



Epigeic earthworms increase soil arthropod populations during first steps of decomposition of organic matter

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ABSTRACT

Earthworms and soil arthropods are major groups involved in soil decomposition processes. Although the interaction between these organisms can influence decomposition rates, little is known about their population dynamics during the decomposition of organic matter. In this study, we used the pig manure decomposition process to evaluate the effects of the presence of the epigeic earthworm *Eisenia fetida* on seven groups of soil arthropods: springtails, astigmatid, prostigmatid, mesostigmatid and oribatid mites, psocids and spiders. We carried out an experiment in which low and high doses (1.5 and 3 kg, respectively) of pig manure were applied in consecutive layers to small-scale mesocosms with and without earthworms. The presence of *E. fetida* increased the overall number of soil arthropods regardless of the dose of manure applied. This result was mainly due to the presence of large populations of springtails and mesostigmatid mites. Springtails were more abundant in the new layers of the mesocosms, which indicated a preference for substrates with fresh organic matter and higher microbial biomass. The other arthropod groups were consistently favored by the presence of earthworms, but remained at low densities throughout the decomposition process. Only the psocids were negatively affected by the presence of *E. fetida*. These results suggest that the development of large populations of soil arthropods, mainly springtails, in the mesocosms with earthworms is a characteristic feature of the initial stages of the earthworm-driven decomposition process.

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Introduction

Soil invertebrates are known to play an important role in regulating the number and activity of decomposer microorganisms in soil systems (Lavelle and Spain 2001). These invertebrates are usually present in diverse communities, and their impact on the decomposition process depends on the result of complex interactions (Scheu 2002). Soil invertebrates can affect microbial decomposer activity by grazing directly on microorganisms, ingesting organic particles inhabited by fungi and bacteria, and by increasing the surface area for microbial colonies after comminution of organic materials (Lavelle and Spain 2001). These activities enhance the turnover rate and productivity of microbial populations, thereby increasing the amount of decomposed organic matter (Berg and Laskowski 2006). The relative abundance of the different groups of soil animals will depend on the type of microorganisms available and on the physicochemical characteristics of the environment (Beare et al. 1992). When the availability of water is restricted and the pH is low, as in surface litter environ-

ments, decomposer fungi are more abundant than bacteria. Such conditions support a dominantly fungivorous fauna, mainly fungal feeding nematodes and microarthropod groups (Beare et al. 1992). However, fungi are absent from or are dormant in anaerobic soils and water-rich environments such as animal faeces (Garrett 1981) and the bacterial biomass may be twice that of fungi (Aira et al. 2006). Such environments present a dominantly bacterivorous fauna, mostly composed of protozoa and bacterial feeding nematodes (Monroy et al. 2008). Ultimately, the type of decomposer community and the trophic relationships among its members will be important in determining the rates of organic matter decomposition (Beare et al. 1992).

The activity of large soil organisms, such as earthworms, can alter the physicochemical conditions that affect the composition of the microbial decomposer community, entailing changes in the availability of resources for the different groups of small soil invertebrates (Lavelle and Spain 2001). The influence of earthworms on soil animals may also be direct, mainly through the ingestion of microfaunal groups (protozoa and nematodes) that are present within the organic detritus consumed (Monroy et al. 2008). Other larger soil animals, such as soil arthropods, are not directly consumed by earthworms (Edwards and Bohlen 1996), and their populations may benefit indirectly from the formation of macrop-

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Table 1
Results of the repeated measures ANOVA for density (No. of ind. g⁻¹ dw) of soil arthropod groups in the mesocosms with pig manure.

