ECOSYSTEMS

Exotic Ecosystem Engineers Change the Emergence of Plants from the Seed Bank of a Deciduous Forest

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ABSTRACT

The anthropogenic spread of exotic ecosystem engineers profoundly impacts native ecosystems. Exotic earthworms were shown to alter plant community composition of the understory of deciduous forests previously devoid of earthworms. We investigated the effect of two exotic earthworm species (*Lumbricus terrestris* L. and *Octolasion tyrtaeum* Savigny) belonging to different ecological groups (anecic and endogeic) on the emergence of plants from the seed bank of a northern North American deciduous forest using the seedling emergence method. We hypothesized that (1) exotic earthworms change the seedling emergence from the plant seed bank, (2) *L. terrestris* increases the emergence of plant seedlings of the deeper soil layer but decreases that of the upper soil layer due to plant seed burial, and (3) *O. tyrtaeum* decreases plant seedling emergence due the damage of plant seeds. Indeed, exotic earthworms altered the emergence of plant seedlings from the seed bank and the functional composition of the established plant seedlings. Surprisingly, although *L. terrestris* only marginally affected seedling emergence, *O. tyrtaeum* changed the emergence of native plant species from the seed bank considerably. In particular, the number of emerging grass and herb seedlings were increased in the presence of *O. tyrtaeum* in both soil layers. Moreover, the impacts of earthworms depended on the identity of plant functional groups; herb species benefited, whereas legumes suffered from the presence of exotic earthworms. The results highlight the strong effect of invasive belowground ecosystem engineers on aboveground ecosystem characteristics and suggest fundamental changes of ecosystems by human-spread earthworm species.

Key words: above- and belowground interactions; exotic earthworms; *Lumbricus terrestris*; *Octolasion tyrtaeum*; plant seedlings; seedling emergence; soil seed bank.

INTRODUCTION

Human alterations of Earth's ecosystems and their functions are substantial and multifaceted (Vitousek and others 1997). One major mechanism by which human activity alters ecosystem functions is

the introduction of exotic species (Vitousek and others 1996). In particular, the spread of ecosystem engineers profoundly impacts native ecosystems (Morrison 2002; Cuddington and Hastings 2004; Anderson and Rosemond 2007).

Previous studies on species invasions primarily focussed on aboveground plant and animal species. Recently, studies on exotic earthworms showed that also belowground invaders strongly impact above- and belowground ecosystem properties (Bohlen and others 2004; Hale and others 2005, 2006, 2008; Eisenhauer and others 2007; Straube and others 2009). Invasive earthworms were shown to alter physical and chemical soil characteristics, nutrient cycling and mineralization, microbial functioning, and the density and diversity of other soil invertebrates (Bohlen and others 2004; Groffman and others 2004; Migge-Kleian and others 2006; Eisenhauer and others 2007; Straube and others 2009). Moreover, exotic earthworms were also reported to profoundly change plant community composition of the understory of deciduous forests by altering seedbed conditions (Hale and others 2005, 2006; Frelich and others 2006; Holdsworth and others 2007).

