Earthworms and Nematodes: The Ecological and Functional Interactions

Jair Alves Dionísio, Wilian Carlo Demetrio and
Arlei Maceda

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Abstract

Soil invertebrate organisms are responsible for several biochemical processes indispensable for the correct functioning of ecosystems. Because of the high diversity of animals that occurs in the soil environment, some invertebrates such as earthworms and nematodes are highly important in trophic chains, with high number of species and the effect that they exert on both natural and agricultural systems. However, although numerous studies have evaluated the implications of these organisms in soil processes and their consequences on crop productivity, the interaction between earthworms and nematodes has received little attention in recent years. This chapter reviews studies focusing on the elucidation of the interaction between earthworms and nematodes in diverse situations in which they occur, for example, the vermicompost process and the native and agricultural systems. Several studies have shown that the direct and/or indirect action of earthworms can highly modify nematode populations. In addition, in the presence of earthworms, the damage caused by phytonematodes can be reduced in some crops.

Keywords: biological control, plant growth, vermicomposting, plant parasitic nematode, soil food web

1. Introduction

The first studies on earthworms were initiated by Darwin, with the classic "The Formation of Vegetable Mold through the Action of Worms, with observations on their Habits" [1]. Since then, thousands of studies related to the biology and ecology of earthworms have been performed worldwide. However, even in ancient Rome, these invertebrates had already attracted the attention of Aristotle, who described them as “the intestines of the earth” in 340BC [2].

At present, the importance of earthworms for the functioning of natural and agricultural ecosystems is recognized [3–6]. These organisms can influence the growth of plants via several mechanisms, which were described by Edwards [2] and Scheu [7], such as increasing soil organic matter mineralization; modifications of soil porosity and aggregation that change the availability of water and oxygen to plants; production of plant growth regulators via the stimulation of microbial activity; pest and parasite control; and stimulation of symbiotic microorganisms.

However, the benefits mediated by these organisms in the soils led to erroneous interpretations, mainly because of their high diversity; there are about 3500 earthworm species described worldwide, with potential of more than 7000 species [8–10]. In addition, also it is high the diversity of earthworms occurring in an area with natural vegetation or agricultural system. This has already been noted by Steffen et al. [11], who identified about 56 earthworm species in natural and agricultural ecosystems, of which 26 were native and 30 exotic, belonging to six families. In addition, the greatest diversity of these species was related to the type of ecosystem evaluated: their richness is greater in areas of forest fragments and native fields. Brown et al. [12] evaluated earthworm populations in different land use systems and observed high earthworm abundance in conservation systems with values ranging from 116 to 179 ind. m^{-2} in no-tillage and minimum tillage, respectively. The authors suggested that the greater presence of these organisms can be attributed to the lack of soil management in no-tillage, promoting the accumulation of organic material on the soil surface, and small mechanical movement, benefiting the community of these organisms. In addition to the effect of management on earthworm populations, Tanck et al. [13] found seasonality effects in the communities of *Amynthas* spp. (exotic earthworm) under no-tillage and native forests, with densities of about 170 and 93 ind m^{-2} and biomass of 50 and 65 g m^{-2}, respectively.

The remarkable diversity of earthworm species can be divided into three distinct ecological categories: epigeic, anecic, and endogeic [14]. Epigeic earthworms comprise animals living on the soil surface, by using the litter and organic horizons as habitat, feeding on organic materials at the beginning of the decomposition process, and incapable of digging galleries in the soil; they are normally used in vermicompost processes. Conversely, endogeic species live in greater depths of soil; are geophageous, taking from the soil the food necessary for their survival; and include most of the earthworms described. The anecic earthworms are organisms that live in the soil-surface interface and are considered the most active of the three categories mentioned above [15].

These ecological categories are based on the environments in which earthworms live, ingesting and transporting organic and mineral particles at different distances horizontally and vertically in the soil profile [16–18]. Because of their size and dietary habits, earthworms also unintentionally ingest a large diversity of organisms, ranging from microorganisms such as bacteria and fungi to small animals such as nematodes [15, 19, 20].

Nematodes are highly representative invertebrates in soils, with densities ranging from 106 to 10^7 m^{-2} and biomass of up to 100 kg ha^{-1} [21]. Like earthworms, these organisms also present remarkable ecological diversity, with free-living species—bacteriophages, plant-parasitic, mycophages, omnivores, and predators—responsible for the regulation of several trophic chains in the soil, and parasitic nematodes of plants or animals [22]. Population densities of

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these animals are of the order of 10^6 m^{-2} and can consume up to 800 kg ha^{-1} of bacteria [23]. However, plant-parasitic nematodes, a group with high agricultural interest, and bacteriophages, nematodes that feed on both pathogenic and saprophytic bacteria and other beneficial species, are the most representative groups in soils [24].

Considering the small size of free-living and plant-parasitic nematodes, they are inevitably ingested by other organisms, mainly by earthworms [25]. Several studies have attempted to elucidate the interactions between these groups of invertebrates; however, because of the remarkable ecological variability already mentioned, the results have not been consistent, and these interactions have not been clearly defined [26–28]. Thus, little is known about the effects of earthworms on microbial diversity and soil microfauna [29].

