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Trophic dynamics in a simple experimental ecosystem: Interactions among centipedes, Collembola and introduced earthworms

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ABSTRACT

Invasive earthworms in North America are known to have dramatic influences on soil ecosystems, including negative effects on other soil fauna. In general, studies examining this phenomenon have focused on invasive earthworm impacts on organisms at the same or lower trophic level as the earthworms themselves (i.e., detritivores and decomposers). In contrast, there have been relatively few studies of invasive earthworm impacts on higher trophic levels or food web interactions. Invasive earthworms might alter food webs either directly as prey items, or indirectly through their profound alteration of soil physical characteristics, which might in turn alter established predator/prey interactions. In this study, we created experimental mesocosms to investigate the influence of an invasive earthworm on a native predator-prey interaction. We incubated several combinations of a widespread Asian invasive earthworm (*Amynthas agrestis*), a generalist centipede predator (family: Cryptopidae), and a putative microarthropod prey species (*Sinella curviseta*) in an experiment to determine their interactions. We hypothesized that collembolan abundance would be reduced in mesocosms containing centipedes. We further hypothesized that earthworm feeding on litter substrate in the mesocosms would reduce the complexity of the substrate, and thus increase the likelihood of centipede/collembolan encounters, with the ultimate effect of more pronounced reduction of Collembola populations in mesocosms containing both earthworms and centipedes. Unexpectedly, we found that earthworms had a negative effect on collembolan abundance early in the incubation and that centipedes did not. Collembolan populations were less variable through time in the presence of earthworms, suggesting that invasive earthworms exerted some regulatory pressure on food or habitat supply for the collembolans. Centipedes lost biomass when only Collembola were available for food, but gained biomass when incubated with earthworms. We noted a simultaneous significant decrease in earthworm biomass (mainly in the form of earthworm mortality) in experimental units that contained centipedes relative to those without centipedes. Taken together, these results suggest that this invasive earthworm may represent a novel prey resource for the centipedes, and that their presence in ecosystems could have consequences on both higher and lower trophic levels.

1. Introduction

Biological invasions induced by human activities have forced ecologists to quantify the consequences of these invasions for ecosystem structure, ecological function, and ecosystem services. Less attention has been paid to the underlying processes that determine how invasive species interact and co-exist in the food web of a given ecosystem. Biotic interactions have long been considered one potential mechanism to explain species coexistence at a local scale (Wardle, 2006), but the contribution of an invading species to the preexisting assemblage of biotic interactions is not always clear, especially in belowground ecosystems.

Regulation of prey populations by predators is a well-known phenomenon in soil food webs (de Ruiter et al., 1995; Wardle, 2002), and many studies have found that populations of soil animals are controlled by their predators, emphasizing the role of top-down control (Wardle, 2002). Populations of soil animals occupying lower trophic levels (e.g., detritivores and fungivores such as

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Collembola) can be directly controlled through predator-prey interactions, i.e. density constrained by their predators, such as spiders (Lawrence and Wise, 2000) and centipedes (Poser, 1988). On the other hand, bottom-up regulation of trophic dynamics has also been demonstrated, either through direct availability of food resources (e.g., Scheu and Schaefer, 1998; Chen and Wise, 1999) or through non-trophic interactions, that alter the strength of top-down control through predation. For example, in a mesocosm experiment, the predator-prey interaction effect was altered by manipulating habitat complexity, with decreased habitat complexity resulting in greater control of collembolan populations by their centipede predators (Kalinkat et al., 2013). These results suggested that top-down control of predators on microbi-detritivore prey is less effective in litter-rich (i.e., complex habitat) ecosystems (Kalinkat et al., 2013). These examples reveal the importance of top-down vs. bottom-up controls in soil food-webs and the complexity of these interactions, supporting the overall view endorsed by Hunter and Price (1992) that both forces can act individually or simultaneously within ecosystems depending on conditions. Indeed, interpretation of results from experiments designed to examine the relative importance of top-down vs. bottom-up forces can change depending upon the duration of the experiments themselves (Lawrence and Wise, 2017). In light of the apparent context dependency of predator-prey outcomes in soil ecosystems, we wished to examine the influence of adding an “engineering” variable, such as the behavior of a novel invasive earthworm, and evaluate the strength of top-down control for a predator-prey food chain.

