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The influence of *Hormogaster elisae* (Oligochaeta, Hormogastridae) on the colonisation of defaunated soil by microarthropods in laboratory cultures

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Summary

Controversy surrounds the effect of earthworms on soil microarthropod abundance and distribution. To shed further light on the topic, the present work investigated the capacity of soil microarthropods to colonise defaunated soil in the presence and absence of earthworms.

Microcosms composed of plastic boxes were prepared with a central cage containing two endogeic earthworms (*Hormogaster elisae*). In one experiment, the cage contained defaunated natural soil while that outside was non-defaunated. In a second experiment, the soil outside the cage was defaunated while that inside the cage was non-defaunated. All microcosms were kept at 13 °C with 20% soil–water content for 21 days before extracting microarthropods for enumeration by standard methods.

In the first experiment, the majority of microarthropod groups were not able to colonise the defaunated soil containing earthworms, but did colonise it when earthworms were absent. In the second experiment, nearly all the microarthropod groups left the central cages containing earthworms, while in the controls without earthworms the majority stayed inside. The results indicate that different microarthropod taxa are affected unequally by the presence of the earthworms. Due to their greater mobility Tarsonemidae and sometimes Gamasida were able to colonise the defaunated soil even when earthworms were present. In contrast, Oribatida, members of which disperse slowly and are very sensitive to soil perturbations, were generally unable to colonise the soil whether earthworms were present or not. However, the presence of *H. elisae* had a negative effect on the numbers of most groups of microarthropods and on their ability to colonise new

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environments. Physico-chemical perturbations produced by endogeic earthworms acting as ecosystem engineers, competition for organic matter and passive predation are discussed as possible causes of this negative effect.

Introduction

Earthworm activity modifies soil's physical, chemical and biological properties. Earthworms influence carbon and nitrogen cycles as well as the structure of the soil, favouring the infiltration and retention of water (Lee, 1985; Brown, 1995; Edwards and Bohlen, 1996). In addition, they interact with other soil organisms and play an important role in the soil system via different direct and indirect effects. In general, earthworms act as ''ecosystem engineers'' modifying the soil and influencing its other inhabitants (Lavelle and Spain, 2001).

It might therefore be expected that earthworms affect the number and species richness of soil microarthropods in the organic layers of the soil (McLean and Parkinson, 1998). A survey of the literature, however, reveals disagreement over this premise. Many authors suggest that earthworms influence the diversity and abundance of other soil organisms positively (Marinissen and Bok, 1988; Loranger et al., 1998; Salmon and Ponge, 1999, 2001; Tiunov, 2003; Salmon et al., 2005), while others have found a negative impact (Dash et al., 1980; Lagerlöf and Lofs-Holmin, 1987; McLean and Parkinson, 1998; Maraun et al., 1999; Migge, 2001). Numerous studies on the effects of earthworms on soil microarthropods have been performed in the laboratory using experimental microcosms, in which environmental conditions can be controlled, thus avoiding the variations seen in the field (Parkinson and McLean, 1998). However, the results of such experiments have been inconsistent. Wickenbrock and Heisler (1997) reported *Aporrectodea caliginosa* and *Lumbricus terrestris* to have had positive effects on Collembola, as have Salmon and Ponge (1999, 2001) and Salmon et al. (2005) for *Allolobophora chlorotica*, *Aporrectodea giardi* and *L. terrestris*.

McLean and Parkinson (1998) observed positive effects of *Dendrobaena octaedra* on microarthropods after 3 months, but after 6 months, when the soil was completely replaced by earthworm faeces, the abundance of microarthropods decreased. Migge (2001) also reported a decline in microarthropod numbers in the presence of *L. terrestris* and *Octolasion tyrtaeum*, especially at the end of the experiment (after 12 months). Gutiérrez et al. (2003) performed similar laboratory experiments with the endogeic earthworm *Hormogaster elisae* and reported a marked negative effect of this species on the abundance of most microarthropod groups enumerated.

