



Earthworm invasion in North America: Food resource competition affects native millipede survival and invasive earthworm reproduction

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ABSTRACT

The invasive non-native earthworm *Amyntas agrestis* (Goto and Hatai, 1899) has recently been documented invading forests of the Appalachian Mountains in the southeastern United States. This epigeic earthworm decreases the depth of organic soil horizons, and this may play a role in the decrease of millipede richness and abundance associated with *A. agrestis* invasion. To investigate the mechanisms behind these effects, *A. agrestis* and the millipede *Sigmoria ainsliei* (Xystodesmidae) were placed into microcosms with soil and either L horizon, F and H horizon, or a combination L/FH treatment. Microcosms were destructively sampled and reconstructed with the same treatments every four weeks to assess faunal fresh weight change and survival. Soils from earthworm treatments were wet-sieved for cocoons to assess treatment effects on reproduction. On average, millipede mortality occurred 88 days sooner in treatments that did not have FH horizon material, and within all litter treatments millipedes tended to survive longer when *A. agrestis* was absent. Earthworms maintained higher fresh weight in L/FH than FH or L treatments. With a single exception, no *A. agrestis* cocoons were recovered from microcosms that also contained *S. ainsliei*. The results suggest that *A. agrestis* and *S. ainsliei* may compete for food resources, particularly the smaller particle material in the FH horizons of the forest floor. Millipedes may exert some biotic resistance to *A. agrestis* invasion, as diminished earthworm fecundity was observed in experimental units containing both species.

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1. Introduction

Non-native earthworm invasion is a truly global phenomenon in which invasive earthworm species are invading every continent, except Antarctica (Hendrix et al., 2008). These earthworm species also have origins on every continent, except Antarctica. In North America, earthworms of Asian origin (the genera *Amyntas*, *Metaphire*, *Pheretima*, and *Pithemera*) have recently been documented in the northeastern (Steinberg et al., 1997; Burtelow et al., 1998; Bohlen et al., 2004a,b), central (Snyder, unpublished results), and southeastern (Callaham et al., 2003; Snyder et al., 2011) regions of the United States, although these earthworms have been known in North America since the early 20th century (Garman, 1888; Gates, 1937).

Earthworm invasion can significantly alter forest ecosystems. Physical changes to the forest floor through consumption of organic horizons, mixing of organic and mineral horizons, and burrowing and casting activities can impact biogeochemical cycling (Bohlen et al., 2004a,b,c). Earthworm invasion can also impact soil fauna communities through competition and through the significant alteration of soil profile and structure (Bohlen et al., 2004b,c; Frelich et al., 2006). Although much is known about the interactions of invasive earthworms with soil micro- and mesofauna, less is known about interactions with detritivorous macrofauna, such as millipedes (Migge-Kleian et al., 2006). Bonkowski et al. (1998) found that earthworms (*Octolasion lacteum*) benefited from consuming millipede (*Glomeris marginata*) fecal pellets in a European Beech forest. However, in a microcosm experiment, millipedes were negatively affected by earthworms (*Amyntas corticis*), but earthworms may have similarly consumed millipede fecal material (Snyder et al., 2009). Snyder et al. (2009) found that although the millipede *Pseudopolydesmus erasus* was epigeic and *A. corticis* was endogeic, *P. erasus* acquired less C during the four-

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week course of the experiment in the presence of *A. corticis*, and it is likely that over longer time scales, this C deficit could affect growth, weight maintenance, survival, and/or reproductive output.

Amyntas gracilis invasion in forests of New York, USA was found to reduce O horizon organic matter (Steinberg et al., 1997; Burtelov et al., 1998). Similarly, invasion of *Amyntas agrestis* in the Great Smoky Mountains, USA, reduced the depth of the FH horizon (a combination of the F and H horizons) (Snyder et al., 2011). Millipedes reside in and consume FH horizon, and Snyder et al. (2011) found that millipedes were negatively affected by this *A. agrestis* invasion, both in terms of abundance and species richness. The field observations of Snyder et al. (2011) motivated us to explore the mechanisms behind this interaction, and a microcosm experiment was performed to test whether these two taxa competed for food resources in the L or FH horizons, and whether earthworms and millipedes benefited from the presence of these resources. This microcosm experiment was novel in its approach toward creating a longer-term study (i.e., months instead of weeks). Earthworms, and to a lesser extent millipedes, burrow in the soil and this prevents regular monitoring of faunal survival and fresh weight without causing disturbance. In order to facilitate data collection, all microcosms were destructively sampled every four weeks and fauna were put into newly constructed microcosms of the same treatment.

2. Methods

Millipedes and earthworms were collected by manually searching through leaf litter at the Great Smoky Mountains Institute at Tremont (Blount Co., Tennessee, USA; 35°38'22"N, 83°41'17"W), within the Great Smoky Mountains National Park (GSMNP) in early June 2007. Earthworms and millipedes were kept separate during transport to the laboratory. The two taxa were also stored separately until the beginning of the experiment in containers with soil and litter from the collection site.