Non-native earthworms promote leaf litter decomposition in forest ecosystems across North America (Liu and Zou, 2002; Hale et al., 2008; Fahey et al., 2013) and therefore likely possess the ability to alter environmental complexity for other soil and litter dwelling organisms. Among these introduced species, *Amynthas agrestis* is a widespread invasive species that lives in the litter layer of forested ecosystems (Ishizuka, 2001) and is known to substantially promote leaf litter decomposition and decrease litter horizon depth (Qiu and Turner, 2016). *Amynthas agrestis* are native to Japan, but have expanded into forests in 17 states in the eastern United States since being introduced (Callaham et al., 2003; Reynolds and Wetzel, 2008), and it has been suggested that *A. agrestis* may have potential to further expand their distribution in the USA (Ikeda et al., 2015).

If invasive worms like *A. agrestis* consume substantial amounts of leaf litter in the forest, habitat structure for native micro-arthropods, like Collembola, should be reduced and simplified. We therefore expect that a “concentration effect” (as in Kalinkat et al., 2013) may be observed if Collembola are forced to live in such habitats. Identifying the influence of perturbations (such as invasive earthworms) on food web dynamics can help understand the mechanisms of species co-existence and inform management of biotic resources in forest ecosystems.

In this study, we sought to examine the effects of an invasive earthworm (*A. agrestis*) on the interaction between a generalist predator (centipede) and its putative prey (Collembola: *Sinella curviseta*). Invasive earthworm activity (specifically earthworms in the genus *Amynthas*) has been shown to decrease the complexity of the leaf litter habitat in mesocosms (Greiner et al., 2012; Snyder et al., 2013), as well as in field settings (Snyder et al., 2011). Thus, we hypothesized that invasive earthworm activity would strengthen the top-down control of centipedes on collembolan populations due to the assumed decrease in habitat complexity, resulting in lower collembolan populations in treatments with both the earthworm and centipede predator present. A corollary hypothesis was that if the collembolan abundance were adequate to meet the needs of centipede consumption, then centipede biomass should increase over the course of the experiment when incubated with Collembola alone, and that this increase in centipede biomass would be more pronounced in treatments with earthworms.

2. Materials and methods

2.1. Collection and culture of earthworms, centipedes and Collembola

The earthworms used in this experiment were *Amynthas agrestis*, an invasive species that is wide-spread in the eastern part of the United States. We collected earthworms from the litter layer in a mixed hardwood forest at the Chattahoochee National Forest, in northern Georgia, USA (34.91°N, 83.62° W). Until they were placed into experimental mesocosms, earthworms were kept with sufficient litter, soil, and moisture in plastic containers at 20 °C.

Collembola used in this experiment were *Sinella curviseta* (Collembola, Entomobryidae) from a laboratory culture population (obtained from D.A. Crossley, Jr.). We cultured Collembola in plastic containers filled with hardened plaster of Paris/activated charcoal medium with sufficient moisture and food (baker's yeast) at 20 °C until sufficient numbers of Collembola had been produced for the needs of this experiment.

Centipedes (family: Cryptopidae) were captured by hand from the litter layer of a mixed hardwood stand at Whitehall Forest, Georgia, USA (35°03′N, 83°25′ W), and from the Oconee National Forest (33°76′N, 83.28′W). Each collected centipede was kept in an independent plastic container with fresh litter and sufficient moisture at 20 °C until the experiment began.

