecosystems. Further research is needed on the interactive effects of agricultural practices on soil fauna, reported with a higher taxonomic resolution, as they often occur over short time periods and repeated times during the cropping calendar.

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Data availability The datasets generated during the current study are available in the BonaRes repository: https://doi.org/10.20387/bonares-hm7v-3d76.

Declarations

The authors declare no competing interests.

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