In this context, a series of studies were performed in order to elucidate the interactions between earthworms and nematodes, as well as the implications of these interactions with other soil organisms and plants in natural and agricultural systems. A simplified version of these interactions is shown in **Figure 1**.

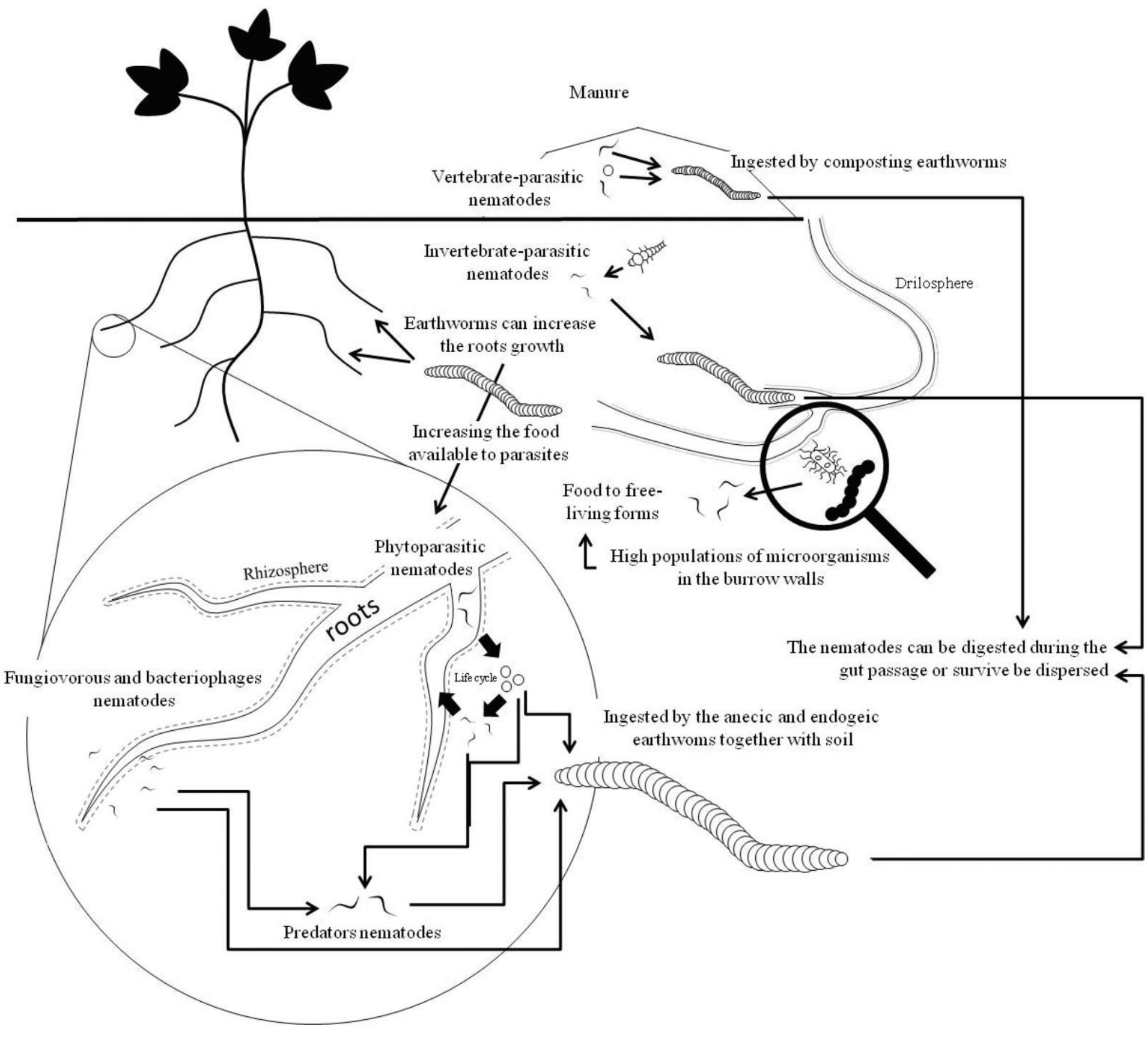

Figure 1. Interactions between earthworms and nematodes in the soils.

2. Effects of earthworms on nematode communities

The effects of earthworms on nematode communities (free living or phytonematodes) can be analyzed under four different situations. First, the effects of earthworms on the populations of nematodes during the vermicomposting process of unstabilized organic residues; second, the effects of the products generated by the action of earthworms (vermicompost) or the byproducts (vermicompost tea) as controlling agents of phytonematodes; third, when soil interaction only occurs between worms and nematodes; and fourth, when the interaction of earthworms and phytonematodes occurs in the presence of plants, the latter being more complex, with greater variability of results and thus greater difficulty of interpretation.