Although the native earthworm fauna of northern North America is restricted to Pacific coastal regions (McKey-Fender and Fender 1982), European earthworms have been colonizing the North American continent since European settlement (Gates 1982; Addison 2009). Currently, a variety of ecosystems are being invaded by exotic earthworms in southern Alberta (Scheu and McLean 1993; Addison 2009). Eisenhauer and others (2007) reported the recent invasion of the two exotic earthworm species, *Lumbricus terrestris* L. (Figure 1C) and *Octolasion tyrtaeum* Savigny (Figure 1D), into an aspen forest in the mountain ranges of the Rocky Mountains west of Calgary (Kananaskis Valley, Alberta). The anecic species *L. terrestris* forms vertical permanent burrows up to 2 m deep, consumes, accumulates and incorporates surface litter into deeper soil layers, and transports mineral soil materials to the soil surface by casting, thereby forming earthworm middens (Lee 1985; Edwards 2004). *Octolasion tyrtaeum*, as an endogeic species, lives in upper mineral soil layers mainly consuming soil organic matter. Both species were shown to function as keystone detritivores and ecosystem engineers (Jones and others 1994; Lavelle and others 1998; Eisenhauer and others 2007).
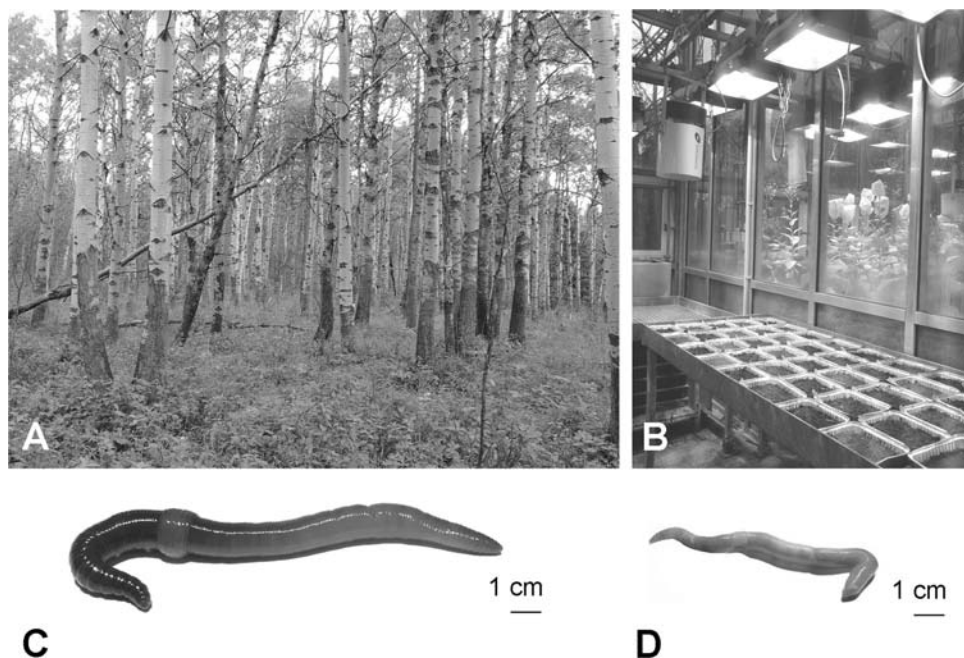
Figure 1. Photograph (**A**) of the studied aspen forest in southwest Alberta (Canada) showing the dense herbaceous understory (Photo: N. Eisenhauer), (**B**) showing a bench with some of the 80 numbered and randomized experimental trays (seedling emergence experiment) under greenhouse conditions at Darmstadt University of Technology (Photo: N. Eisenhauer), (**C**) of *Lumbricus terrestris* L., a large-bodied anecic earthworm species (Photo: H. Schuy), and (**D**) of *Octolasion tyrtaeum* Savigny, a large-bodied endogeic earthworm species (Photo: H. Schuy). Both earthworm species are exotics currently invading the studied aspen forest.