Source of variation	df	Collembola		Astigmata		Mesostigmata		Prostigmata		Oribatida		Psocoptera		Araneae	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P
<i>Between subjects</i>															
Dose	1, 8	1.31	ns	42.47	<0.001	1.22	ns	7.69	0.024	2.77	ns	5.38	0.050	0.01	ns
EW	1, 8	8.07	0.022	9.61	0.015	20.82	0.002	1.53	ns	5.11	0.054	7.41	0.026	16.67	0.004
Dose × EW	1, 8	0.08	ns	26.88	<0.001	3.46	ns	1.43	ns	3.04	ns	1.03	ns	0.06	ns
<i>Within subjects</i>															
Age	11, 88	2.82	0.027 ^a	3.98	0.006 ^a	1.12	ns	5.39	<0.001 ^a	0.71	ns	3.36	0.011 ^a	0.66	ns
Age × Dose	11, 88	0.92	ns	4.29	0.003 ^a	1.00	ns	2.39	ns ^a	1.02	ns	2.36	ns ^a	1.17	ns
Age × EW	11, 88	3.40	0.08 ^a	2.34	ns ^a	0.92	ns	1.60	ns	0.53	ns	1.59	ns	0.78	ns
Age × Dose × EW	11, 88	1.20	ns	1.93	ns ^a	0.82	ns	1.00	ns	1.10	ns	1.86	ns ^a	1.29	ns

Dose = dose of pig manure: low (1.5 kg), high (3 kg); EW = presence/absence of earthworms (*Eisenia fetida*); Age = age of the layers of the mesocosms (2–36 weeks); ns = not significant.

^a Huynh–Feldt's adjusted values of *P*.

ores and the availability of earthworm excreta (Salmon 2004). The occurrence of earthworms at high densities (Monroy et al. 2006) is expected to increase their effect on the soil fauna, promoting rapid changes in the populations of the different invertebrate groups. In fact, it has been shown that dense earthworm populations can cause significant reductions in the number of soil nematodes after 72 h (Aira et al. 2008).

In the case of soil arthropods, earthworm-mediated changes in populations during organic matter decomposition are expected to be positive. Some of the most abundant soil arthropod groups (e.g., springtails and oribatid mites) are fungivorous organisms, and therefore increases in fungal biomass during decomposition (Aira et al. 2006, 2008) would favor their presence. Because of this trophic link, changes in their numbers are probably driven by microbial population dynamics. Furthermore, the decomposition of organic matter is a donor-controlled process (Pimm 2002), in which the rate of detrital input is expected to be a major factor influencing the interactions within the decomposer community. The supply of additional food resources may have contrasting effects depending on the decomposer group considered (Maraun et al. 2001).

In the case of epigeic earthworms (earthworm species that feed and live in the litter layer), variation in the amount of detritus involves variation not only in the availability of food but also of space. If the availability of these resources influences the feeding behavior of earthworms and their effect on the composition of the microbial community (Monroy et al. 2009), it is also expected to have a significant impact on the presence and abundance of soil arthropods.

In the present study, we used the pig manure decomposition process to evaluate the effect of epigeic earthworms on the decomposer community (Aira et al. 2006). We carried out an experiment with small-scale mesocosms to investigate the effect of the presence of earthworms, time and application doses of pig manure on the number of soil arthropods. Since soil arthropods constitute a major group of microbial consumers (Lavelle and Spain 2001) and earthworm activity can increase the microbial biomass during the decomposition process of pig manure (Aira et al. 2006), we hypothesized: (1) that the addition of earthworms would have a positive effect on the number of soil arthropods in the pig manure, and (2) that this increase would depend on the dose of manure provided.