2.1. Earthworms and nematodes in vermicomposting process

Because of the high diversity of organisms involved and the ecological complexity of soils, the interactions between earthworms and nematodes have been completely dependent on the particularities of the surveys conducted. Domínguez et al. [28] evaluated the effects of *Eisenia fetida* (earthworms worldwide used in vermicomposting) on the population of free-living nematodes (bacteriophages and fungivorous) in cattle manure and sewage sludge. In both substrates, bacteriophage nematode populations were reduced during the evaluated period in the presence of earthworms. However, assessment of the fluctuations in nematode populations revealed that fungivorous communities were more affected by the presence of oligochaetes (**Figure 2**). The fungi represent one of the main food sources for earthworms, which might

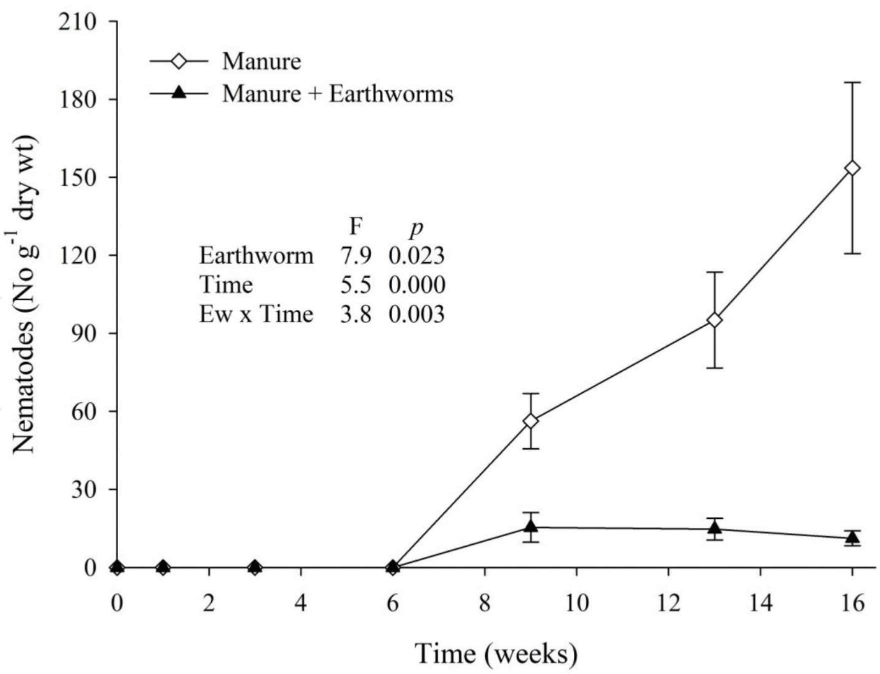

Figure 2. Fungivore nematode abundance (mean ± SE) in the presence and absence of the earthworm *Eisenia andrei* during vermicomposting of cow manure. The figure includes the results of repeated-measures ANOVA for the presence of earthworms (Source: Redrawn from [28]).

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explain the greater effect of vermicomposts on fungivorous populations than on bacteriophage populations. Conversely, earthworms can also facilitate the dispersion of these microorganisms by the excretion of their spores in the coprolites [30]. However, the dispersion of nematophagous fungi by earthworms might also be responsible for the reduction of the nematode populations in the substrates evaluated [31]. Monroy et al. [32] also observed a reduction of bacteriophage populations by the activity of several earthworm species. Kokhia et al. [33] showed that the changes in nematode communities by earthworms did not occur only at the population level, but rather led to the restructuring of all biodiversity when these invertebrates were present.

The effect of earthworms on nematode populations can be attributed to the direct ingestion and digestion, or reduction by indirect effects [34]. The indirect effect is attributed to the reduction of fungal populations by integrating the diet of the earthworms, thereby reducing communities of fungivorous nematodes [30].

2.1.1. Vermicomposting and byproducts in the control of nematodes

Although the action of vermicompost earthworms shows the reduction of populations of free-living nematodes, the application of vermicompost in soils has shown to have adverse effects. Arancon et al. [35] observed a reduction of the communities of plant-parasitic nematodes after the application of vermicompost from different plant materials. However, considering the effect similar to the use of organic compounds in this experiment, the addition of organic materials to the soil was assumed to increase the availability of food for fungivorous and bacteriophage nematodes, increasing the competition between them with other groups. Gabour et al. [36] also observed this effect of vermicompost application on the populations of the plant-parasitic nematode *Rotylenchulus reniformis*.

In addition to vermicompost, recent studies have shown that the application of vermicompost tea has the potential to control plant parasitic nematodes. In this sense, Edwards et al. [37] observed a significant suppression in the number of galls caused by *Meloidogyne hapla* in tomato crop when the plants were subjected to aerated vermicompost tea (**Figure 3**).

Mechanisms of nematode control by vermicompost tea are still poorly understood. The effects of this substance are likely caused by the death of nematodes by the release of toxic substances such as hydrogen sulfate, ammonia, and nitrite produced during vermicomposting process [38]; promotion of the growth of nematode predatory fungi that attack their cysts [39]; favoring of rhizobacteria that produce toxic enzymes and toxins [40]; or indirectly by favoring populations of microorganisms, bacteria, and fungi, which serve as food for predatory or omnivorous nematodes, or arthropods such as mites, which are selectively opposed to parasitic nematodes of the plant [41].