Earthworms are known to engineer seedbed conditions for plants and recent studies highlighted the importance of direct and indirect interactions between earthworms and plant seeds for plant community composition (Eisenhauer and Scheu 2008; Eisenhauer and others 2008a, 2009; Regnier and others 2008). It is increasingly recognized that after the displacement of seeds from the parent plant to the soil surface, earthworms play an important role in the subsequent displacement of seeds on the soil surface and burial into the soil (Grant 1983; Willems and Huijsmans 1994; Decaens and others 2001, 2003; Milcu and others 2006; Eisenhauer and Scheu 2008; Eisenhauer and others 2008a, b). Furthermore, earthworms affect plant seeds and seedling fates in both positive and negative ways by a number of mechanisms. They enhance seed survival by reducing exposure of seeds to aboveground seed predators (Heithaus 1981), create nutrient-rich gaps for seed germination (Milcu and others 2006; Eisenhauer and others 2008a), break seed dormancy, and increase germination and root initiation of plant seeds (Tomati and others 1988; Ayanlaja and others 2001; Eisenhauer and others 2009). However, seeds may also be buried below some critical depth where they fail to emerge (Traba and others 1998; Regnier and others 2008) and get damaged or digested during earthworm gut passage (McRill and Sagar 1973; Grant 1983; Shumway and Koide 1994; Eisenhauer and others 2009). A recent field study revealed that *L. terrestris* very efficiently buries plant seeds from the soil surface to deeper soil layers (Regnier and others 2008), thereby presumably decreasing the number of germinable seeds in the upper soil layers while increasing the number in deeper soil layers. However, it has been shown that both anecic and endogeic earthworm species affect the fate of plant seeds (Eisenhauer and others 2009). Although several studies focussed on the effects of exotic earthworms on the vegetation of ecosystems previously devoid of earthworms (Hale and others 2005, 2006; Frelich and others 2006; Eisenhauer and others 2007; Holdsworth and others 2007), impacts of exotic earthworms on soil seed banks of these ecosystems are unexplored. Generally, seed banks are a source for the re-establishment and recovery of plant species and function to escape unfavorable environmental conditions and seed predation (Juan and others 2006; Wellstein and others 2007). Consequently, impacts of exotic earthworms on seed banks might drive plant community composition of invaded ecosystems with important

consequences for local plant diversity (Hale and others 2006; Holdsworth and others 2007).

We studied the impacts of exotic earthworms on the emergence of herbaceous plant species from the soil seed bank of the above-mentioned aspen forest. We sampled locations without the presence of *L. terrestris* and *O. tyrtaeum*, with only one of these species and with both species present. Moreover, we distinguished two soil layers (0–8 and 8–16 cm) to account for the different ecology of the investigated earthworm species. We hypothesized that (1) exotic earthworms change the seedling emergence from the plant seed bank, (2) *L. terrestris* increases the emergence of plant seedlings from the deeper soil layer but decreases that of the upper soil layer due to plant seed burial, and (3) *O. tyrtaeum* decreases plant seedling emergence due the damage of plant seeds.

METHODS

Study Site

This study was conducted in a deciduous forest located in Kananaskis Valley in the front range of the Canadian Rocky Mountains in southwest Alberta (51°2′ N, 115°4′ W) at about 1410 m above sea level. The dominating tree species in the investigated forest is trembling aspen (*Populus tremuloides* Michx.) interspersed with some balsam poplar individuals (*Populus balsamifera* L.). The understory is dense and mainly consists of herbs (for example, *Aster conspicuus* Lindl., *Aster laevis* L., *Viola canadensis* L., *Epilobium angustifolium* L., *Delphinium glaucum* Wats., *Heracleum lanatum* Michx.), roses (*Rosa acicularis* Lindl., *Rosa woodsii* Lindl.), and grasses (for example, *Bromus* sp., *Danthonia* sp., *Agropyron* sp.) (see Table 1 for plant species list; Figure 1A). The soil was classified as orthic gray luvisol (Karkanis 1972). The climate is characterized by long, cold winters with intermittent warm Chinook winds and short dry summers. The soil usually remains frozen from November until March. The mean annual precipitation at the study site is 625 mm and the mean annual temperature in the organic layer is 3.8°C (Mitchell 1974).