Experimental results, however, have varied with earthworm species and ecological category. A recent field study (Eisenhauer et al., 2007), for example, showed that anecic earthworms do not always negatively affect the density and diversity of soil microarthropods; indeed, they may locally increase microarthropod density by concentrating organic material in middens. At the same time, the authors also report that endogeic earthworms had negative effects on soil microarthropods densities and diversity (in particular on Oribatida) through mixing organic and mineral soil materials, by compacting the soil, and by reducing microbial biomass.

The mechanisms behind the negative effect of earthworms on microarthropods may involve changes in the soil's physico-chemical properties, the environmental heterogeneity caused by earthworm activity (via the production of casts and galleries, causing mechanical disturbances), competition for food, and even active or passive predation (McLean and Parkinson, 2000).

The aim of the present work was to gain further insight on the nature of the effects of earthworms on microarthropods by studying the capacity of different microarthropod groups to colonise soil in the presence and absence of *H. elisae*.

Materials and methods

The soil and organisms used in the present experiments were derived from a plot at El Molar (42 km northeast of Madrid; U.T.M.30TVL525095 at an altitude of 817 m). The climatic and edaphic characteristics of the site are described by Valle et al. (1997) and Gutiérrez et al. (2006). *Hormogaster elisae*, an endogeic earthworm endemic to the centre of the Iberian Peninsula and member of the family Hormogastridae (Álvarez, 1977), was used in all experiments. The initial water content of the soil was determined by heating a sample to 105 °C for 24 h and calculating the weight loss.

The microcosms used were similar to those employed by Gutiérrez et al. (2003), and consisted of plastic containers ($19 \times 14 \times 7\,cm^3$) with a central 2 mm wire mesh cage ($15 \times 10 \times 5\,cm^3$). This mesh size allowed free movement of microarthropods, but not of earthworms.

Two experiments were set up (DefTI and DefTII), each with 12 microcosms, six with earthworms inside the cages (two earthworms weighing a total of 5.75 ± 0.25 g with gut content) and six without earthworms (controls). In both experiments 500 g of untreated soil from El Molar with a water content of 20% were placed inside and outside the cage. In DefTI, the soil used inside the cages was defaunated; in DefTII the soil outside the cages was defaunated (Figure 1). Thus, in DefTI, earthworms were inside the cages and microarthropods outside, and in DefTII both earthworms and microarthropods were inside the cages. To determine microarthropod numbers at the beginning of the experiment (i.e., at time 0) six samples of 500 g of non-sieved soil were analysed.

Defaunation of the soil was performed following a method adapted from Huhta et al. (1989); Wright et al. (1989); Bruckner et al. (1995) and Salmon et al. (2005). The soil was first frozen at $-32\,^{\circ}C$ for 24 h, then allowed to thaw for 24 h, and then heated to $60\,^{\circ}C$ for another 24 h. This method removes the microfauna but not the microflora. Other methods, such as the use of microwaves or biocides, were ruled out because they are known to change the biological and physico-chemical properties of the soil such as water retention (Huhta et al., 1989). To test the reliability of the defaunation method, microarthropod extraction was performed on six defaunated soil samples; no live microarthropods were detected.

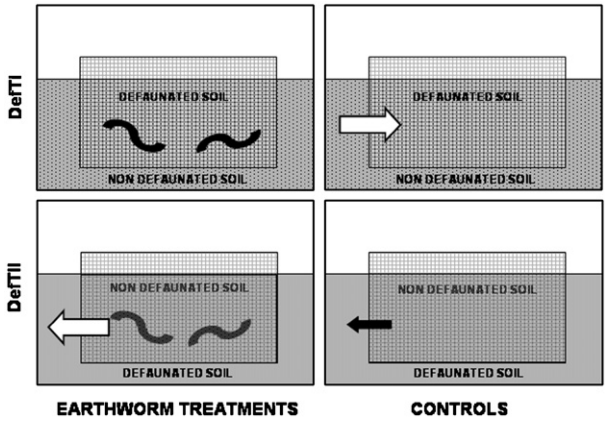

Figure 1. Experimental setup: white arrows indicate the trend in abundance of the majority of the microarthropod groups. The black arrow indicates the relative abundance of the members of Gamasida and Tarsonemidae.

