Quantifying seeds egested by field-collected earthworms: a dynamic and overlooked pool in forest soil seed banks

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Abstract
Although awareness of the influence of earthworms on soil seed banks in Canadian forests is growing, there have been few direct field measurements. We used a novel pairing of field-collected earthworms from a central Great Lakes forest in Ontario with a laboratory seed egestion assay to obtain a snapshot of the number of seeds passing through earthworms compared with seeds found in the surrounding soil. We identified a pool of seeds egested by earthworms that accounted for 2.4% of all seeds found in the earthworms and the top 0–10 cm of soil. Individual earthworms contained 0–5 seeds. The large-bodied adult anecic non-native Dew Worm or Common Nightcrawler (*Lumbricus terrestris*) egested a disproportionate number of seeds for its abundance (50% of egested seeds from 17% of earthworms), but smaller earthworms were also an important source of egested seeds (the other 50%). This small-scale proof-of-concept study demonstrates a method of directly measuring earthworm–seed interactions in the field. It can also detect seeds egested by earthworms below ground that would otherwise be missed by other seed accounting methods and it highlights the importance of granivory by non-surface casting earthworms.

Key words: Granivory; seed dispersal; aboveground–belowground interaction; *Lumbricus terrestris*; novel method; forests

Introduction

Forest soil seed banks can be modified by earthworms that act as seed predators and dispersers by actively or passively ingesting seeds (Grant 1983; Thompson 1987; McCormick *et al.* 2013). Earthworms ingest seeds from the total available seed pool, destroying some through digestion and egesting others back into the soil below ground or at the soil surface after a relatively short gut transit, e.g., 8 h for Dew Worm/Common Nightcrawler (*Lumbricus terrestris*; Hartenstein and Amico 1983), a non-native species in Canada (Addison 2009). Many egested seeds remain viable and may be transported through the soil vertically (Willems and Huijsmans 1994; Zaller and Saxler 2007; Regnier *et al.* 2008) or horizontally (McTavish and Murphy 2021) and may experience increased or reduced germination (Ayanlaja *et al.* 2001; Clause *et al.* 2015).

Most studies of earthworm–seed interactions have been indirect or observational, with few direct measurements in the field, and key questions remain regarding the overall importance of these interactions in ecosystems (Cassin and Kotanen 2016; McTavish

and Murphy 2020). Notably, we lack accurate measures of the pool of seeds that passes through earthworms under field conditions. Because of logistic challenges, most manipulative experiments occur in the laboratory—with a few exceptions, such as Cassin and Kotanen (2016) and McTavish and Murphy (2020)—and most rely on indirect measures, such as associations between earthworm density and seed bank or vegetation composition (Nuzzo *et al.* 2015), seed removal (Cassin and Kotanen 2016), or quantification of seeds in surface casts, which are produced by only some species (Willems and Huijsmans 1994; Decaëns *et al.* 2003). No studies have attempted to directly quantify the pool of seeds actively passing through earthworms in the field.

The purpose of our study was to examine earthworms as a transient/ephemeral belowground seed pool, evaluate the overall importance of earthworm granivory, and enhance the accounting of the total forest soil seed bank. We used a novel pairing of live earthworm collection from the field with an immediate earthworm seed egestion assay in the laboratory to obtain an instantaneous snapshot of the seeds passing

through earthworms and compared this to the density of seeds found in the surrounding soil. This proof-of-concept study occurred at a central Great Lakes temperate forest field site in Ontario, Canada.

Methods

Sampling occurred at the University of Toronto's Koffler Scientific Reserve at Joker's Hill, Newmarket, Ontario, Canada (44°02′10.0″N, 79°32′11.9″W). The study area consisted of mature, secondary growth forest dominated by Sugar Maple (*Acer saccharum* Marshall), American Beech (*Fagus grandifolia* Ehrhart), Eastern Hemlock (*Tsuga canadensis* (L.) Carrière), and Red Oak (*Quercus rubra* L.). The understorey was not characterized at the time of this study (which took place during the late fall); however, taxa known from the study area include Brown Knapweed (*Centaurea jacea* L.), plume thistles (*Cirsium* Miller), pepperweed (*Lepidium* L.), Butter-and-Eggs (*Linaria vulgaris* Miller), Bouncing-bet (*Saponaria officinalis* L.), White Trillium (*Trillium grandiflorum* (Michau) Salisbury), and Common Mullein (*Verbascum thapsus* L.; M.J.M. and A.R. unpubl. data). Soils are sandy loam, grey-brown podzols overlaying morainal sand (Cassin and Kotanen 2016). The study area was a 60 m × 30 m block between two walking trails with 24 quadrats (30 cm × 30 cm) placed randomly throughout.