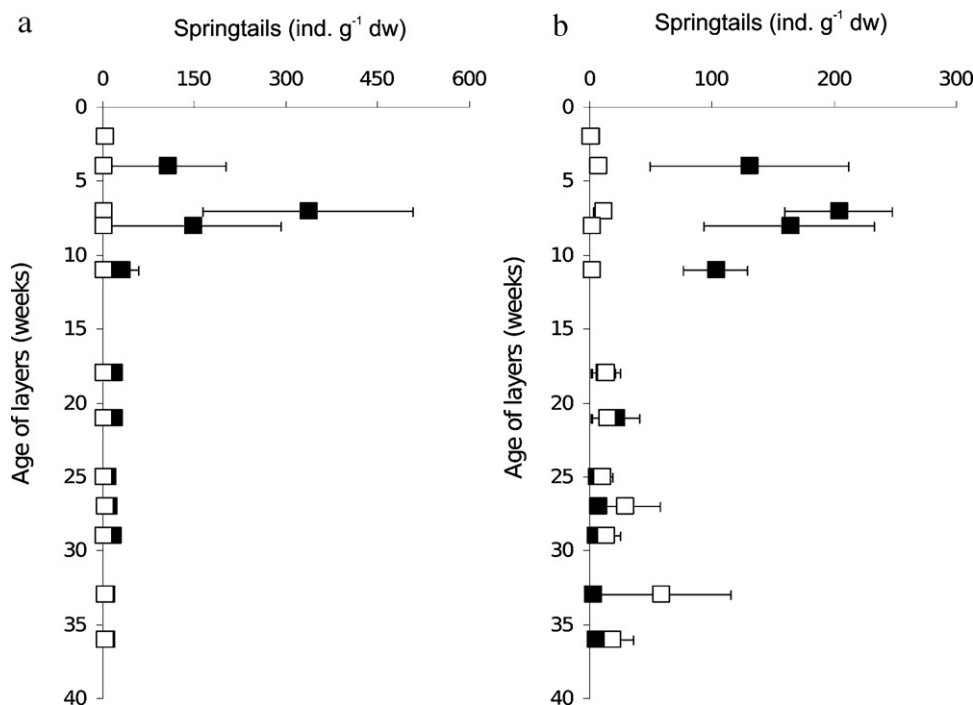


Fig. 1. Springtail (Collembola) numbers in mesocosms ($n = 3$) supplied with doses of 1.5 kg (a) and 3 kg of pig manure (b), and with *Eisenia fetida* (filled symbols) and without *E. fetida* (open symbols). Variable values (means \pm SE) corresponding to the age of the layers of pig manure are shown on the y axis. Note the different scaling of the x axes in the two graphs.

