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Influence of two exotic earthworm species with different foraging strategies on abundance and composition of boreal microarthropods

Erin K. Cameron [a,*], Kyle M. Knysh [a,1], Heather C. Proctor [a], Erin M. Bayne [b]

[a] Department of Biological Sciences, CW 405, Biological Sciences Building, University of Alberta, Edmonton, Alberta, Canada T6G 2E9
[b] Integrated Landscape Management Group, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

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ABSTRACT

In North America, many species of European earthworms have been introduced to northern forests. Facilitative or competitive interactions between these earthworm species may result in non-additive effects on native plant and animal species. We investigated the combined versus individual effects of the litter-dwelling earthworm *Dendrobaena octaedra* Savigny, 1826 and the deep-burrowing species *Lumbricus terrestris* L., 1758 on microarthropod assemblages from boreal forest soil by conducting a mesocosm experiment. Soil cores from earthworm-free areas of northern Alberta, Canada, were inoculated with *D. octaedra* alone, *L. terrestris* alone, both worm species together, or no earthworms. After 4.5 months, microarthropods were extracted from the soil, counted, and identified to higher taxa. Oribatid mites were further identified to family and genus. Abundance of microarthropods was significantly lower in the treatment containing both species than in the no earthworm treatment and the *L. terrestris* treatment. Oribatida and Prostigmata/Astigmata differed significantly among treatments and were lowest in the treatment containing both earthworm species, followed by the *D. octaedra* treatment, although post-hoc pairwise comparisons were not significant. Within the Oribatida, composition differed between the control and *L. terrestris* treatments as compared to the *D. octaedra* and both-species treatments, with *Suctobelbella* and *Tectocepheus* in particular having higher abundances in the control treatment. Effects of the two earthworm species on microarthropods were neither synergistic nor antagonistic. Our results indicate that earthworms can have strong effects on microarthropod assemblages in boreal forest soils. Future research should examine whether these changes have cascading effects on nutrient cycling, microbial communities, or plant growth.

1. Introduction

As the numbers of non-native species increase in many ecosystems worldwide (Cohen and Carlton, 1998; Ricciardi, 2001; Lockwood et al., 2007), the potential for interactions to occur among these species has also grown. Positive interactions such as mutualism or facilitation among exotic species can result in larger effects on native species than would otherwise be expected (Simberloff and Von Holle, 1999; Simberloff, 2006). Facilitation between non-native species may even result in an invasional meltdown, in which there is an accelerating increase in the number of introduced species and/or in the severity of their impacts (Simberloff and Von Holle, 1999; Simberloff, 2006). Conversely, negative interactions such as competition or predation among invading species can decrease their success and may lead to reduced effects on native species (e.g., Yang et al., 2011).

Non-native species that act as ecosystem engineers may have particularly strong effects on the species with which they interact, due to their ability to modify biological and physical characteristics of the environment (Lavelle et al., 1997). Among the non-native ecosystem engineers currently spreading in northern North American forests are earthworms (Annelida: Haplotaxida: Lumbricina Burmeister, 1837). Due to glaciation, there are no native species of earthworms in most of Canada and the northern United States (Gates, 1970, 1982). Recent invasions of European earthworms into North American forests have resulted in changes such as reductions in thickness of organic soil layers (Gundale, 2002) and decreases in abundance and diversity of understory plants (Gundale, 2002; Hale et al., 2008; Eisenhauer et al., 2007; Nuzzo et al., 2009).

In addition to altering soil and plant composition, non-native earthworms can affect other groups of soil invertebrates such as

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[*] Corresponding author. Tel.: +1 780 492 6873; fax: +1 780 492 9234.
E-mail address: ecameron@ualberta.ca (E.K. Cameron).

[1] Present address: Biology Department, University of Prince Edward Island, 550 University Avenue, Charlottetown, PEI, Canada C1A 4P3.

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millipedes (Snyder et al., 2011) and microarthropods (Acari and Collembola) (McLean and Parkinson, 2000; Eisenhauer et al., 2007; Straube et al., 2009). Microarthropod densities can exceed 100,000/m^2 of soil (Coleman et al., 2004), and changes in their abundance and diversity can have strong effects on nutrient cycling (Wickings and Grandy, 2011) and decomposition (Eisenhauer and Schaedler, 2011). Microarthropods may be affected by earthworms via changes in the physical structure of the soil, by predation, or by competition for food (McLean and Parkinson, 1998, 2000; Eisenhauer, 2010). However, the response of microarthropods to earthworms in invaded forests varies substantially across studies (Eisenhauer, 2010). Increases in microarthropod richness and abundance due to earthworm invasions tend to be observed primarily over short time periods (e.g., several months) or at low earthworm densities, while non-significant or negative effects are more commonly observed over longer time periods (McLean and Parkinson, 1998; Migge-Kleian et al., 2006; Eisenhauer, 2010).