Experimental Design

The studied forest has been colonized in a patchy way by the exotic earthworm species *L. terrestris* and *O. tyrtaeum* (Eisenhauer and others 2007; Straube and others 2009). Locations in the forest without presence of *L. terrestris* and *O. tyrtaeum*, with only one of these species and with both species present

Table 1. List of Herbaceous Plant Species in the Understory of the Investigated Aspen Forest and Their Classification to Plant Functional Groups

Plant species	Plant functional group
Agropyron sp.	Grass
Aster conspicuus Lindl.	Herb
Aster laevis L.	Herb
Bromus sp.	Grass
Danthonia sp.	Grass
Delphinium glaucum Wats.	Herb
Disporum hookeri Torr.	Herb
Epilobium angustifolium L.	Herb
Fragaria virginiana Dcne.	Herb
Galium boreale L.	Herb
Heracleum lanatum Michx.	Herb
Lathyrus ochroleucus Hook.	Legume
Lonicera utahensis Wats.	Herb
Osmorhiza depauperata Phil.	Herb
Pyrola asarifolia Michx.	Herb
Smillacina stellata L.	Herb
Taraxacum officinale L.	Herb
Thalictrum occidentale Gray	Herb
Vicia americana Muhl.	Legume
Viola canadensis L.	Herb

were carefully selected. Identification of these sites was based on sampling three transects from the edge to the center of the forest to determine earthworm distribution patterns (see Straube and others 2009 for more details) and on the inspection of the locations for earthworm activity (casts and middens). We identified 20 sampling sites: 10 with presence of *O. tyrtaeum* and 10 without. At each of these 20 sites, two soil cores were taken: one in the center of *L. terrestris* middens (with *L. terrestris*) and another one at approximately 1 m away from the midden (without *L. terrestris*) to investigate the effects of *L. terrestris* presence/middens and *O. tyrtaeum* presence on the soil seed bank in a full factorial design ($n = 40$). The four different sampling sites did not vary significantly in total plant coverage (84 ± 3%; $F_{3,36} = 0.59$, $P = 0.45$) and in the coverage of grasses (29 ± 3%; $F_{3,36} = 1.41$, $P = 0.24$), herbs (77 ± 5%; $F_{3,36} = 2.19$, $P = 0.15$), and legumes (15 ± 2%; $F_{3,36} = 2.81$, $P = 0.11$; visual estimation of 1 m^2 in intervals of 5%, modified after Daubenmire 1959). Furthermore, the sites did not differ in plant species richness (8.70 ± 0.25 species/m^2; $F_{3,36} = 0.05$, $P = 0.82$), in the Shannon–Wiener index (1.93 ± 0.03; $F_{3,36} = 0.14$, $P = 0.71$) and in the evenness of the plant community (0.90 ± 0.01; $F_{3,36} = 1.38$, $P = 0.25$). Samples were taken using a metal corer (5 cm in diameter, ~20 cm^2) which was driven into the soil to a depth of 16 cm. Soil cores were separated into

two layers mainly consisting of organic (0–8 cm, layer 1) and mineral soil material (8–16 cm, layer 2; ~160 cm^3, ~155 g soil fresh weight; $n = 80$), respectively. The samples were taken in September 2007 and stored at 5°C.

Seedling Emergence Experiment

The content of viable plant seeds in the different soil cores was analyzed by the seedling emergence method (Cosyns and Hoffmann 2005; Eichberg and others 2007). In November 2007, soil samples were frozen for 2 weeks (-10°C) to break seed dormancy. Then, the soil of each soil core and layer was placed in individual trays (15 cm × 22 cm × 5 cm) and exposed to light (450–650 µE/m^2 s) under controlled greenhouse conditions (day/night regime of 16/8 h and 20/10 ± 2°C; Figure 1B). The soil was kept moist continuously. Trays were randomized weekly and emerging seedlings were identified, counted, and removed every week for 4 months. To expose seeds to light that initially were located at the bottom of the trays, the soil was mixed thoroughly every 2 weeks starting after 1 month. No further seedlings emerged 3 months after experimental start.