2.2. Earthworms and nematodes in the soils

Poinar [42] reviewed several works and published a list regarding the natural relationships between oligochaetes and nematodes, with more than 150 nematode citations, also containing a brief summary of the groups of nematodes, mainly endoparasite species, found in

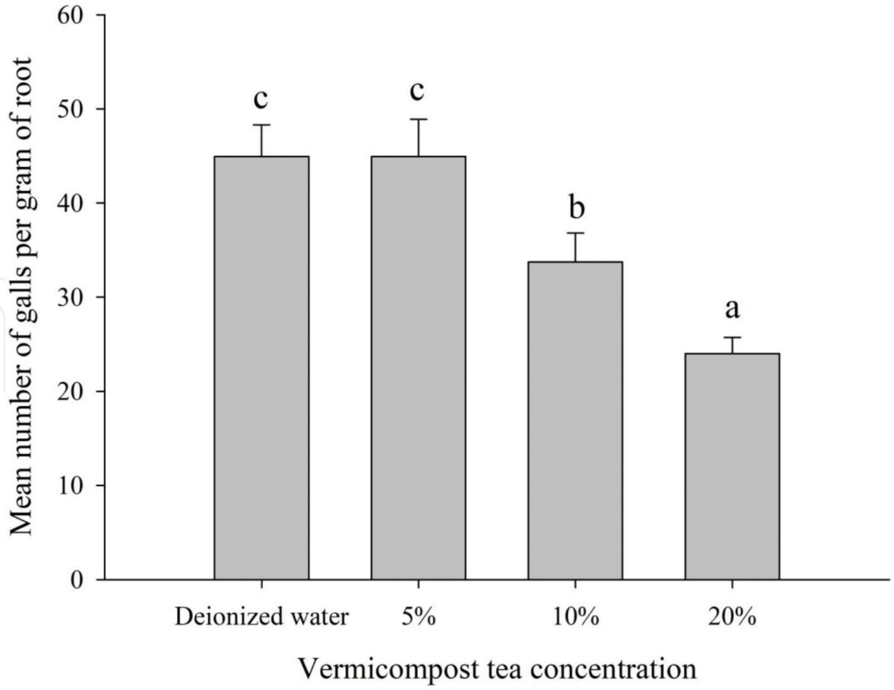

Figure 3. Mean numbers of *Meloidogyne hapla* galls (mean ± SE) on tomato roots infested with the nematodes and treated with soil drenches of vermicompost tea. Columns with different letters are significantly different ($p < 0.05$). All plants were grown in MM 360 and received all needed nutrients (Source: Redrawn from [37]).

earthworms. However, it does not present information on these endoparasites in presence of some tropical earthworm species such as *Pontoscolex corethrurus* and *Amynthas* spp. (especially *A. gracilis* and *A. corticis*), which are frequently used in studies evaluating the interaction between these organisms [26, 43–46].

The effects of geophageous earthworms on soil nematodes also differ across studies, and this variability occurs among studies that use the same worm species, which is probably related to the high diversity of these organisms, especially nematodes found in situ. Dash et al. [34] observed reductions of nematode populations in the soil in the presence of *Lampito mauritii*, an effect that occurred without the distinction of groups; however, plant-parasitic species were less affected, likely because of the low palatability of this group, which is lower than that of the free life forms. Senapati [47] also evaluated the effect of *L. mauritii* on nematode communities, but the results showed an increase in bacteriophage populations and a decrease in plant-parasitic populations, whereas Tao et al. [48] evaluated effects in the presence of *Metaphire guillelmi* in field experiments and revealed reduction of all groups of nematodes to the depth of 20 cm.

Studies by Boyer et al. [43] on *P. corethrurus*, an exotic earthworm distributed globally in tropical regions, in the laboratory by using sterilized soil showed that this species had the potential to reduce phytonematodes. They suggested that some compounds such as proteolytic enzymes released into the digestive system of earthworms seem to have an antagonistic effect on these invertebrates (**Figure 4**).

Further, Villenave et al. [46] evaluated the interaction between nematodes and *P. corethrurus* and found an increase in the population of soil nematodes, mainly of the plant-parasitic