Effects of earthworms on soil communities can differ depending on the earthworm species' foraging strategies. Microarthropod abundances are typically much higher in the organic than mineral layers (e.g., Battigelli et al., 2004), and therefore earthworms that are active in the organic soil might be expected to have a particularly strong effect on microarthropod populations. Anecic earthworms inhabit deep burrows but feed on leaf litter, while endogeic and epigeic species live and feed in the mineral soil and leaf litter, respectively (Bouché, 1977). In invaded forests, the anecic species *Lumbricus terrestris* L., 1758 has either negative effects (Migge, 2001; Burke et al., 2011) or no significant effects on microarthropods at the habitat-scale (Migge, 2001; Eisenhauer et al., 2007; Straube et al., 2009). Endogeic species such as *Octolasion tyrtaeum* Savigny, 1826 generally cause decreases in abundance of microarthropods in forests (Migge, 2001; Eisenhauer et al., 2007), although there are exceptions (Straube et al., 2009). Considerably less research has examined effects of epigeic earthworms on microarthropods. Microarthropod abundance decreased in the presence of the epigeic species *Dendrobaena octaedra* Savigny, 1826 in a field study conducted in a pine forest in Alberta, Canada (McLean and Parkinson, 2000). In the only other study on exotic epigeic earthworm effects on microarthropods, which was conducted in a laboratory using pine forest soil, microarthropod abundance increased in the presence of *D. octaedra* after 3 months, but declined significantly after 6 months (McLean and Parkinson, 1998).

In northern forests in Canada and the United States, non-native earthworm species often co-occur (Gundale et al., 2005; Hale et al., 2005; Suarez et al., 2006; Cameron et al., 2007). In particular, endogeic and anecic earthworms occur mainly in areas that have also been colonized by epigeic and epi-endogeic species, whereas epigeic species frequently occur on their own. The frequent co-occurrence of multiple earthworm species raises the possibility that their effects on native forest biota could be strongly affected by facilitative or competitive interactions between earthworm species. Despite this, manipulative experiments have not typically examined how effects of single earthworm species differ from effects of multiple species together.

We used a greenhouse mesocosm experiment to investigate the effects of the non-native European earthworms *D. octaedra* (epigeic) and *L. terrestris* (anecic) on microarthropods in boreal forest soil. Both of these earthworm species are common invaders in northern forests in North America (Gundale et al., 2005; Hale et al., 2005; Cameron et al., 2007), although *D. octaedra* is more widespread in boreal regions (Cameron et al., 2007). We predicted that the epigeic *D. octaedra* would cause a larger decrease in microarthropod abundance and diversity in the organic soil horizons than the anecic *L. terrestris*. *L. terrestris* may have fewer direct interactions with microarthropods in the organic layers because it feeds in those layers, but lives in deep burrows. Due to the two species' differing feeding strategies and effects on soil structure, a treatment containing both species was expected to disturb all soil layers and have the largest impact on microarthropods. However, *L. terrestris* can negatively affect the reproduction of *D. octaedra* (Cameron and Bayne, 2011), suggesting the effect of both earthworm species when together might be lower than what would be expected by simply adding together individual effects. We also predicted that Mesostigmata (predatory mites) would be less negatively affected by earthworms than groups that are more detritivorous or microbivorous (Collembola, Prostigmata, and Oribatida including Astigmata) due to competition for food resources or greater disruption of these resources (Salmon et al., 2005; Eisenhauer, 2010). Because oribatid mites are a highly diverse group and tend to be sensitive to disturbances (Wallwork, 1983; Maraun and Scheu, 2000), we further examined the effects of earthworms on oribatids at the genus/family level.

2. Materials & methods

2.1. Experimental design

We used a mesocosm experiment to examine the effects of non-native earthworms on microarthropods in boreal forest soil collected from an earthworm-free area. The experiment included four treatments, each with ten replicate mesocosms: 1) no earthworms (control); 2) two *L. terrestris*; 3) 30 *D. octaedra*; and 4) both species (two *L. terrestris* and 30 *D. octaedra*). We chose these earthworm densities based on field densities found at invaded sites in northern forests in Alberta and Minnesota. Field averages range from 0 to 7.6 for *L. terrestris* and 0 to 40 for *D. octaedra* for areas the size of our mesocosms (0.07 m^2) (Hale et al., 2005, 2008; Cameron et al., 2007; Eisenhauer et al., 2007), and there were therefore different total biomasses per mesocosm for the two species. In our samples, *L. terrestris* weighed ~5.3 g each and *D. octaedra* weighed ~0.15 g each, and all earthworms were adults. We collected *D. octaedra* from the field and obtained *L. terrestris* from a local bait shop; however, based on our conversations with bait-shop owners and bait distributors, earthworms sold for bait in Alberta are not captive-bred, but are also captured from the wild.

Mesocosms consisted of 30 cm diameter by 38 cm high plastic buckets with five 2.2 cm drainage holes drilled in the bottom. To prevent earthworm escape and soil loss, landscaping fabric was glued into the bottom of the buckets. As well, the top 5 cm of the inner rim of each bucket was covered with coarse sand using white glue in order to discourage earthworm escape. The buckets were filled with 18 cm of mineral soil, which was first sorted to remove large roots, large arthropods (e.g., Coleoptera: Carabidae), and rocks. A 4–6 cm thick disc of intact forest floor (FH layers) the same diameter as the bucket, as well as 3 cm of aspen leaf litter, were placed on top of the mineral soil. Soil and litter were collected from a forest stand in northeastern Alberta (54°36′N, 110°59′W) that was dominated by trembling aspen (*Populus tremuloides* Michx) and white spruce (*Picea glauca* (Moench) Voss) and had gray luvisolic soil. Previous sampling indicated the site was earthworm-free (Cameron et al., 2007; Cameron and Bayne, 2009).

The experiment took place from 9 May 2009 to 20 October 2009. Mesocosms were randomly placed in a greenhouse at the University of Alberta and earthworms were added to half of the mesocosms in treatments 2, 3, and 4 after two weeks. We waited an additional two weeks before adding earthworms to the remaining mesocosms in treatments 2, 3, and 4 because data collection at the end of the experiment was expected to take approximately a month in total, and this ensured that all of the mesocosms were exposed to the