Statistical Analyses

Seedlings were separated to plant functional groups (total, grass, herb, and legume seedlings) due to the low emergence of single plant species. Prior to statistical analyses, the data were log-transformed to improve normality of the distribution and homogeneity of variance, if necessary. Data on the total number of established seedlings, number of grass, herb, and legumes seedlings were analyzed using fixed factor repeated measures analysis of variance (GLM) with soil layer (LAY; 0–8 and 8–16 cm) as repeated factor, and presence/middens of *L. terrestris* (LUM; center of the midden and control ~1 m away from the midden) and presence of *O. tyrtaeum* (OCT; with and without) as categorical factors ($n = 80$). Furthermore, protected analyses of variance were performed for the two single soil layers (Scheiner and Gurevitch 2001). Moreover, two-factorial ANOVAs were performed to analyze the effect of earthworm presence (LUM and OCT) on the relative number of grass, herb, and legume seedlings. Therefore, we only used samples with established plant seedlings and summed up the number of plant seedlings of layers 1 and 2 ($n = 20$). Furthermore, single-factor ANOVAs were performed to analyze the effect of the four different sampling sites (with and without *L. terrestris* and *O. tyrtaeum*, respectively) on the coverage of the vegetation and the

coverage of grasses, herbs, and legumes ($n = 40$). Statistical analyses were performed using SAS V9.1 (SAS Institute Inc., Cary, USA). Means (±standard error) presented in text and figures were calculated using non-transformed data.

RESULTS

Generally, the number of established seedlings per soil core was low (0.80 ± 0.14 seedlings/160 cm^3). The number of total seedlings and herb seedlings were significantly higher in layer 1 (0.60 ± 0.07 and 0.30 ± 0.13 seedlings/160 cm^3) than in layer 2 (0.20 ± 0.13 and 0.08 ± 0.06 seedlings/160 cm^3; Table 2, Figure 2A, C). The presence/middens of *L. terrestris* did not affect the number of seedlings irrespective of the plant functional group identity and soil depth (Tables 2, 3). On the contrary, the number of total seedlings was increased significantly in presence of *O. tyrtaeum* ($\times$ 2.56; Table 2). However, this increase was only significant in layer 1 (Table 3, Figure 2A) and was due to the considerable increase of the number of grass ($\times$ 6.0) and herb seedlings ($\times$ 4.0) in the presence of *O. tyrtaeum* (Table 2). Although the number of grass seedlings was only increased significantly in layer 1 in the presence of *O. tyrtaeum* (Table 3, Figure 2B), there was a tendency of increased numbers of herb seedlings in both soil layers (Table 2, Figure 2C). However, the number of herb seedlings also depended on the presence of both earthworm species (Table 2). Although no herb seedlings established in the absence of earthworms, the number of herb seed-

Table 2. MANOVA Table of *F*-Values on the Effects of Earthworms and Soil Depth on the Number of Plant Seedlings

	Df	Total	Grasses	Herbs	Legumes
Between subject factors					
LUM	1	0.67	0.18	0.30	1.08
OCT	1	**6.74***↑	**4.59***↑	**6.86***↑	0.05
LUM × OCT	1	0.47	1.65	**3.95***	2.82
Error	36				
Within subject factors					
LAY	1	**5.36***↓	0.14	**4.14***↓	2.33
LAY × LUM	1	0.02	1.25	0.01	1.71
LAY × OCT	1	0.66	1.25	0.46	0.09
LAY × LUM × OCT	1	0.34	0.14	1.63	0.26
Error	36				