All microcosms were kept in a culture chamber at $13\,^{\circ}C$ for 21 days, allowing sufficient time for the earthworms to consume all the soil according to the rate of cast production of *H. elisae* (3.18 g cast per earthworm $g^{-1}\,d^{-1}$ in natural soil) (Díaz Cosín et al., 1996). After this time the microcosms were dismantled and microarthropods were collected from the soil from both sides of the cage using the Berlese–Tullgren method (Krantz, 1978). Extracted microarthropods were preserved in Scheerpeltz solution (70% ethanol, 29% distilled water, 1% acetic acid and glycerine), identified and counted (Krantz, 1978; Dindal, 1990).

Prior to statistical analysis, relative proportions of microarthropod taxa inside and outside the cage were calculated. The dataset was tested for the requirements of an analysis of variance (Shapiro–Wilks and Kolmogorov–Smirnov tests). Subsequently, numerous MANOVAs and protected ANOVAs were performed analysing different taxonomic levels. The first MANOVA for total Arthropoda was done using total Collembola, total Acari and other groups as independent variables. Additional MANOVAs for total Collembola were performed using the collembolan families and for total Acari using the mite taxa. Afterwards, protected ANOVAs and post-hoc tests (Duncan) for the single collembolan families and mite taxa were conducted to determine significantly different means. When data were not normally distributed, ANOVAs and the Duncan test were replaced with a Kruskal–Wallis analysis and distribution-free multiple comparisons based on Kruskal–Wallis rank sums (Hollander and Wolfe, 1973). Mean numbers at the beginning and at the end of the experiment were also compared with an ANOVA in order to determine the evolution of each taxa during both experiments. All calculations were made using SPSS software v. 15.0 and S.A.S.

Results

DefTI (defaunated soil inside the cage)

The MANOVA results for total Arthropods using total Collembola, total Acari and other groups showed significant differences between treatments (Wilks' Lambda $F = 9.67$; $p < 0.001$), demonstrating that the presence of earthworms had a general effect on the abundance of soil arthropods. Similar results were obtained for total Collembola in the MANOVA using collembolan families (Wilks' Lambda $F = 4.02$; $p < 0.001$) and for total Acari using mite taxa (Wilks' Lambda $F = 2.68$; $p < 0.01$).

In the presence of earthworms, total Arthropods were more abundant outside the cage than inside (Table 1). However, in the absence of earthworms, their abundance was similar outside and inside the cages. The results obtained for total Collembola and for the family Isotomidae were similar.

Abundance of the Poduromorpha followed the same trend as observed for total Collembola and Isotomidae (Table 1). This group was also more abundant at time 0 than at the end of the experiment in all treatments (ANOVA; $F = 14.40$; $p < 0.001$).

The Collembola families Onychiuridae and Sminthuridae showed very low numbers at all times and in all treatments. No members of the family Entomobryidae were found in this experiment.

Total Acari were more abundant outside the cage than inside in the presence of earthworms, while densities did not vary in the absence of earthworms.

The Gamasida showed a very similar behaviour pattern to that of total Acari. When the cages contained earthworms, members of this group were more abundant outside the cage than inside; in the absence of earthworms Gamasida distribution inside and outside the cage was similar.

Members of the suborder Astigmata showed a similar behaviour to that of Poduromorpha; there were more mites at time 0 than at the end of the experiment (ANOVA; $F = 3.04$; $p < 0.05$). Earthworm presence and absence did not significantly affect Astigmata abundance inside and outside the cage.

The suborder Prostigmata was present in very low numbers, except for the family Tarsonemidae and as observed for the Astigmata, neither earthworm presence or absence affected abundance inside or outside the cage. Members of Oribatida (i.e., both Macropylina and Brachypylina) remained more abundant outside than inside the cage in the presence of earthworms. The abundance of Brachypylina inside and outside the cage did not differ in the absence of earthworms, while Macropylina individuals were more abundant outside than inside the cage in the absence of earthworms.

The remaining arthropods were found in very low numbers and no clear patterns were seen in their behaviour.

DefTII (defaunated soil outside of the cage)

Total Arthropods showed no significant differences between treatments (MANOVA; Wilks' Lambda $F = 1.55$; $p = 0.160$). However, the MANOVA performed for total Collembola using collembolan families (Wilks' Lambda $F = 2.64$; $p < 0.01$) and for total Acari using mite taxa (Wilks' Lambda $F = 7.87$; $p < 0.001$) showed significant differences between treatments, demonstrating that the presence of earthworms had an overall effect on the abundance of Collembola and Acari.