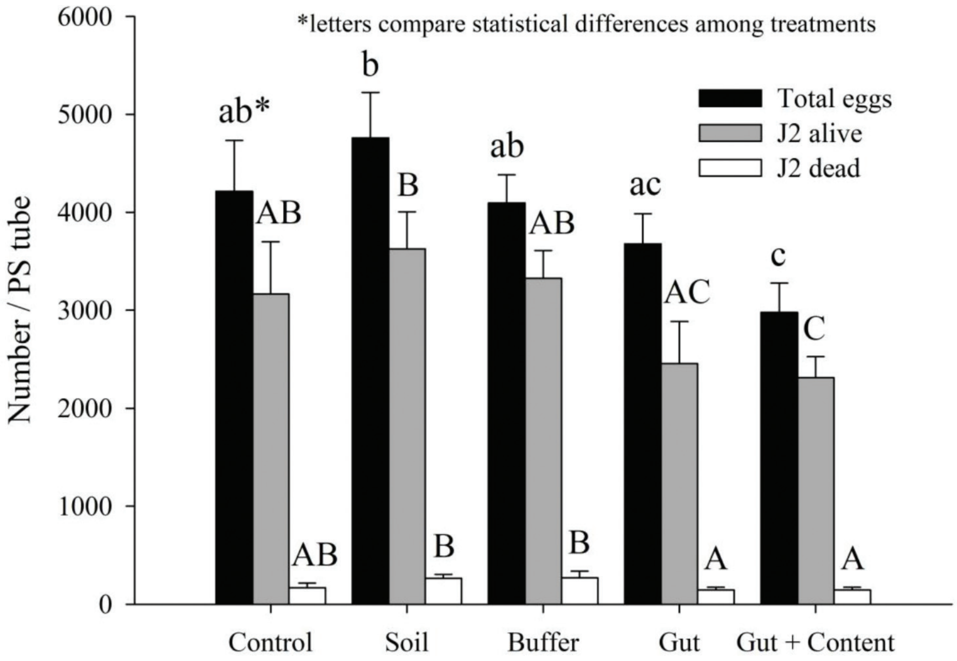

Figure 4. Living and dead J2 larvae and total eggs per polystyrene (PS) transparent tube obtained 5 weeks after exposure of J2 *Heterodera sacchari* to the *Pontoscolex corethrurus* gut contents, the *P. corethrurus* gut alone, aqueous soil extracts (Andisol), or phosphate buffer. (Source: Redrawn from [43]).

species, in a field experiment. Although these studies differed in the methodological approach, and a greater number of interactions might occur in experiments in which the substrate is not sterilized, a key factor to be observed is the earthworm density that was used in each experiment. Boyer et al. [43] used a small amount of soil (200 g) and a large number of earthworms, which would represent around 2000 m^{-2} individuals (up to 20 cm deep). However, in the experiment by Villenave et al. [46], the densities were approximately 122 earthworms m^{-2}. However, the disagreement in the results of the studies mentioned above was not necessarily an effect of the methodology used, since another factor to be considered in these interactions is the time of coexistence between worms and nematodes, which was 35 and 150 days for [43, 46], respectively. Experiments with *Lumbricus rubellus* [27] showed a reduction of the general density of soil nematodes; however, this effect occurred in a pronounced way in the first 60 days, with a reduction of bacteriophages and increase in plant-parasitic species after this period. The interaction between earthworms and nematodes, in addition to being dependent on all the variables already discussed, is also influenced by the presence of plants. Yeates [49] studied the interaction of these three components and observed the same results as those of Ilieva-Makulec and Makulec [27]. According to Yeates [49], the positive effect of earthworms on root development also increases the rhizospheric area, which is a highly complex zone in which frequent release of cells, mucilages, exudates, and lysates that contain amino acids, enzymes, proteins, sugars, carbohydrate complexes, alcohols, vitamins, and hormones [50], thereby increasing the food for microorganisms and thus for nematodes (**Figure 5**). Räty and Huhta [51] showed that some abiotic conditions such as soil pH also modify the behavior of earthworms and nematodes in the soil.

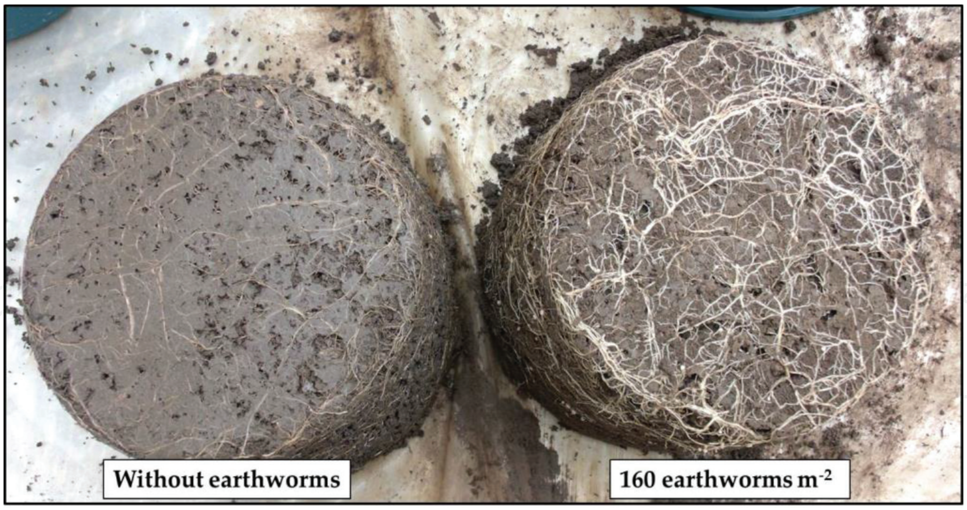

Figure 5. Effects of earthworms on the growth of bean roots (Source: Authors).