2.2. Lab experiment

All mesocosms for the study were constructed using uniform amounts of standard topsoil, fragmented litter, and coarse litter in cylindrical plastic containers (14 cm depth, ~10 cm diameter, ~1 L volume). Soil was a commercially acquired topsoil (classified as sandy loam, with SOM of ~1.0–1.5%) derived from the top 25 cm of a recently cleared forested site in Clarke CO., GA, USA, which had been screened, mixed, air-dried, and stored in bulk in the laboratory (Snyder et al., 2013). Litter was collected from the same site at Chattahoochee National Forest where earthworms were collected and consisted mostly of oak, hickory, and maple species. The litter used in the experiment was defaunated by extracting for one week using the Berlese-Tullgren method with a 60 W bulb placed 15 cm above the litter surface, then rewetting and allowing to sit for one week before repeating the extraction. After 4 cycles of drying (8 weeks in total), rewetting, and extracting, the litter was considered to be effectively defaunated. All litter was then sieved using a standard soil sieve with 4.75 mm aperture. Material passing through the sieve was operationally defined as fragmented litter, and that which did not pass the sieve was defined as coarse litter. Soil was sieved with the 4.75 mm sieve and dried with two cycles using the same method used to defaunate litter. We placed 200 ± 5 g dried soil in each container and added 30 mL tap water to moisten the soil. Then we placed 7 g fragmented dried litter and 7 g coarse dried litter into each mesocosm. Finally, each mesocosm was moistened from the top with 15 mL water with a mister and was fitted with a perforated lid.

We imposed seven faunal treatments as follows: 1) Control – no fauna (hereafter “Control”); 2) Collembola only (“CO”); 3) earthworm only (“ ET”); 4) Collembola and centipede (“CO + CE”); 5) Collembola and earthworm (“CO + ET”); 6) Collembola and earthworm and centipede (“CO + ET + CE”); and 7) earthworm plus centipede (“ET + CE”). Due to a limited number of collembolans available, we used a varying number of replicates (3–6) for each treatment and harvesting time (for exact replication for each treatment at each date, see Supplemental Fig. 1). For all treatments containing earthworms, we added two individuals of *A. agrestis* of similar size and weight (0.721 [s.d. 0.126] g individual^{-1}) into each mesocosm. For those treatments containing centipedes, we placed one centipede (0.130 [s.d. 0.035] g individual^{-1}) into each mesocosm. For treatments containing Collembola, we placed 100 individuals of *Sinella curviseta* into each mesocosm. Collembola were collected from cultures using an aspirator taking no account of adult or immature life stage. During the incubation, mesocosms were watered weekly with a mister, applying a standard amount of water to each mesocosm (approximately 5 mL).

Mesocosms were harvested three times: two, four, and six weeks after the start of the experiment on June 17, 2016. When we harvested the mesocosms, we first counted the number and weight of each recovered earthworm and centipede. Then Collembola were extracted (for three days) from litter and soil, separately, from each mesocosm using the Berlese-Tullgren method. Finally, Collembola and any other extracted soil animals were identified and counted using a dissecting microscope (Lomo 7 × 8, M6C-10).

2.3. Statistical analyses

A three-way factorial ANOVA was used to test the main and interactive effects of other organisms and time on collembolan abundance (factors: ET, CE, Time), earthworm biomass (factors: CO, CE, Time), and centipede biomass (factors: CO, ET, Time). We elected not to include a centipede only treatment (i.e., incubating predators with no putative food source), and so interactive effects of centipede treatments could not be calculated in the analysis. One replicate of the ET + CE treatment harvested after 4 weeks was excluded from analyses, because the centipede in this mesocosm was dead. Analyses were performed by R version 3.2.2 (R core team, 2015) and figures were created using Origin 8.0 and SigmaPlot 13.0.

3. Results

Results of the 3-way ANOVA for each response variable can be seen in Table 1. Abundances of Collembola were higher relative to starting conditions in all treatments on all sample dates (Fig. 1). In the factorial analysis, there were significant main effects of earthworm presence and time on collembolan abundance, as well as a significant interaction between earthworm presence and time (Fig. 2). Collembola abundance was significantly greater in mesocosms without earthworms early in the incubation but decreased sharply after 6 weeks such that there was no effect of earthworm presence on collembolan abundance. When mesocosms were extracted for Collembola, we did collect some microarthropods that were not specifically added to the experimental units (i.e., unintended contamination by mites). We considered the number of these organisms to be negligible on the first two sample dates, as these contaminant species made up less than 10% of the total microarthropod abundance in the mesocosms (data not shown), and on the third sample date the population levels of a mite species that contaminated all the mesocosms made up approximately 30–50% of the total microarthropod abundance in the mesocosms with Collembola. The abundance of mites was not affected by any faunal treatment (data not shown), and so we considered that they were not directly involved in any of the interactions we examined.