Table 1. Experiment DefTI (defaunated soil inside the cage, non-defaunated soil outside): mean numbers of the different microarthropod taxa (in bold) and mean relative proportions (in brackets) under each set of conditions, plus the *F*- and *p*-values for the ANOVA and the χ^2 and *p*-values for Kruskal–Wallis (* = $p < 0.05$)

Taxonomic group	Time 0	Earthworm treatments		Controls		Anova/Kruskal–Wallis	
		Inside	Outside	Inside	Outside	F/χ^2	*p*-Value
Total Arthropods	**71.00**	**11.83** (18.08)A	**55.50** (81.91)C	**34.66** (46.80)B	**38.16** (53.19)B	$F = 49.44$	0.000*
Total Colembola	**24.83**	**3.66** (14.64)A	**24.16** (85.35)C	**8.66** (48.64)B	**8.00** (51.35)B	$F = 40.61$	0.000*
Isotomidae	**7.17**	**2.33** (15.60)A	**16.16** (84.39)C	**4.66** (62.12)BC	**3.50** (37.87)AB	$F = 9.04$	0.001*
Poduromorpha	**15.83**	**1.00** (13.33)A	**5.66** (86.66)B	**0.83** (27.77)A	**1.00** (38.88)AB	$\chi^2 = 8.84$	0.031*
Onychiuridae	**1.00**	**0.00** (0.00)	**1.16** (50.00)	**0.17** (16.66)	**0.83** (66.66)	$\chi^2 = 7.18$	0.066
Entomobryidae	**0.00**	**0.00** (0.00)	**0.00** (0.00)	**0.00** (0.00)	**0.00** (0.00)	–	–
Sminthuridae	**0.83**	**0.33** (12.50)	**1.16** (54.16)	**3.00** (43.97)	**2.66** (39.36)	$F = 1.30$	0.300
Total Acari	**41.83**	**6.83** (18.78)A	**29.16** (81.21)C	**23.16** (43.44)B	**29.00** (56.55)B	$F = 33.33$	0.000*
Gamasida	**5.00**	**0.50** (1.66)A	**4.66** (81.66)B	**3.16** (28.75)AB	**5.00** (54.58) AB	$\chi^2 = 11.41$	0.010*
Astigmata	**8.67**	**1.33** (31.94)	**2.67** (51.38)	**5.83** (55.09)	**3.83** (44.90)	$F = 0.40$	0.753
Prostigmata	**1.50**	**0.50** (27.77)	**0.67** (38.88)	**1.33** (33.33)	**2.00** (66.66)	$\chi^2 = 3.04$	0.384
Tarsonemidae	**6.50**	**2.83** (56.38)	**2.00** (43.61)	**10.67** (55.24)	**7.83** (44.75)	$F = 0.43$	0.732
Oribatida Macropylina	**8.17**	**1.50** (22.71)A	**6.33** (77.28)B	**0.83** (13.88)A	**3.17** (86.11)B	$\chi^2 = 15.92$	0.001*
Oribatida Brachypilina Gymnonota	**8.50**	**0.00** (0.00)A	**6.67** (100.00)B	**0.33** (11.11)A	**3.83** (72.22)AB	$\chi^2 = 18.15$	0.000*
Oribatida Brachypilina Poronota	**3.50**	**0.17** (2.77)A	**6.17** (97.22)B	**1.00** (24.30)AB	**3.33** (75.69)AB	$\chi^2 = 13.73$	0.003*
Other groups	**4.33**	**1.33** (35.31)	**2.17** (64.68)	**2.83** (60.55)	**1.17** (39.44)	$F = 1.31$	0.298

Different letters indicate significantly different means differing as indicated by the Duncan test and by the distribution-free multiple comparisons based on the Kruskal–Wallis rank sums test.