The effect of earthworms on the environment are not only restricted to the changes that occur in the soil ingested by these animals. Tiunov et al. [52] evaluated the populations of nematodes on the walls of the galleries of *L. terrestris* and found communities of bacteriophage nematodes associated with this environment. Thus, like coprolites, the walls of earthworm galleries are rich in nitrogen compounds that promote the development of microorganisms in these sites, which might also favor the development of nematodes.

In addition to all the results cited above, earthworms can also act as a transport vehicle for these small invertebrates. Shapiro et al. [53] reported the ability of *L. terrestris* and *A. trapezoides* to disperse within the soil *Steinernema carpocapsae*, the parasitic nematode of over 250 species of insects.

2.3. Interaction between earthworms and nematodes and their effects on plants

Few studies have investigated the effects of earthworm and nematode interactions on plant growth [26, 44, 45, 54].

Dionísio et al. [26] evaluated the effect of the inoculation of earthworms *P. corethrurus* and *Amynthas* spp. in tomato plants infested with the plant-parasitic species *Meloidogyne paranaensis* in a greenhouse. Six adult worms of *Amynthas* spp. or *P. corethrurus*, isolated or in the same proportion (3, 3), were inoculated in pots containing soil sterilized in a steam oven. After 1 week, tomato seedlings (Rutgers" cultivar) were transplanted into the pots, and 5 mL of a suspension of *M. paranaensis* containing 5000 eggs and/or juveniles was inoculated per pot. The authors observed a reduction in the number of galls plant per plant after 65 days in the treatments in which the earthworms were inoculated, with reduction varying from 39.2 to 55.2% for *Amynthas* spp. and *P. corethrurus*, respectively (**Figure 6**). Nonetheless, the combination of the two species resulted in the reduction of 50.0% incidence of galls.

The authors indicated that the action of the earthworms occurred probably after the inoculation of the nematodes, because tomato is highly susceptible to attack by nematodes, especially

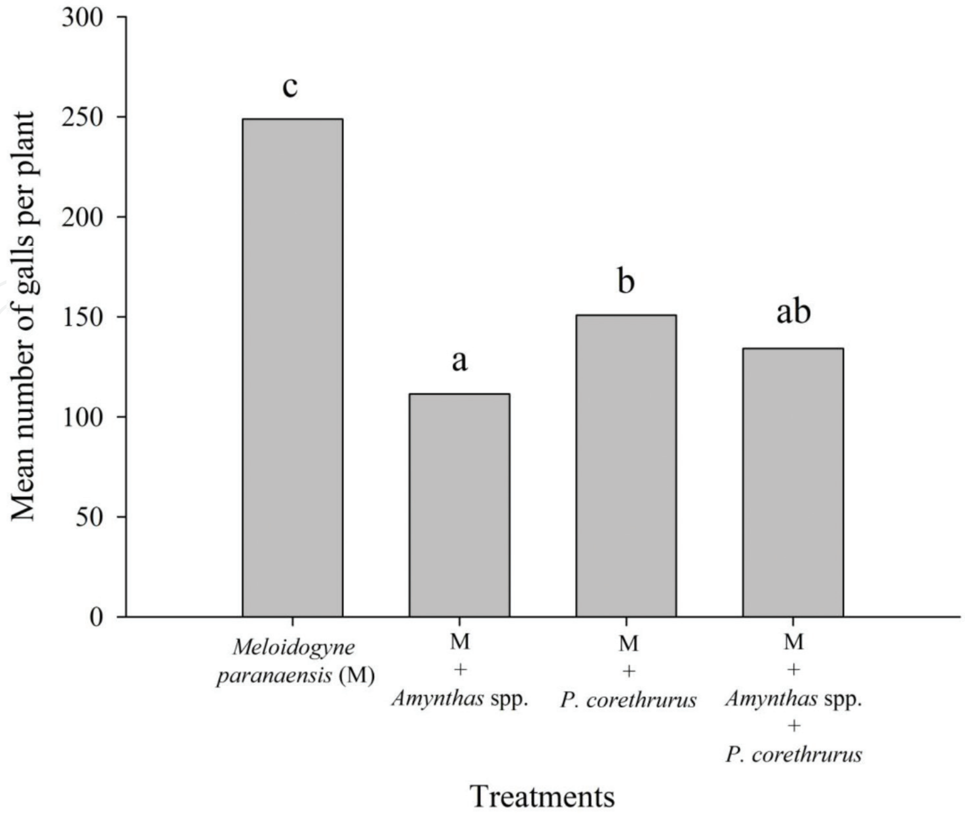

Figure 6. Galls per tomato plant (*Solanum lycopersicum* "Rutger") inoculated with earthworms (*Amynthas* spp. and *P. corethrurus*) and plant parasite nematodes. Letters indicate statistical differences ($p < 0.05$) by Tukey's test (Modified from [26]).

at the seedling stage [55]. Thus, two explanations were presented. First, the earthworms *Amynthas* spp. and *P. corethrurus* are epigeic and endogeic, respectively, and ingested a greater (*P. corethrurus*) or smaller (*Amynthas* spp.) soil quantity. Further, they might also have ingested eggs/juveniles of *M. paranaensis*, which might have been destroyed or inactivated in the passage through the digestive system, thereby reducing the possibility of gall formation in plants. Second, the eggshell of *M. paranaensis* might have been destroyed by the enzymes in the digestive tract of earthworms, mainly chitinase [30], releasing the larvae inside. Thus, the released larvae remained in the infested state in the tissues, coelom, and hemocele without essential development and, normally, without growth, what is called as paratenosis [56]. Therefore, future experiments are needed to perform parasitological tests of the earthworm tissues to better interpret the results.