Centipede biomass dynamics over the course of the incubation are shown in Fig. 3. In the factorial analysis, there were significant main effects of collembolan presence and earthworm presence, but no significant effects of time or any interactions (Table 1). Due to the lack of a full factorial design in the absence of mesocosms with centipedes alone, it was not possible to calculate all interaction terms (See Table 1 for details). Centipedes gained significantly more biomass in mesocosms where Collembola were absent (Fig. 4a), and gained significantly more biomass when earthworms were present (Fig. 4b).

Earthworm biomass dynamics during incubation in all treatments are shown in Fig. 5. In the factorial analysis there were significant main effects of centipede presence and time, as well as a significant interaction between collembolan presence and time (Table 1.). Earthworms lost more biomass when centipedes were present (Fig. 6a), and this loss was due to earthworm mortality, primarily in treatments where centipedes were present (see Fig. 5 for general trends). The interaction between collembolan presence and time was due to a positive effect of Collembola on earthworm biomass on the first sample date, but a reversal of this trend by the end of the incubation (Fig. 6b).

4. Discussion

Collembolan abundance was depressed over time and by the presence of earthworms, with those factors interacting, such that after two and four weeks Collembola abundance was lower in mesocosms where earthworms were present, but after six weeks the effect of earthworm presence had diminished. This interactive effect was likely due to most earthworms losing biomass in all treatments as the incubation proceeded (Fig. 5), such that the large effect of earthworm presence early in the experiment was dampened by the final sample date (Fig. 2). The negative effect of earthworms on Collembola is supported by other experiments with similar findings (Donghui Wu, unpublished data). The reason for the effect is unclear, but may be related to earthworm consumption of collembolan eggs deposited on leaf litter. Another possible explanation for this negative effect of *Amynthas agrestis* on the Collembola is that the active feeding and burrowing behavior of the earthworm disrupted the growth of fungi in the mesocosms, and therefore decreased the amount of fungi available as food for the Collembola (Chang et al., 2016).

Unexpectedly, the presence of centipedes did not negatively affect collembolan abundance. In contrast, centipede biomass was significantly lower when they were combined with Collembola relative to treatments where Collembola were absent (Fig. 4 a). These observations suggest that *S. curviseta* is not a preferred food for these centipedes. This result is in contrast with other studies, which reported that centipedes have strong negative effects on collembolan abundance (Poser, 1988; Salmon et al., 2005). One possible explanation is that the centipedes that we used (family Cryptopidae) do not consume Collembola and must specialize on another type of prey.

Although Collembola abundance was negatively affected by the presence of earthworms after two and four weeks, by the end of the incubation, Collembola abundance was unaffected by earthworm presence (Fig. 2). We suspect that this diminished effect may have been due to the loss of earthworm biomass including mortality of all earthworms in the CO + ET + CE treatment by the six week sample date. This supports the idea that earthworms can suppress Collembola abundance, but that this effect does not persist when earthworms are no longer active. Another possible reason for this phenomenon is that the dead earthworms in this treatment provided direct or indirect food resource for collembolan population.

Population dynamics of the collembolan used in this study have been shown to peak in cultures and then decrease over time even under optimal conditions (Gist et al., 1974), similar to what we observed in the CO treatment during our experiment. The observed peak abundance of collembolans was delayed in all treatments containing earthworms and centipedes (Fig. 1), and there was no significant decline from this peak in the CO + ET + CE treatment.

Table 1
Analysis of Variance results for 3-way analyses of variance for collembolan numbers and centipede and earthworm biomass response variables. Some interactivity terms could not be calculated for the "Centipede biomass change from initial" response variable due to unbalanced experimental design. "*" indicates significance at $p < 0.05$; "**" indicates significance at $p < 0.01$; "***"indicates significance at $p < 0.001$.