Significant effects (*P ≤ 0.05) are given in bold.
Df = degrees of freedom; ↑ = increase (in presence of earthworms or with increasing soil depth); ↓ = decrease; LUM = Lumbricus terrestris; OCT = Octolasion tyrtaeum; LAY = soil layer; 0–8 and 8–16 cm. Seedling categories: Total, grasses, herbs, and legumes.
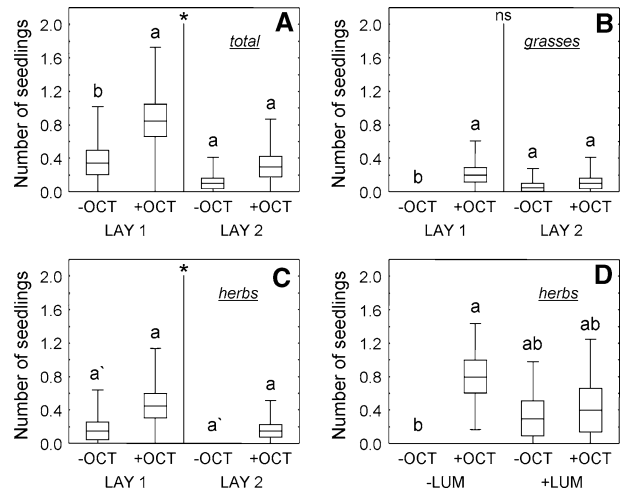
Figure 2. Variations in the number of established seedlings per soil core (diameter 5 cm, height 8 cm) (**A–C**) as affected by presence of *Octolasion tyrtaeum* (−OCT = without and +OCT = with) and soil depth (LAY 1 = 0–8 cm and LAY 2 = 8–16 cm) and (**D**) as affected by presence of *Octolasion tyrtaeum* and presence of *Lumbricus terrestris* (−LUM = without and +LUM = with). Means with standard error (*boxes*) and standard deviation (*error bars*). Means with *different letters* vary significantly (Tukey's HSD test, α < 0.05), and *asterisks* indicate significant differences between soil layers ($P < 0.05$) and inverted commas virtually significant differences between means ($P < 0.1$).

lings was increased significantly in the presence of *O. tyrtaeum* only (Figure 2D). Remarkably, this effect disappeared in the presence of *L. terrestris*. Generally, the number of legume seedlings was not affected by earthworm presence and soil depth (Tables 2, 3).

Table 3. Table of *F*-Values of Protected ANOVAs on the Effects of Earthworms on the Number of Plant Seedlings in Two Soil Layers

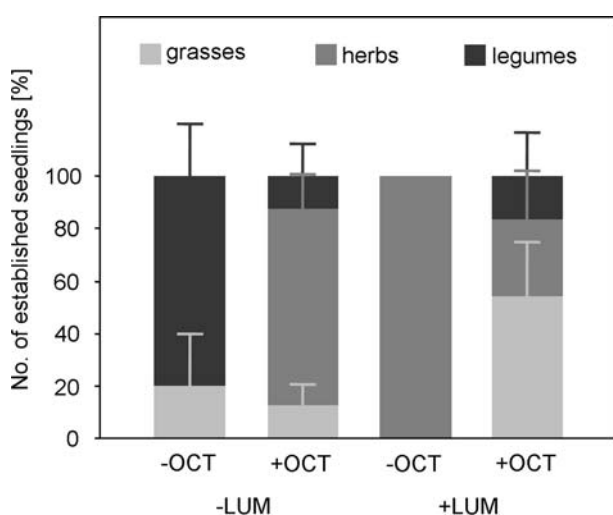|	Df	Total	Grasses	Herbs	Legumes
Layer 1					
LUM	1	0.32	1.20	0.07	1.77
OCT	1	**3.99***↑	**4.80***↑	**3.56**(*)↑	0.09
LUM × OCT	1	0.00	1.20	**3.56**(*)	1.77
Error	36				
Layer 2					
LUM	1	0.25	0.33	0.36	0.00
OCT	1	1.66	0.33	**3.24**(*)↑	0.00
LUM × OCT	1	1.16	0.33	0.36	2.00
Error	36				

Significant effects (P ≤ 0.05) and distinct tendencies (P < 0.1) are given in bold.
Df = degrees of freedom; * = P ≤ 0.05; (*) = P < 0.1; ↑ = increase (in presence of earthworms); LUM = Lumbricus terrestris; OCT = Octolasion tyrtaeum; LAY = soil layer; 0–8 and 8–16 cm. Seedling categories: Total, Grasses, Herbs, and Legumes.