Contrary results are cited by Lafont et al. [44] evaluating the effects of *P. corethrurus* and *Radopholus similis* (cave nematodes) on banana plants (*Musa acuminata*, subgroup Cavendish, "Grande-Naine"). The study was conducted in a greenhouse by using pots containing soil, which was previously frozen (−20°C) for 2 days to eliminate the native microfauna. The total biomass of inoculated *P. corethrurus* was 5.0 (g pot^{-1}); 4 weeks later, the plants were inoculated with a *R. similis* suspension containing 450 eggs. The results showed the absence of the control of nematodes in the soil; however, the plants developed better in the presence of earthworms (**Figure 7**) and also showed a reduction in the severity of necrosis in the root system. Similar

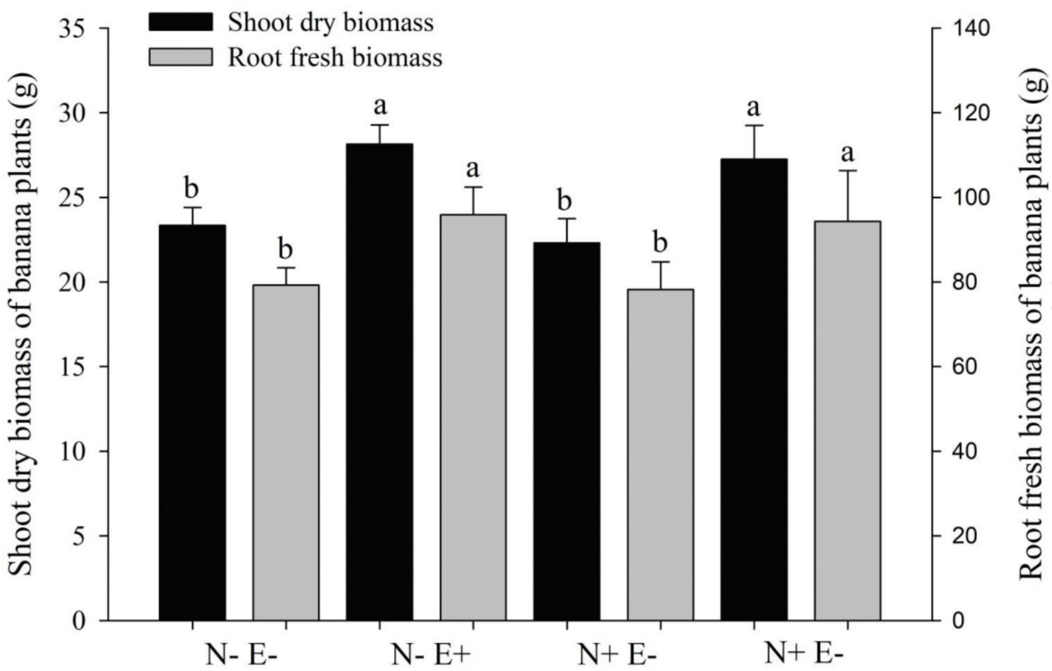

Figure 7. Shoot dry and root fresh biomass of banana plants under different treatments at the end of the experiment: N- E- Absence of fauna; N- E+ *P. corethrurus earthworms* alone; N+ E- *R. similis* nematodes alone; N+ E+ earthworms plus nematodes. Bars indicate standard errors, n = 12. For each treatment, the means with the same letter are not significantly different based on Bonferroni test at $p < 0.05$ (Source: Adapted from [44]).

results have also been reported by Loranger-Merciris [45] by using *P. corethrurus* in banana plants infected with *R. similis*, *Helicotylenchus multicinctus*, and *Pratylenchus coffeae*.

The reduction of nematode damage in plants in the presence of earthworms was also observed by Demetrio et al. [54], who evaluated the potential of the earthworm *Amynthas* spp. in reducing the infection of *Meloidogyne javanica* (worldwide parasite of tomato crop) as well as the effects of the inoculation of these organisms on some soil biological attributes. Under similar conditions as those used in [26], different densities of *Amynthas* spp. were inoculated (0, 2, 4, 6, and 8 animals per pot) in the presence of tomato plants, which received a suspension containing 3000 eggs and/or juveniles of *M. javanica*. At the end of the experiment, the increase in carbon content of the microbial biomass and positive correlation of this attribute with the dry mass of the plants was verified. The results of this experiment showed that the earthworms were not able to reduce the infection of the plant-parasitic species in the tomato roots; however, in the presence of these invertebrates, the damage caused was reduced. Further, a positive correlation was noted between the number of inoculated earthworms and the dry mass of tomato (**Figure 8a**).