Response Variable: Collembolan Abundance Change From Initial

Source	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Centipede	1	10 824	10 824	0.1510	0.700336
Earthworm	1	917 558	917 558	12.7991	0.001201**
Time	2	561 380	280 690	3.9154	0.030842*
Centipede:Earthworm	1	109 354	109 354	1.5254	0.226391
Centipede:Time	2	242 246	121 123	1.6896	0.20169
Earthworm:Time	2	488 256	244 128	3.4054	0.046473 *
Centipede:Earthworm:Time	2	57 938	28 969	0.4041	0.671163
Residuals	30	2 150 670	71 689		

Response Variable: Earthworm Biomass Change From Initial

Source	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Collembola	1	0.0120	0.0120	0.0581	0.81083
Centipede	1	5.9573	5.9573	28.9313	4.045e-06***
Time	2	6.9414	3.4707	16.8551	5.752e-06***
Collembola:Centipede	1	0.1677	0.1677	0.8145	0.37249
Collembola:Time	2	1.6692	0.8346	4.0531	0.02538*
Centipede:Time	2	0.1970	0.0985	0.4783	0.62349
Collembola:Centipede:Time	2	0.4836	0.2418	1.1743	0.32001
Residuals	38	7.8247	0.2059		

Response Variable: Centipede Biomass Change From Initial

Source	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Collembola	1	0.0013616	0.00136160	8.9284	0.0056655 **
Earthworm	1	0.0025953	0.00259527	17.0180	0.0002844 ***
Week	2	0.0000280	0.00001399	0.0917	0.9126153
Collembola:Week	2	0.0006291	0.00031455	2.0626	0.1453692
Earthworm:Week	2	0.0006143	0.00030713	2.0139	0.1517055
Residuals	29	0.0044226	0.00015250		

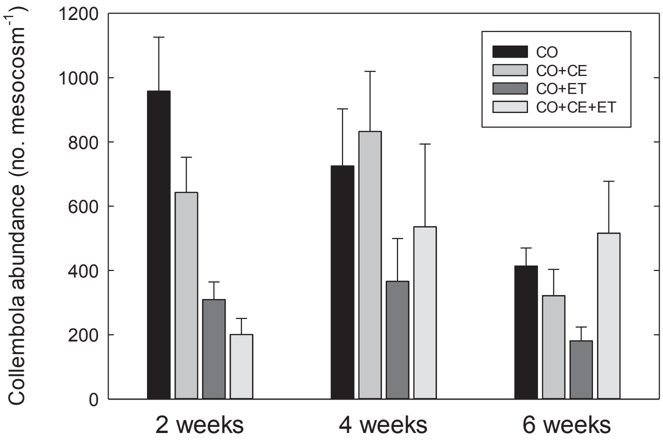

Fig. 1. Changes in Collembola abundance from initial conditions over the course of the study. Bars represent the mean number of Collembola per mesocosm recovered in excess of the original 100 individuals; error bars indicate standard error. CO = treatments with Collembola (*Sinella curviseta*) added; CE = treatments with centipedes (Family: Cryptopidae) added; ET = treatments with earthworms (*Amynthas agrestis*) added.

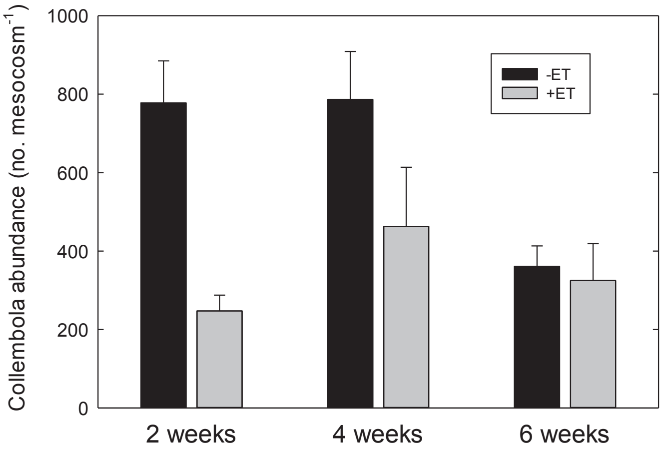

Fig. 2. Changes in Collembolan abundance from initial conditions. Interactive response of collembolan abundance to absence (-ET) and presence (+ET) of *Amynthas agrestis* earthworms and sample date (Time). Bars represent the mean number of Collembola per mesocosm recovered in excess of the original 100 individuals; error bars indicate standard error.