The proportion of grass seedlings of the total number of plant seedlings was not affected by earthworms ($25 \pm 9\%$; Table 4, Figure 3). On the contrary, the proportions of herb ($46 \pm 11\%$) and legume seedlings ($29 \pm 10\%$) of the total number of plant seedlings were significantly affected by an interaction between the two earthworm species (Table 4). Although herb seedlings only established in the presence of earthworms (with maximum proportions of total seedlings in presence of *L. terrestris* only), the proportion of legume seedlings was considerably lower in the presence of earthworms, particularly in the sole presence of *L. terrestris* (Figure 3).

Table 4. ANOVA Table of *F*-Values on the Effects of Earthworms on the Proportion of the Number of Plant Seedlings Belonging to the Plant Functional Groups Grasses, Herbs, and Legumes

	Df	Grasses	Herbs	Legumes
LUM	1	0.32	2.45	**3.93**(*)↓
OCT	1	1.51	0.01	1.77
LUM × OCT	1	2.63	**17.77*****	**4.84***
Error	17			

Significant effects ($P \leq 0.05$) and distinct tendencies ($P < 0.1$) are given in bold. Df = degrees of freedom; *** = $P < 0.001$; * = $P < 0.05$; (*) = $P < 0.1$; ↓ = decrease (in presence of earthworms); LUM = Lumbricus terrestris; OCT = Octolasion tyrtaeum.

Figure 3. Variations in the proportion of the number of established seedlings belonging to the plant functional groups grasses, herbs, and legumes as affected by the presence of *Lumbricus terrestris* (−LUM = without and +LUM = with) and *Octolasion tyrtaeum* (−OCT = without and +OCT = with). Means with standard error.

DISCUSSION

Exotic earthworms profoundly change above- and belowground properties of northern North American deciduous forests (Bohlen and others 2004; Hale and others 2005, 2006; Frelich and others 2006; Eisenhauer and others 2007; Holdsworth and others 2007; Straube and others 2009). By altering seedbed conditions, exotic earthworms were reported to be a threat for plant diversity of forests previously devoid of earthworms (Hale and others 2006; Holdsworth and others 2007). Conforming to hypothesis (1), this study indicates that exotic earthworms change native seed banks. Although plant species composition of the standing vegetation did not differ significantly between the four sampling sites, total seedling numbers and seedling numbers of the plant functional groups grasses, herbs, and legumes varied considerably. Thus, we assume that changes in plant seedling emergence were due to earthworm presence and not due to different characteristics of the four sampling sites. Although, the invasion of the investigated forest by *L. terrestris* and particularly by *O. tyrtaeum* presumably started quite recently (Eisenhauer and others 2007), changes in plant seedling emergence are likely to change plant community composition. However, in contrast to hypothesis (2), the presence/middens of *L. terrestris* did not affect plant seedling numbers significantly, irrespective of soil depth. Previous studies showed that this anecic earthworm species buries plant seeds efficiently (Milcu and others 2006; Eisenhauer and Scheu 2008; Eisenhauer and others 2008b) and forms nutrient-rich plant regeneration niches (Eisenhauer and Scheu 2008; Eisenhauer and others 2008a). Furthermore, *L. terrestris* was shown to affect plant seeds directly via ingestion and digestion of plant seeds and indirectly via breaking seed dormancy due to physical and chemical stimuli (Shumway and Koide 1994; Ayanlaja and others 2001; El Harti and others 2001; Eisenhauer and others 2009). Moreover, a recent field study highlighted that *L. terrestris* concentrates plant seeds in its burrows (sixfold higher concentration of seeds in burrows than in the surrounding soil) and incorporates plant seeds into deeper soil layers (0.5–22 cm deep; Regnier and others 2008). However, in contrast to hypothesis (2), seedling emergence from the deeper soil layer was not increased in the presence of *L. terrestris* in this study. Similarly and surprisingly, *L. terrestris* burrows also had little effect on soil abiotic (pH, C, and N concentrations) and biotic (microbial respiration and biomass and microarthropod densities) properties in the investigated aspen forest (Straube and others 2009).