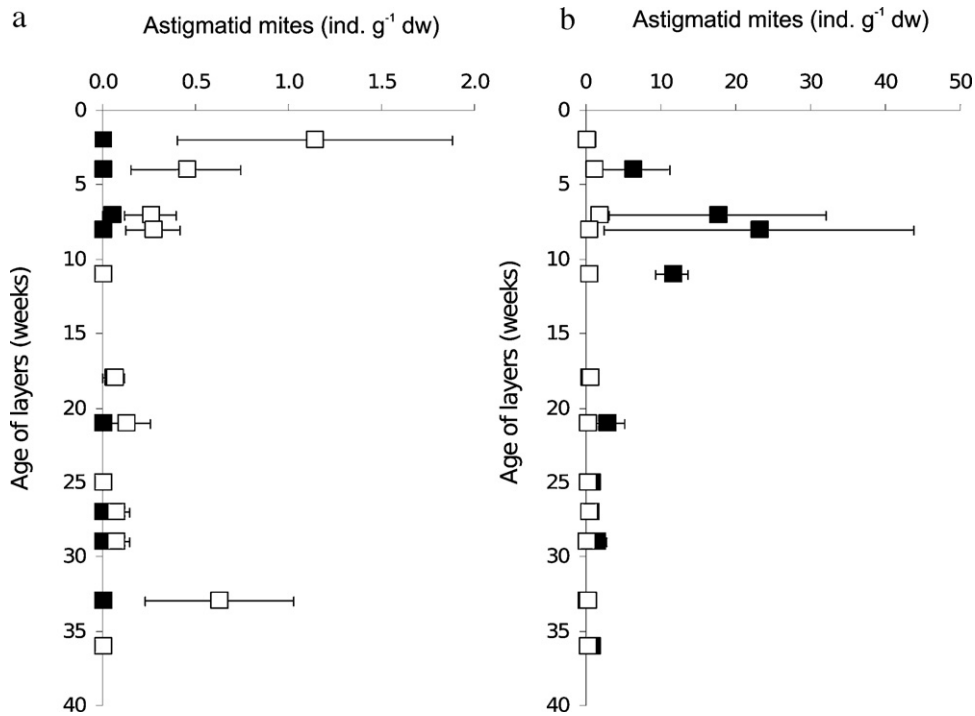


Fig. 2. Number of astigmatid mites in mesocosms ($n=3$) supplied with doses of 1.5 kg (a) and 3 kg of pig manure (b), and with *Eisenia fetida* (filled symbols) and without *E. fetida* (open symbols). Variable values (means \pm SE) corresponding to the age of the layers of pig manure are shown on the y axis. Note the different scaling of the x axes in the two graphs.

Materials and methods

Earthworms and pig slurry manure

Specimens of the lumbricid earthworm *Eisenia fetida* (Savigny, 1826) were obtained from stock cultures reared under laboratory

conditions ($20 \pm 2^\circ\text{C}$). Fresh pig slurry manure was used as a food source for the earthworms and was obtained from a pig-breeding farm near the University of Vigo. The solid fraction (15% dry weight) of the slurry manure was selected in order to avoid any harmful effects that leachates may have on earthworms. The manure was homogenized, stored in sealed plastic containers and kept at

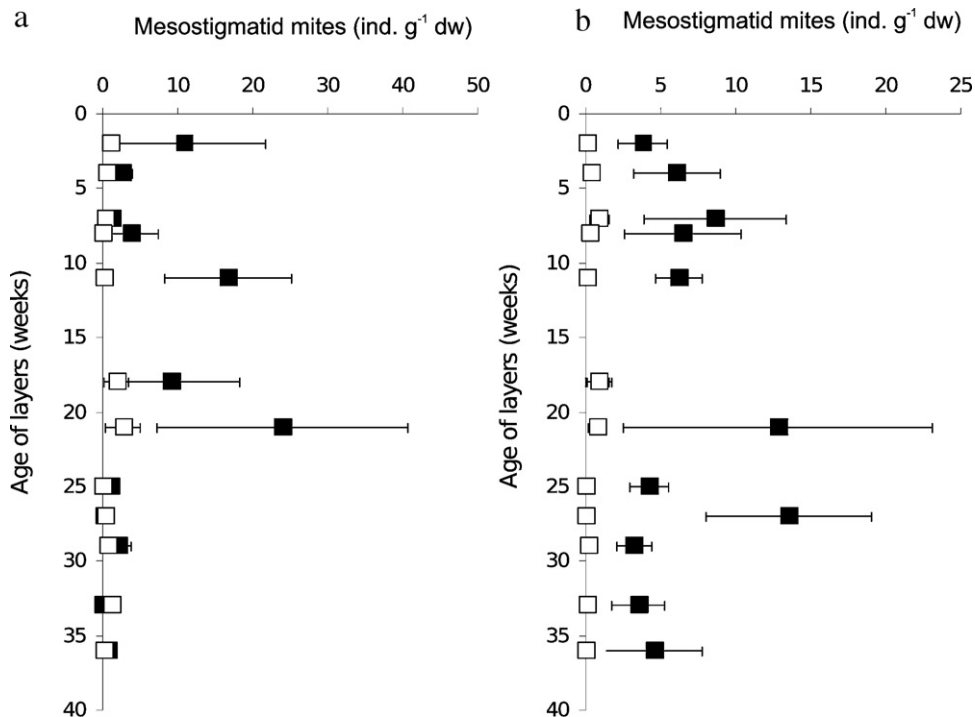


Fig. 3. Number of mesostigmatid mites in mesocosms ($n=3$) supplied with doses of 1.5 kg (a) and 3 kg of pig manure (b), and with *Eisenia fetida* (filled symbols) and without *E. fetida* (open symbols). Variable values (means \pm SE) corresponding to the age of the layers of pig manure are shown on the y axis. Note the different scaling of the x axes in the two graphs.