We speculate that interactions in this most complex trophic system resulted in the most stable collembolan population. In the context of broader soil foodweb trophic ecology, others have shown that earthworms can function as "trophic whales," stabilizing erratic population oscillations of other species by moderating the effects of certain disturbances (Schwarzmuller et al., 2015). It is possible that the results from our mesocosm study represent another demonstration of earthworms as a stabilizing force in population dynamics, although this experimental system is admittedly very simple. This possibility is particularly interesting given that the invasive earthworm in this system is both the disturbance and the "trophic whale," potentially complicating the interpretation of overall effects of the invasion of *Amynthas agrestis* on soil properties. Clearly, more research in this avenue with additional earthworm species and invasives/natives would be valuable for untangling such complex trophic interactions.

Centipede biomass significantly increased when earthworms were present compared to the treatment without earthworms (-ET in Fig. 4 b). Additionally, centipede biomass was significantly lower

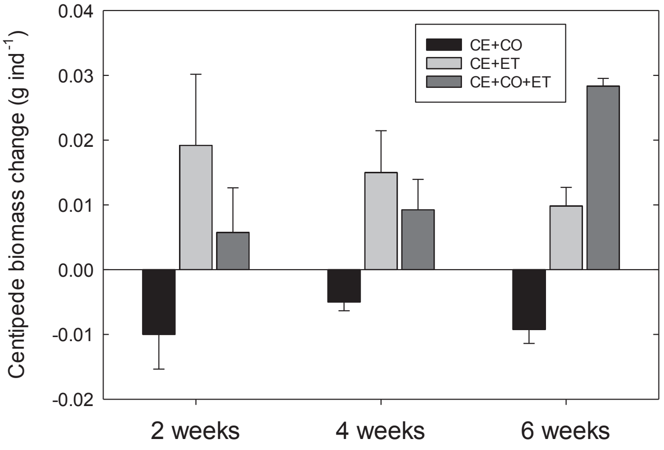

Fig. 3. Changes in Centipede biomass (g mesocosm^{-1}) from initial. Bars represent the mean increase or decrease in biomass per individual centipede relative to initial mass; error bars indicate standard error. Treatment abbreviations as in Fig. 1.