Table 2. Experiment DefTII (defaunated soil outside the cage, non-defaunated soil inside): mean numbers of the different microarthropod taxa (in bold) and mean relative proportions (in brackets) under each set of conditions, plus the *F*- and *p*-values for the ANOVA and the χ^2 and *p*-values for Kruskal–Wallis (* = $p<0.05$)

Taxonomic group	Time 0	Earthworm treatments		Controls		Anova/ Kruskal–Wallis	
		Inside	Outside	Inside	Outside	F/χ^2	*p*-Value
Total Arthropods	**251.50**	**112.66** (50.60)BC	**110.33** (49.39)AB	**196.00** (58.97)C	**133.00** (41.02)A	$F = 6.61$	0.003*
Total Colembola	**159.83**	**76.00** (50.16)AB	**75.50** (49.83)AB	**108.33** (58.36)B	**69.66** (41.63)A	$F = 2.77$	0.068
Isotomidae	**91.17**	**59.83** (47.14)AB	**67.17** (52.85)AB	**94.33** (59.06)B	**59.33** (40.93)A	$F = 3.17$	0.047*
Poduromorpha	**65.50**	**12.33** (68.78)C	**6.00** (31.21)A	**7.33** (58.40)BC	**4.83** (41.59)AB	$F = 8.47$	0.001*
Onychiuridae	**1.50**	**2.17** (59.16)	**1.00** (40.83)	**2.67** (64.72)	**0.83** (35.27)	$F = 0.85$	0.479
Entomobryidae	**0.33**	**0.17** (16.66)	**0.00** (0.00)	**0.00** (0.00)	**0.17** (16.66)	$\chi^2 = 2.09$	0.554
Sminthuridae	**1.33**	**1.50** (51.11)	**1.33** (48.88)	**4.00** (51.36)	**4.50** (48.63)	$F = 0.01$	0.997
Total Acari	**88.16**	**35.66** (51.46)AB	**34.00** (48.53)AB	**87.33** (58.66)B	**62.66** (41.33)A	$F = 4.17$	0.019*
Gamasida	**3.50**	**1.67** (62.22)	**1.17** (37.77)	**1.33** (29.36)	**3.17** (70.63)	$F = 1.89$	0.162
Astigmata	**19.00**	**7.83** (45.68)AB	**7.83** (54.31)AB	**21.50** (64.96)B	**11.50** (35.03)A	$F = 2.86$	0.062
Prostigmata	**13.83**	**3.83** (93.88)B	**0.33** (6.11)A	**10.17** (90.63)B	**0.83** (9.36)A	$\chi^2 = 18.64$	0.000*
Tarsonemidae	**16.33**	**8.00** (31.68)A	**16.67** (68.31)B	**23.83** (34.55)A	**41.83** (65.44)B	$F = 11.21$	0.000*
Oribatida Macropylina	**18.67**	**7.00** (61.14)C	**4.50** (38.85)B	**13.67** (77.30)D	**3.83** (22.69)A	$F = 19.77$	0.000*
Oribatida Brachypilina Gymnonota	**6.83**	**1.67** (47.91)AB	**0.33** (18.75)AB	**5.33** (92.36)B	**0.33** (7.63)A	$\chi i^2 = 9.66$	0.022*
Oribatida Brachypilina Poronota	**10.00**	**5.67** (65.50)C	**3.17** (34.49)B	**11.50** (89.60)D	**1.17** (10.39)A	$F = 50.49$	0.000*
Other groups	**3.50**	**1.00** (40.00)	**0.83** (43.33)	**0.33** (25.00)	**0.67** (58.33)	$\chi^2 = 1.57$	0.665

Different letters indicate significantly different means as indicated by the Duncan test and by the distribution-free multiple comparisons based on the Kruskal–Wallis rank sums test.

No significant differences were detected between the numbers of total Arthropods inside and outside the cage in the presence of earthworms (Table 2). However, total Arthropods were more abundant inside the cage in the absence of earthworms. Similar results were observed for total Collembola and Isotomidae.

A significant reduction in Poduromorpha mean abundance was observed at the end of the experiment under all conditions (ANOVA; $F = 73.71$; $p<0.001$). However, this group was more abundant inside than outside the cage in the presence of earthworms. No significant differences were detected when earthworms were absent.

The Collembola families Onychiuridae, Sminthuridae and Entomobryidae were present in very low numbers and were not affected by earthworm presence.