5 °C until use. The main physicochemical characteristics of the pig manure are described elsewhere (Monroy et al. 2009).

Experimental set up

Time-associated changes in the number of soil arthropods in the pig manure were studied by use of continuous feeding vermireactors (Aira et al. 2006). These small-scale mesocosms consisted of PVC modules resembling sieves, with an external diameter of 30 cm. The mesh size was 5 cm, which allowed mobility of earthworms between modules. To set up the mesocosms, a module with fresh pig manure was placed on top of another module containing vermicompost and earthworms. Pig manure was applied in doses of 1.5 or 3 kg fresh weight, using 2- or 4-cm high modules (low and high doses, respectively). New modules with the same amount of pig manure were added sequentially, as required (depending on the feeding activity of the earthworm population). This procedure allowed us to determine the age of the added modules at the end of the experiment.

The experimental set up consisted of twelve of the above-mentioned mesocosms. Six of the mesocosms received a low dose of pig manure and the other six a high dose. For each dose, three mesocosms were inoculated with 500 mature specimens of *E. fetida* and three were left without earthworms (control). Addition of 500 earthworms to the mesocosms provided an initial density of $\approx 7000 \text{ ind. m}^{-2}$, which is within the range observed for *E. fetida* in the field (Monroy et al. 2006). After 36 weeks, the mesocosms provided modules of increasing age, resembling a time profile. Twelve modules, of ages 2, 4, 7, 8, 11, 18, 21, 25, 27, 29, 33 and 36 weeks, were dismantled and isolated, to prevent the earthworms escaping. The earthworms were then manually removed from the substrate, counted and weighed and samples were taken from all the modules in order to quantify the number of soil arthropods.

Faunal analysis

The soil arthropods were separated from the pig manure by the use of a modified Tullgren extractor (Edwards 1991). Samples of 30 g (fresh weight) of pig manure were placed on 2-mm sieves under light bulbs (40 W), for 72 h. The arthropods fell through metal funnels placed under the sieves and were collected in glass jars containing 70% ethanol. The individuals thus collected were counted under a dissecting microscope (40 \times) and sorted into four main groups: mites (Acari), springtails (Collembola), psocids (Psocoptera) and spiders (Araneae). Mites were additionally sorted into the orders Astigmata, Prostigmata, Mesostigmata and Oribatida, following the descriptions given by Dindal (1990).

Statistical analysis

Data were analyzed by use of the R environment (R Development Core Team 2010). A repeated-measures analysis of variance (ANOVAR) was performed on the number of Collembola and the different groups of Acari. A linear model was assumed, where the repeated subject (the mesocosm) was random and the remaining effects were fixed (Potvin et al. 1990). This model was analyzed by including the Error () statement within the aov () function (Venables and Ripley 2002), with the mean square of the repeated subject (the mesocosm) as the appropriate error term. Before the analysis, soil arthropod counts were $\log(x+1)$ -transformed. Violation of the sphericity assumption of the ANOVAR (Maulchy's test) was addressed with the application of the Huynh–Feldt correction to the significance levels (Potvin et al. 1990). Values given throughout the text are means \pm SE.

Results

Earthworm population

After 36 weeks, the mean population of *E. fetida* in the mesocosms with earthworms was 2800 ± 200 individuals, with a mean biomass of 700 ± 30 g. This signified a 5- and 8-fold increase, respectively, in the initial number and biomass of the inoculated population of *E. fetida*. There were no significant differences in the size of the earthworm populations in the mesocosms with low and high doses of manure. Seventy percent of the earthworms were located in the 2- and 4-week-old manure layers, with ca. 1000 individuals per layer. The rest of the earthworms were distributed throughout the 7-, 8-, 11- and 18-week-old layers, with no more than 200 individuals per layer. No earthworms were found in the remaining, older layers (21, 25, 27, 29, 33 and 36 weeks old).