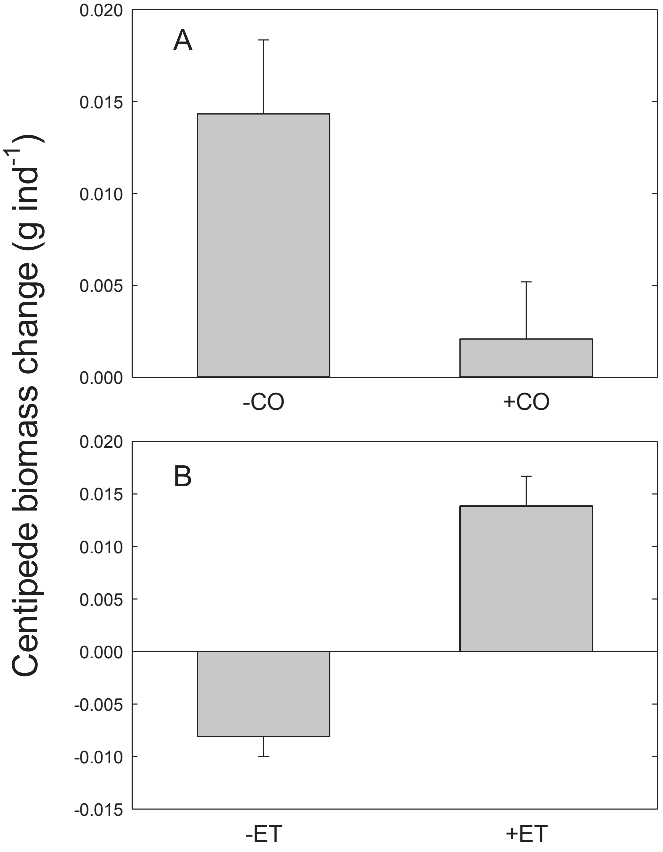

Fig. 4. Changes in Centipede biomass (g mesocosm^{-1}) from initial. (A) Response of centipede biomass to the absence (-CO) and presence (+CO) of Collembola; (B) Response of centipede biomass to the absence (-ET) and presence (+ET) of earthworms. Bars represent the mean increase or decrease in biomass per individual centipede relative to initial mass; error bars indicate standard error.

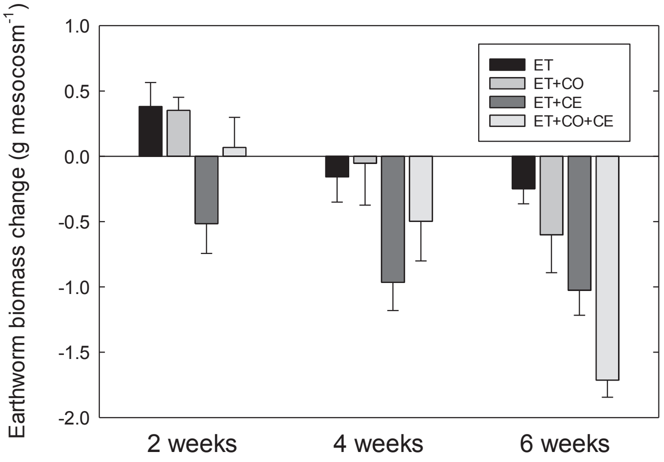

Fig. 5. Changes in earthworm biomass (g mesocosm^{-1}) from initial conditions. Bars represent the mean increase or decrease in biomass per mesocosm relative to initial mass; error bars indicate standard error. Treatment abbreviations as in Fig. 1.

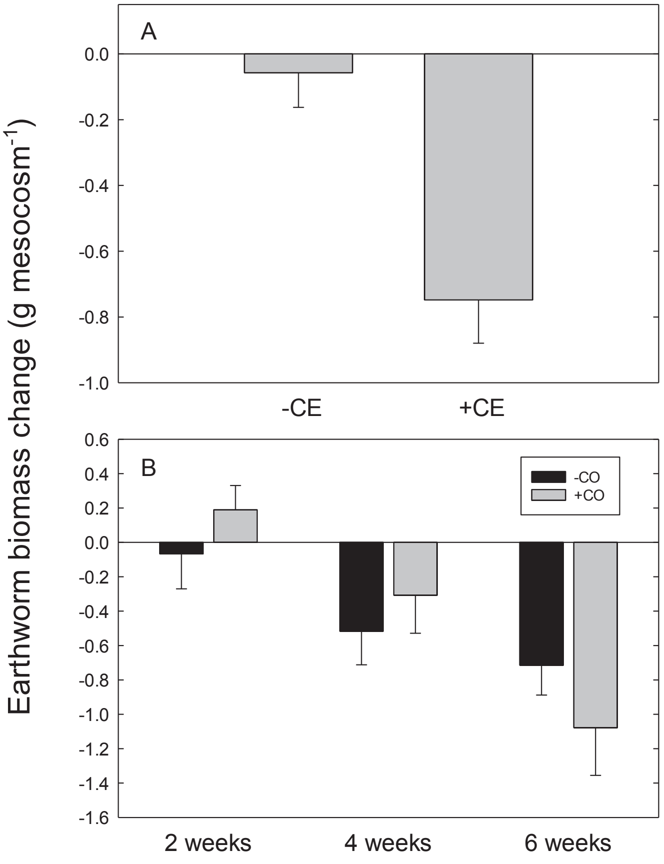

Fig. 6. Changes in earthworm biomass (g mesocosm^{-1}) from initial. (A) Response of earthworm biomass to the absence (-CE) and presence (+CE) of centipedes; (B) Interactive response of earthworm biomass to the absence (-CO) and presence (+CO) of Collembola and sample date (Time). Bars represent the mean increase or decrease in biomass per mesocosm relative to initial mass; error bars indicate standard error.