More total Acari were found inside the cage in the absence of earthworms while the presence of earthworms did not significantly affect the relative proportions of total Acari inside and outside the cage.

No significant differences between the relative proportions of Gamasida inside and outside the cage were detected, regardless of the presence or absence of earthworms.

The members of Tarsonemidae were more abundant outside the cage than inside in both treatments, with and without earthworms.

In the presence of earthworms, the members of Astigmata and Oribatida Brachypylina Gymnonota were found in similar numbers inside and outside the cage. However, they were more abundant inside than outside the cage in the absence of earthworms.

The members of Prostigmata and Oribatida Macropylina and Brachypylina Poronota were more abundant inside the cage both in the presence and absence of earthworms.

Other arthropods were present only in very low numbers, except at time 0, and their abundance showed no clear trends in the absence or presence of earthworms during the course of the experiment.

Discussion

There is growing evidence that earthworms influence the density and diversity of the soil micro- and meso-fauna, as well as their activity (Brown, 1995). In the laboratory, several authors have reported reductions in the number and diversity of microarthropods with increasing

earthworm densities (McLean and Parkinson, 1998; Parkinson and McLean, 1998; Migge, 2001). Similar results were found in the present study and our work confirms that *H. elisae* has a negative effect on some microarthropods present at El Molar, as previously reported by Gutiérrez et al. (2003).

In DefTI, most of the microarthropods (total Microarthropods, total Collembola, Isotomidae, Poduromorpha, total Acari, Gamasida, and Oribatida Brachypilina) were unable to colonise the defaunated soil inside the cage in the presence of earthworms, although they were able to do so in their absence. Poduromorpha abundance decreased notably at the end of the experiment both in the presence and absence of earthworms indicating that experimental conditions were not favourable for this group. A similar reduction was reported by Gutiérrez et al. (2003) who performed experiments under the same conditions. Migge (2001) reported reductions in the number of Collembola of the genus *Tomocerus*; this was the dominant genus in the field but disappeared from experimental microcosms. The Collembola of the Onychiuridae, Sminthuridae and Entomobryidae were present in very low numbers and showed no clear pattern of distribution.

Members of the Tarsonemidae were able to colonise the inside of the cage irrespective of earthworm presence, which might be due to their high mobility. The taxon Tarsonemidae consists mainly of obligate phytophagous mites (Lindquist, 1986) that generally rely on passive dispersal by wind for their transfer from one plant to another, or on a phoretic association with insects (Krantz, 1978). In addition, sex determination among the Tarsonemidae is largely arrhenotokous, with females diploid and males haploid. This ensures a constant presence of males, which could be an advantage in dispersion (Lindquist, 1998). Although time and living space was limited in this experiment, the members of Tarsonemidae naturally show a strong dispersion capacity that could have contributed to their colonisation of the inside of the cage.

Oribatida were unable to colonise the defaunated soil when earthworms were present. Macropylina also did not colonise the defaunated soil when earthworms were absent. Abundance of Brachypilina did not differ significantly inside and outside the cage in the absence of eathworms, but they were much more abundant outside the cage in the presence of earthworms. Bruckner et al. (1995) reported that the majority of soil microarthropods, such as Collembola, were able to colonise defaunated soil while members of Oribatida were not. Oribatida presumably are very sensitive to soil perturbations (Norton and Palmer, 1991); results from Maraun et al. (1999) indicate them to be more sensitive to such events than Collembola since Oribatida growth is slower. Modifications in the microhabitat caused, for example by earthworms, might therefore affect their ability to colonise the soil. It is possible that Oribatida, which are slow dispersers, had insufficient time to colonise the inside of the cage during the 21 days of the experiment.

In the DefTII experiment nearly all microarthropods studied were able to colonise the defaunated soil, moving out from the inside of the cage when earthworms were present. Individuals of the groups Poduromorpha, Prostigmata and Oribatida Macropylina and Brachypilina Poronota stayed inside the cage or left it only very slowly. In the absence of earthworms, the majority of microarthropod groups remained inside the cage. The members of Gamasida and Tarsonemidae, however, were found in greater abundance outside the cage in the controls (significantly so for Tarsonemidae); that is, even when there were no earthworms present these groups showed a tendency to leave the cage.