Soil arthropod populations

Collembola were the most abundant arthropod group in the mesocosms (52.1%). The number of springtails was 67 times greater in the mesocosms with *E. fetida* than in those without earthworms (Table 1). In the mesocosms with earthworms, the number of these arthropods also depended on the age of the layers of pig manure (age \times earthworm interaction, Table 1). Springtails were more frequent in the young layers (4–11 weeks old) of the mesocosms, where the *E. fetida* population was located (Fig. 1a and b). The dose of pig manure had no effect on the number of springtails (Table 1).

Acari were the second most abundant group of soil arthropods (33.5%) present in the mesocosms. Astigmatids and mesostigmatids were the most frequent mites (23.3% and 51.4%, respectively), while prostigmatids and oribatids represented less than 12% of the total mite population. As with springtails, the numbers of mites generally increased in relation to the presence of *E. fetida* (ANOVAR $F_{1,8} = 16.23$, $P = 0.004$), although the extent of the effect depended on the order of mite considered. The presence of earthworms only increased astigmatid mite numbers in the mesocosms with high dose of pig manure (Fig. 2b). In the low dose mesocosms, the presence of *E. fetida* had rather a negative effect on the number of these mites (dose \times earthworm interaction, Table 1; Fig. 2a). Variation in astigmatid numbers also depended on the age of the layers (Table 1), with the greatest numbers of the mites found in the young layers (2–11 weeks old) of the mesocosms (Fig. 2a and b).

Mesostigmatid mites were 11.5 times more abundant in the mesocosms with earthworms than in those without. Neither the age of the layers nor the dose of pig manure affected the number of these mites (Table 1, Fig. 3a and b). In contrast with the observed effects in mesostigmatids, the presence of earthworms had no significant effect on the number of prostigmatids (Table 1). In general, prostigmatids were more abundant in the young layers (2–11 weeks) of the high dose mesocosms (Table 1). Oribatid mites were more frequent in the mesocosms with *E. fetida*, especially in those with low doses of pig manure. However, this effect was only marginally significant (Table 1). Oribatids were absent from several layers of the mesocosms and their populations were not affected either by the age of the layers or the dose of pig manure (Table 1).

Psocids were the only arthropod group that was consistently lower in the presence of earthworms (Table 1). Furthermore, psocids were 3.7 times more abundant in the mesocosms with high doses of pig manure than in those with low doses. In the low dose mesocosms, the negative effect of *E. fetida* led to the absence of psocids from most layers. Independently of the dose of pig manure and the presence of earthworms, psocids were more abundant in the young layers of the mesocosms (Table 1). Variation in the numbers of spiders was directly related to the presence of *E. fetida* (Table 1). Spiders were absent from most of the layers of the mesocosms