One possible explanation for the missing *L. terrestris* effects may be that the earthworm burrows did not run completely vertically and, therefore, were not included in the sampled soil core (5 cm in diameter) in deeper soil layers.

In contrast to *L. terrestris*, the presence of *O. tyrtaeum* affected plant seedling emergence considerably. Contrary to hypothesis (3), emergence of grass and herb seedlings from the seed bank was increased significantly in presence of this endogeic earthworm species (sixfold and fourfold increase in seedling numbers, respectively). Remarkably, this trend of increased seedling numbers was consistent for both soil layers. Obviously, positive effects of *O. tyrtaeum* on plant seeds, such as the physical and chemical acceleration and breakage of seed dormancy (Tomati and others 1988; Ayanlaja and others 2001; El Harti and others 2001; Eisenhauer and others 2009), were more important than negative ones, such as damaging and digesting of seeds (Grant 1983; Decaens and others 2001, 2003; Eisenhauer and others 2009). However, interactions between earthworms and grassland plant seeds were shown to be species specific and idiosyncratic (Eisenhauer and others 2009). Results of this study underline previous observations by showing increased numbers of herb seedlings in the presence of *O. tyrtaeum*. This increase was particularly pronounced for the most abundant herb species *A. leavis* (not shown); interestingly, coverage of this species was positively correlated with the density of *O. tyrtaeum* in 2004 (Eisenhauer and others 2007). Thus, certain plant species, such as *A. leavis*, might benefit from the presence of exotic earthworms at the expense of other species. However, this topic deserves further attention.

Results of this study suggest that the functional composition of emerging plants and, therefore, of the whole plant community is altered by exotic earthworms. Earthworm presence enhanced the emergence of herb seedlings but decreased the proportion of legume seedlings. Remarkably, only herb seedlings emerged in the presence of *L. terrestris* only. Again, this underlines observations from 2004 showing that shoot biomass of grasses and legumes declined at a higher density of *L. terrestris* (Eisenhauer and others 2007). These differences in earthworm impacts on plant seedling emergence of certain plant functional groups might have been due to variations in seed coat morphology. Previous studies suggested that slight physical and chemical damage to plant seed coats by earthworms breaks seed dormancy and enhances plant germination (Tomati and others 1988; Ayanlaja and others 2001; Eisenhauer and others 2009). In contrast to the majority of grass and herb species, both legume species occurring in the investigated aspen forest (*Vicia americana* Muhl. and *Lathyrus ochroleucus* Hook.) have thick seed coats that probably were not affected by earthworms. However, for example, the seed coat of the herb species *A. leavis* is comparatively thin allowing for strong *O. tyrtaeum* effects. Thus, the number of emerging legume seedlings was not affected by earthworms inducing lower proportions of legume seedlings of the total number of plant seedlings in the presence of earthworms. These results indicate that effects of exotic earthworms on the plant community composition of invaded forests are not only due to changes in seedbed conditions, for example, soil structure and nutrient availability, but also due to interactions between earthworms and plant seeds and, therefore, alterations in plant recruitment.

CONCLUSIONS

This study shows for the first time that exotic earthworms alter the seedling emergence from forest seed banks and the functional composition of the established plant seedlings. Surprisingly, *L. terrestris* only marginally affected seedling emergence, whereas *O. tyrtaeum* strongly increased the emergence of native plant species from the seed bank. However, earthworm impacts depended on the plant functional group; particularly herb species benefited, whereas legumes suffered from the presence of exotic earthworms. This highlights the strong effects of invasive belowground ecosystem engineers on aboveground ecosystem characteristics and foreshadows fundamental changes of native ecosystems by human-spread earthworm species.

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