In general, most of the groups had a similar abundance inside and outside the cage during the course of the experiment. Had the experiment continued for longer, it is possible that more microarthropods would have moved beyond the cage. Migge (2001) suggested that the behaviour of each microarthropod taxa in the presence of earthworms and also the moment at which the perturbations caused by the earthworms becomes limiting could be different for each species. Maraun and Scheu (2000) affirmed that some species that have coexisted with earthworms for a long period of time could have adapted to the disturbance produced by earthworms, but groups that cannot cope with the changing environment due to fragility or low reproduction (like Oribatida) are driven to extinction by earthworms at some locations. A study at the species level of the microarthropods considered in this experiment might provide more insight.

Several hypotheses exist regarding the negative effect of earthworms on certain microarthropod species. Earthworms greatly affect the functioning of the soil system and its physico-chemical structure by means of their casts and galleries. They act as ''ecosystem engineers'', building and maintaining the soil structure and taking an active part in energy and nutrient cycling. They modify the physical, chemical and biological properties of the soil, influencing the structure of the soil, the carbon and nitrogen cycles and the water regimes (Lee, 1985; Lavelle, 1988; Brown, 1995; Edwards

and Bohlen, 1996). Microarthropods may be affected by these modifications in soil properties (Marinissen and Bok, 1988; Loranger et al., 1998), which in the long term lead to the homogenisation of the soil environment and a reduction in the number of microarthropod niches (McLean and Parkinson, 1998). In the present experiments earthworms presumably perturbed all the soil inside the cages likely with significant effects on its structure.

It is important to distinguish the different effects of each type of earthworm on soil processes; the degree of mixing of soil layers varies with earthworm species and ecological categories. Epigeic species cause limited mixing of mineral and organic layers. Anecic species form vertical permanent burrows, incorporate litter from the soil surface into deeper soil layers and also transport mineral soil materials to the surface by casting. Endogeic species live in mineral soil layers mainly consuming the organic matter present in mineral layers. Anecic earthworms may have a positive effect on the density and diversity of soil microarthropods by concentrating litter in middens while endogeic earthworms usually have a negative effect on soil microarthropods by mixing organic and mineral soil materials and compacting the soil (Eisenhauer et al., 2007). *H. elisae*, an endogeic earthworm, is usually responsible for pronounced changes in the soil's physical structure which can affect the abundance of soil microarthropods.

Moreover, earthworms and microarthropods possibly compete for food resources since both (Hale, 1971) (Lee, 1985; Edwards and Bohlen, 1996) prefer habitats rich in organic matter. This hypothesis has also been proposed by Wallwork (1971); Brown (1995) and Gutiérrez et al. (2008). In the experimental conditions of the present work, the quantity of soil available was very limited and the earthworms probably consumed much of it, thus provoking competition with microarthropods. Gutiérrez et al. (2008) showed that the negative effect of *H. elisae* on microarthropods disappeared when topsoil (which is rich in organic matter) was added to the microcosms.

The possibility that earthworms prey upon microarthropods is unlikely; certainly no such relationship has been demonstrated to date (McLean and Parkinson, 1998). After analysing the faeces and intestinal contents of *H. elisae*, Gutiérrez et al. (2006) concluded that it was improbable that this species actively preys upon microarthropods.

In conclusion, the present results show that, under the experimental conditions employed, *H. elisae* has a mainly negative effect on most microarthropod groups. The densities of most taxa decreased in the presence of earthworms since they either escaped or died. Nevertheless due to their greater mobility, the Tarsonemidae and sometimes the Gamasida, were able to colonise the defaunated soil even when earthworms were present. In contrast, the Oribatida, which are very sensitive to soil perturbations, were generally unable to colonise it whether or not earthworms were present.

Presumably, the behaviour of each microarthropod taxa in the presence of earthworms could be different. Some species could have adapted to the disturbance produced by earthworms and may not be affected at all (such as the members of the family Tarsonemidae), but those ones with poor adaptive capacity to earthworm-induced changes in the microenvironment (like Oribatida), would try to escape the earthworm presence more quickly.

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