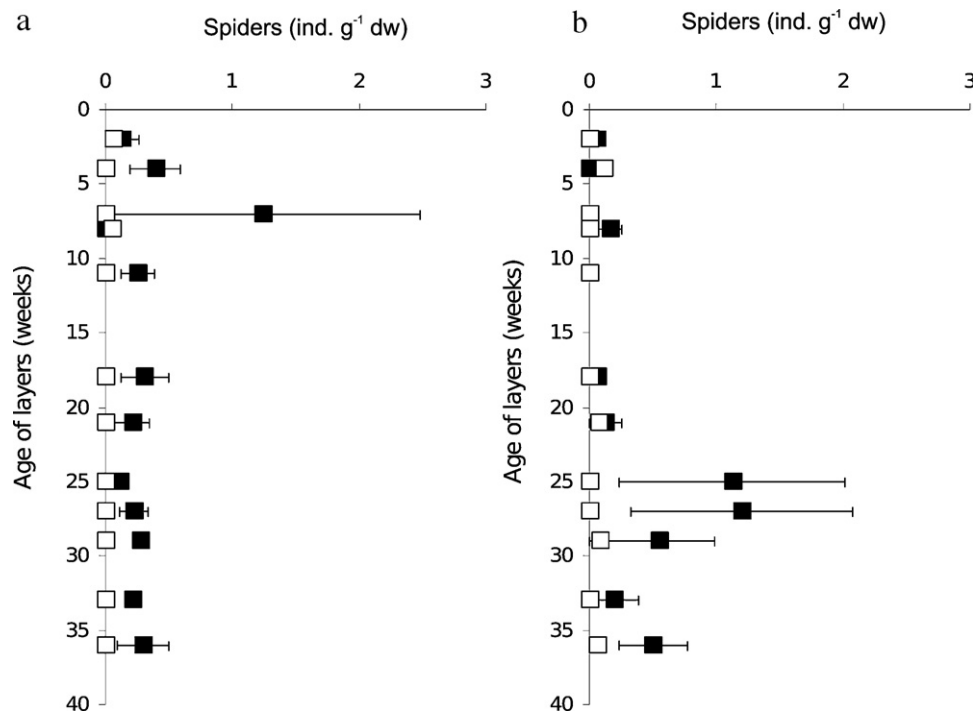


Fig. 4. Number of spiders (Araneae) in mesocosms ($n=3$) supplied with doses of 1.5 kg (a) and 3 kg of pig manure (b), and with *Eisenia fetida* (filled symbols) and without *E. fetida* (open symbols). Variable values (means \pm SE) corresponding to the age of the layers of pig manure are shown on the y axis.

without earthworms. The number of spiders increased in the mesocosms with *E. fetida*, independent of both the dose of pig manure and the age of the layers (Fig. 4a and b).

Discussion

The presence of *E. fetida* generally favored the establishment of large populations of soil arthropods. This effect was associated with the observed increase in microbial activity and carbon mineralization caused by earthworms in these types of mesocosms (Aira et al. 2007a,b). In the present study, the numbers of the most abundant group of arthropods (springtails) were greater in the layers with the highest values of microbial biomass (Aira et al. 2007a). Microorganisms were more abundant in the young layers of the mesocosms, where the earthworm population was located. In the older layers, the microbial biomass decreased as a result of the depletion of nutrient pools (Domínguez 2004; Aira et al. 2007a), as did the numbers of Collembola. The results are consistent with the idea that microorganisms constitute major food resources for springtails (De Ruiter et al. 1994), and that their availability may therefore control the abundance of this arthropod group. This consumer–resource relationship is further supported by the fact that neither the microbial biomass (Aira et al. 2007b) nor the density of springtails in the mesocosms was affected by the dose of pig manure.

Although *E. fetida* increased microbial biomass in the mesocosms 1.3-fold (Aira et al. 2007b), this increase did not correspond with the observed 67-fold increase in springtail density. This mismatch suggests that factors other than changes in microbial populations had a major impact on the number of springtails. For instance, Collembola populations may have been favored by physical modifications brought about by *E. fetida* in their habitat. Earthworm burrowing and casting activities increase substrate porosity (Haimi and Huhta 1987; Brown et al. 2000), thus extending the living space available for Collembola and improving access to their food resources (Wickenbrock and Heisler 1997; Salmon 2004).