in the presence of Collembola compared to the treatment where Collembola were not present (+CO vs. −CO in Fig. 4a). An important caveat with these results is that a centipede-only treatment was not included and therefore we cannot know with certainty the possible interactive effects of earthworms and Collembola on the biomass of centipedes. Although earthworms lost biomass over the course of the experiment in all treatments, earthworms incubated with a centipede (+CE in Fig. 6 a) lost more biomass than those in treatments without a centipede (-CE, Fig. 6 a). In fact, we recovered no earthworms from the CO + ET + CE treatment by the end of the experiment, and this earthworm mortality accounted for the biomass reductions compared to the previous sample dates. At the same time, centipedes in the CO + ET + CE treatment gained the most biomass by the end of the experiment.

The earthworm species used in this study is epigeic and known to consume leaf litter. We provided leaf litter collected from the earthworms' invaded habitat and sufficient moisture every week (Görres et al., 2016), and so the reason for earthworm biomass decrease was neither food availability nor moisture constraints. It is possible that these earthworms were in a reproductive state, and were losing mass as a result of cocoon production, which is known to occur near the end of their annual life cycle (Snyder et al., 2013). Some centipedes have been reported to be active predators of earthworms (Weil, 1958; Blandin et al., 1980; Lewis, 1981; Poser, 1988). It is likely, given the results of our incubation, that the centipedes we collected for the study used earthworms as a food source. The centipedes were collected from a different location than the earthworms would not likely have previously been exposed to these earthworms as a food source. We propose that centipedes may exert some top-down influence on populations of invasive earthworms, although this does not appear to be sufficient to prevent their establishment and spread.

Some predators can serve as an effective controller for invasive earthworms. Birds (Yui, 1988), moles (Imaizumi, 1979) and ground beetles (Sota, 1985a, b) are all major predators for *A. agrestis* in Japan which is the native range for this species. In contrast, we still do not know the major predators for *A. agrestis* in its invaded distribution area, except for salamanders (Ransom, 2012). Results from our study suggest that the invasive earthworm is opportunistically used as a prey item by centipedes, and that this could represent a novel food resource for these native litter-dwelling predators.

In our study, an invasive earthworm influenced a microbe-detritivore population (Collembola) but may itself have been influenced by a common predator (centipede). The apparent interactions we observed between these three organisms were not as hypothesized. Whereas we expected centipedes to feed on collembolans, the centipedes we used in the study may have preferred invasive earthworms as a food source. Centipedes, as generalist predators, are known to have a varied diet, which can change depending on the developmental stage and even with time of year (Ferlian et al., 2012). It is possible, therefore, that the results of our experiment would have been different if we had used younger centipedes, or different species of centipedes in the incubation. Our results highlight the complexity of belowground trophic interactions, and suggest the need for basic research into traits and behaviors of belowground fauna. Techniques for examining food web dynamics such as tracer and natural abundance applications of stable isotopes (e.g., Crotty et al., 2011; Pollierer et al., 2012), or DNA analysis of gut contents (e.g. Juen and Traugott, 2007; Eitzinger et al., 2013) should allow better resolution and greater certainty with respect to actual trophic interactions involving invasive earthworms in the future.

5. Conclusions

Invasive earthworms influenced trophic dynamics in our experimental mesocosm, but not in the way we anticipated. Invasive earthworms directly depressed collembolan populations initially, and benefited centipedes throughout. Invasive earthworms may represent a novel food source for centipedes and other predators, and could potentially disrupt typical trophic relationships in ecosystems where they invade.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.08.001.

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