Microcosms consisted of 1 l transparent plastic containers with perforated snap-on lids. Each microcosm received 500 ± 5 g of air-dried soil that was then mixed with 70 ± 5 mL tap water. Soil was a commercially acquired ultisol (USDA soil taxonomy) from the top 25 cm of a recently cleared forested site in Clarke Co., GA, USA. Soil was screened through a 4.75 mm sieve to remove large aggregates and rocks. Litter was previously collected from GSMNP and defaunated via Berlese extraction for 72 h, followed by air-drying. Dominant tree species at the litter collection site were *Acer* spp., *Quercus* spp., *Liquidambar styraciflua*, *Liriodendron tulipifera*, and *Pinus strobus* (Snyder et al., 2011).

Litter treatments were defined by particle size: litter was 4.75 mm sieved to separate unfragmented leaves (L horizon) from fragmented and partially decomposed organic matter (FH, combined F and H horizons). Large rocks, twigs, seeds and nuts were discarded. Organic layer treatments were L (15 ± 0.1 g of L horizon), L/FH (7.5 ± 0.1 g each of L and FH horizon), or FH (15 ± 0.1 g of FH horizon). Litter was misted with a standard quantity (~7 mL) of tap water when microcosms were constructed. Three fauna treatments were established: two *A. agrestis* individuals (mean fresh weight 0.86 ± 0.036 g each); one adult male *Sigmoria ainsliei* (mean fresh weight 2.26 ± 0.038 g); and two *A. agrestis* and one *S. ainsliei* together. *A. agrestis* were all clitellate or pre-clitellate. All individuals were approximately the same size and due to the annual nature of their life cycle (Reynolds, 1978; Callahan et al., 2003; Snyder et al., 2011), all individuals were similar in age. Individuals were randomly assigned to treatments with 6–7 replicates for a total of 76 microcosms. However, at the end of the experiment four experimental units were found to contain *A. corticis* rather than *A. agrestis*; these were excluded from subsequent analyses.

All microcosms were kept in the dark at 20 °C (±2 °C). Each microcosm was misted with tap water weekly, except early in the incubation when microcosms were misted every 3 d. Incubation began in June 2007 and continued until all fauna died (except *A. corticis* mentioned above).

Microcosms were destructively sampled every four weeks. After destructive sampling, new microcosms were constructed and the surviving fauna were weighed and placed into the new microcosms. Earthworms were rinsed in tap water to remove soil and gently dried on a paper towel prior to weighing. If any fauna (earthworm or millipede) from the original treatment were alive, then a new microcosm was constructed, if all fauna in a particular microcosm had died, then that microcosm was terminated. In this way, longevity of every individual could be assessed. Soils from treatments that included earthworms were wet-sieved through a 2 mm sieve to assess cocoon production. After the first cocoons collected were found to be only slightly larger than 2 mm in diameter, a 1.4 mm sieve was employed to ensure cocoon capture.

Millipede and earthworm survival and fresh weight data were analyzed using a general linear model (GLM), with the LSMEANS option for post-hoc tests. Data used in the GLM analysis for earthworm survival were the calculated average days of survival for the two worms in each microcosm. Fresh weight changes through 12 weeks (millipedes) and 16 weeks (earthworms) were analyzed using a repeated measures analysis; beyond these points there were insufficient replicates for robust analyses. Cocoon production was assessed with a *t*-test comparing between Months 1–3 and 4–7, and GLM comparing between Months 4, 5, 6, and 7. All statistical analyses were completed in SAS (Version 9.2).

3. Results

3.1. Survival and growth

Millipedes lived a mean time of 136.8 ± 10.6 d ($n = 36$) from the beginning of the experiment (Fig. 1). The overall model testing fauna and litter effects was significant ($P = 0.0002$). Millipede survival was significantly affected by litter ($P < 0.0001$), with survival time significantly decreased in L relative to FH ($P < 0.0001$) and L/FH ($P = 0.0012$). However, differences in millipede survival times between L/FH and FH treatments were not statistically significant ($P = 0.0567$). There was a trend for earthworm presence to decrease millipede survival time, but this was not statistically

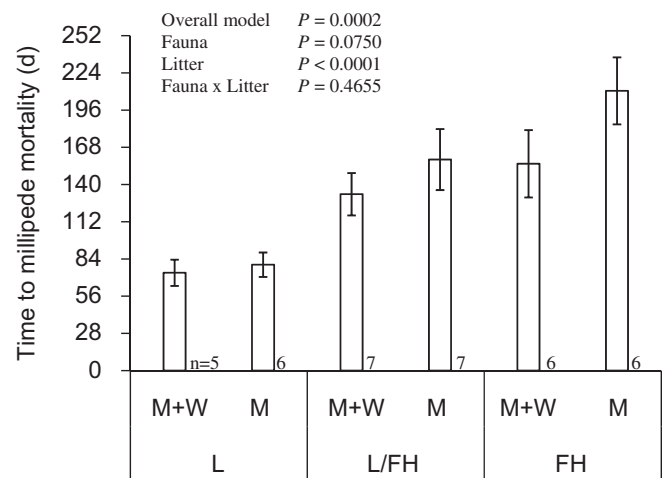


Fig. 1. Mean survival (±SE) of *Sigmoria ainsliei* from initiation of the incubation with (M + W) and without (M) earthworms. Litter treatments were litter (L), litter and FH material (L/FH), and FH only (FH).

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