The high density of springtails was probably a major factor in the recorded rise in mesostigmatid mite populations in the mesocosms with earthworms. These mites are mainly considered as predators (Scheu and Falca 2000) and they can feed effectively on springtails (Hedlund and Ohrn 2000). Like springtails, mesostigmatid mites were probably affected by the presence of earthworms through changes in the physical structure of their environment (McLean and Parkinson 2000). Although mesostigmatids are very sensitive to changes in abiotic conditions (Ruf 1998), they probably benefited from the presence of earthworm burrows and the increased porosity of the pig manure. Both of these factors may have facilitated access for the mites to food resources, including not only Collembola but also other invertebrate groups. For instance, bacterivorous nematodes are very abundant in pig manure (Monroy et al. 2008) and could constitute a suitable prey for this group of mites (Freckman and Caswell 1985). The use by the mesostigmatids of such additional food resources present in the pig manure may explain why their populations did not decrease in the layers of the mesocosms in which springtails were absent.

The presence of *E. fetida* increased the populations of astigmatid mites in the young layers of the high dose mesocosms but not in the young layers of the low dose ones, indicating that the effect of earthworms on some soil arthropod groups may depend on factors other than the enlargement of microbial populations. The observed pattern may be due to the occurrence of different earthworm densities in the low and high dose mesocosms (Eisenhauer 2010), but previous studies suggest that astigmatid mites are not sensitive to this factor (McLean and Parkinson 1998, 2000). Comparison between the populations of astigmatids and those of other arthropod groups suggests that in the low dose mesocosms, astigmatid numbers may have been reduced by the presence of spiders. In turn, the presence of astigmatids in the young layers of the high dose mesocosms with earthworms was probably favored by the low numbers of these predators and their population reached high densities owing to their high reproductive rates and short generation time (Norton 1994).

Unlike astigmatids, prostigmatid mites form a heterogeneous group with respect to their life history traits (Kethley 1990) and therefore, the different taxa may react differently to changes in their environment, thus concealing their response to disturbance (Bedano et al. 2006). Consequently, the prostigmatids were the only group of soil arthropods not affected by the presence of earthworms.

In natural environments, earthworms can exert a negative effect on oribatid populations due to physical perturbation of the habitat (McLean and Parkinson 2000). However, in the present study, the presence of oribatid mites, although very variable and at low densities, was only observed in the mesocosms with earthworms. The presence of *E. fetida* changed the physicochemical characteristics of the pig manure thus allowing an increase in oribatid numbers, although this effect was only marginally significant. Pig manure probably did not provide suitable conditions for the establishment of oribatid populations, since in organic matter-enriched soils mites are generally present at lower densities than other soil arthropods, such as Collembola (Larink 1997).

The presence of *E. fetida* decreased the number of psocids, which were the major group of soil arthropods in the mesocosms without earthworms. Psocids play an important role as the main group in environments with low presence of microarthropods (Whitford 2000). Therefore, the negative effect of *E. fetida* on psocid populations suggests that these arthropods were disturbed either by the activity of earthworms or by the occurrence of large populations of arthropods in the pig manure processed by *E. fetida*. On the contrary, the development of a rich community of soil microarthropods in the mesocosms with earthworms probably favored the establishment of spider populations. This predatory group can exert important effects on the number of collembolans and other microarthropods (Wise et al. 1999; Lawrence and Wise 2000), probably shaping the structure of the arthropod community in the mesocosms with *E. fetida*.

Conclusions

Our results showed that the presence of *E. fetida* increased the abundance of most of the soil arthropods investigated. Collembola were the main group of arthropods in the mesocosms and their presence was probably favored by the increase in microbial biomass and substrate porosity caused by earthworms. Acari were also favored by the presence of earthworms, although their response to *E. fetida* varied with the group considered. As with microbial biomass and activity (Aira et al. 2007b), the dose of pig manure did not influence the effect of *E. fetida* on most soil arthropod groups, indicating a consistent positive effect of earthworms on these soil organisms. We also concluded that the population numbers of some arthropod groups depended not only on the availability of space and/or microbial resources but probably also on the presence of predatory groups like spiders and mesostigmatid mites. The present results support the view that the activity of epigeic earthworms promotes the presence of complex food webs (Domínguez 2004) during the decomposition process of organic matter.

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