The better development of plants even with the formation of galls in the presence of earthworms can be attributed to several factors: physical changes of the soil by the action of these invertebrates, since galleries formed are normally used by plants as a preferred route for root growth, in addition to facilitate the infiltration of water and oxygen throughout the soil profile [57]. Second, chemical changes, which might increase the availability of P and N mainly, because of the acceleration of nutrient cycling, as well as the continuous deposition of NH_4^+

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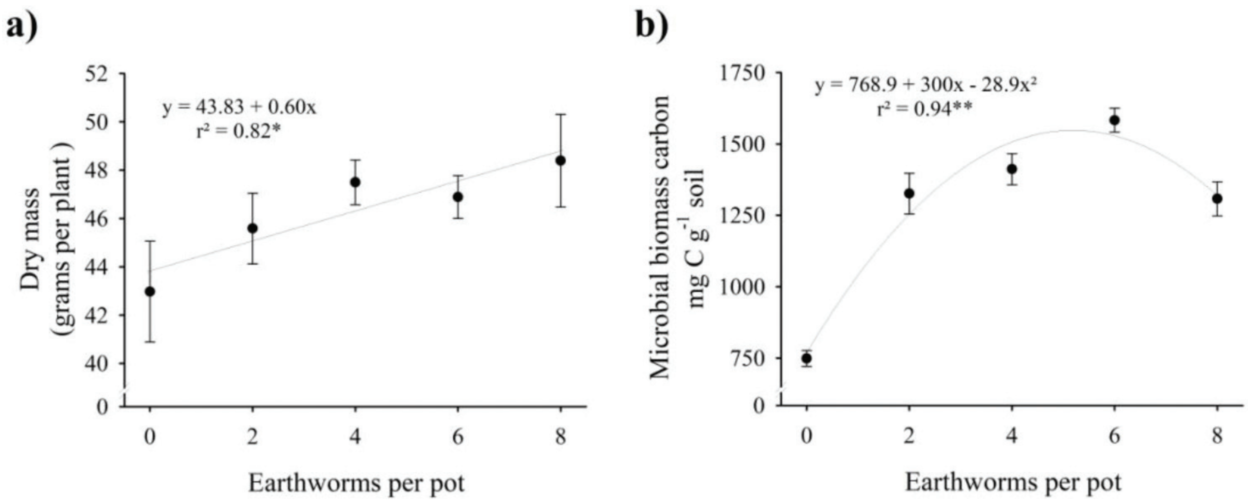

Figure 8. Effects of the levels of earthworms (*Amynthas* spp.) and nematodes (*Meloidogyne javanica*) in (a) dry mass of tomato plants; (b) soil microbial biomass (Source: Modified from [54]). *,** significance at $p < 0.05$ and $p < 0.01$, respectively.

by earthworms, both by the production of casts and organo-mineral excrements. These processes could stimulate communities of nitrifying bacteria and growth-regulating-hormone producers, as well as the deposition of mucus-rich nitrogen compounds on the walls of the galleries [7, 47, 48].

The physico-chemical variations promoted by the earthworms alter the biological component of the soil, thereby mainly stimulating the microorganisms (**Figure 8b**) that can be reflected in the colonization of the roots by arbuscular mycorrhizal fungi [58]. This contributes to the greater absorption of nutrients, mainly phosphorus; the development of plant growth-promoting rhizobacteria [59] such as *Pseudomonas* spp. fluorescents [60], which produce siderophores, that is, increase the availability of Fe^{2+} to plants; or to the production of antibiotics that inhibit the effects caused by clinical and subclinical pathogens [61]. These physico-chemical and biological factors can favor the development of plants and compensate for the damage caused by plant-parasitic species in the roots.

The results of these studies showed that earthworms have a remarkable potential to be used as an alternative in the biological control of plant-parasitic species in several crops; however, further studies are needed to elucidate the mechanisms involved in this process as well as to reveal the interactions with other plants.

3. Final considerations

The complete understanding of the effects of earthworms on nematode communities requires further studies. Considering the studies performed in controlled systems, earthworms seem capable of altering the communities of these invertebrates; however, the effects of other factors such as non-sterilization of the soil and addition of vegetal components could change the number of interactions that exist in this environment, often leading to the generation of contradictory results. The lack of adequate and standardized methodologies for determining the interaction between these organisms and the different habits of life of the nematodes and earthworm species are factors that contribute to the differences found among studies. Nevertheless, this ecological complexity is a part of the soil; therefore, it should be considered in future studies.

Because of the potential to reduce the damage caused by plant-parasitic species, studies with different ecological categories of earthworms need to be performed to understand the interactions occurring in different species and the use of these invertebrates as a tool in the biological control of plant-parasitic nematodes.

Author details

Jair Alves Dionísio[1]*, Wilian Carlo Demetrio[1] and Arlei Maceda[2]

*Address all correspondence to: jair@ufpr.br

1 Federal University of Paraná, Curitiba, Brazil

2 Agricultural Defense Agency of Paraná, Curitiba, Brazil

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