In late October 2019, earthworms were extracted from the soil in each plot by searching and clearing the surface leaf litter and pouring 3 L of mustard solution (10 g mustard powder [Bulk Barn Food Limited, Aurora, Ontario, Canada] per litre water) on the plot over 12 min to extract earthworms (Lawrence and Bowers 2002; Hale 2013). To rapidly collect gut contents, all earthworms were immediately placed in portable, aerated, plastic containers (14 cm × 9 cm × 5 cm; Dollar Tree Canada, Mississauga, Ontario, Canada) lined with moistened viscose cloth (Figure 1). All earthworms from a plot were placed in a single container, with the exception of adult *L. terrestris*, which were placed in a separate container for each plot as they could be reliably distinguished from other earthworm species (thus, up to one container for adult *L. terrestris* and one for other earthworms per plot). Containers were placed in a large plastic bin with the lid closed to create dark conditions known to be more amenable to earthworm activity (M.J.M. pers. obs.). After field collection, the bins were returned to the laboratory (~21°C) and left on a bench for 24 h.

After 24 h, earthworms were removed and rinsed with water over the containers to remove any seeds and then euthanized in isopropyl alcohol, fixed in 10% formalin, and stored in isopropyl alcohol. After fixation, earthworms were identified (no vouchers were

Fɪɢᴜʀᴇ 1. The earthworm egestion collection unit containing an adult *Lumbricus terrestris*. The portable containers (14 cm × 9 cm × 5 cm) were an economical and efficient means of immediately segregating large numbers of live earthworms in the field to collect gut contents. Photo: M. McTavish.

collected) to genus and species where possible using Reynolds (1977) and Hale (2013), assigned to functional groups including litter-dwelling epigeics, mineral soil-burrowing endogeics, and vertically burrowing anecics (*sensu* Bouché 1977, but see Bottinelli *et al.* 2020 for continuing discussion of these functional groups), air dried for 24 h, and weighed. The viscose cloths from the containers were rinsed with water over a 300-µm sieve and air dried to collect egested seeds. After 24 h in the containers, no seeds were expected to remain within the earthworms; all seeds should have been egested.

At each plot, the soil seed bank was sampled after the earthworms were collected using a 5-cm diameter soil corer at the four corners and mid-point of each edge of the quadrat (*n* = 8 soil samples/plot). Because searching for seeds is time-consuming, only the top 0–10 cm of soil (expected to contain the greatest proportion of the soil seed bank) was retained for analysis. Although detailed mapping of the depth distribution of seeds was not available for our study area, similar research suggests that burial of surface-deposited seeds is minimal in the absence of earthworms and that many earthworm-buried seeds can be found in the top 1–10 cm (Willems and Huijsmans 1994; Regnier *et al.* 2008; Cassin and Kotanen 2016; McTavish and Murphy 2021). The eight subsamples from each plot were aggregated, mixed, and sieved (1.70 mm) to remove larger debris. Seeds were extracted using a seed flotation assay described in Malone (1967) and a 300-µm sieve.

Seeds from the earthworm egestion collection units and the seed flotation assay were counted by systematically sorting each sample using a microscope at 10× to 40× magnification. Seeds were distinguished

from other inorganic and organic soil features by cutting into ambiguous samples with a scalpel to check for distinctive organic matter (e.g., seed coat, endosperm). Seeds could not be reliably identified to genus or species morphologically but were between 300 µm and 1.70 mm in size as a result of the collection process. A subset of the soil samples was also subjected to a 3-month cold stratification at 5°C and potted in a greenhouse in an emergence assay; this was intended as an alternative method for quantifying the seed bank and to identify species, but it was abandoned because of a failure of the greenhouse facilities during the course of the experiment.

Soil seed density (in the top 0–10 cm) was calculated per plot by dividing the sum of seeds found across eight subsamples by the total surface area of those eight soil cores. The density of seeds found in earthworms per plot was calculated by dividing the total number of seeds egested by earthworms in a plot by the plot area. Total seed density was calculated as the sum of the soil and earthworm seed densities. Paired t-tests were used to compare soil seed density and earthworm seed density. Because individual egestion could not be directly measured from groups of earthworms in a container, total egestion was pooled across all earthworms in a container (either adult *L. terrestris* or other earthworms) and calculated as an average individual egestion per earthworm. Paired t-tests were used to compare the abundance of total egested seeds per plot between adult *L. terrestris* and other earthworms. Because not all plots contained both adult *L. terrestris* and other earthworm taxa, we could not calculate individual earthworm egestion for

each plot and, therefore, did not have fully paired data. We instead used Welch's test (Welch's unequal variances t-test) for heteroscedastic data (Welch 1951) to compare individual egestion by adult *L. terrestris* and all other earthworms. Correlations between earthworm density, earthworm air-dried biomass, average individual earthworm seed egestion numbers, and soil seed density were assessed using the Pearson correlation in cases when the data demonstrated bivariate normality or the Spearman correlation for data lacking bivariate normality. Test assumptions were checked using the Anderson-Darling test for normality and Levene's test for equal variance. All tests were carried out in R version 3.6.1 (R Core Team 2019) at $\alpha = 0.05$. Values are mean ± SD.

Results

The earthworm community across the 24 plots consisted of four species: epigeic *Dendrobaena octaedra* (Savigny 1826), endogeic *Aporrectodea turgida* (Eisen 1873; synonym *Aporrectodea caliginosa* (Savigny 1826, in part)) and *Aporrectodea tuberculata* (Eisen 1874), and anecic *L. terrestris*. Because no other species were recorded in the plots, juvenile *Aporrectodea* spp. and *Lumbricus* sp. were presumed to be either *A. turgida/A. tuberculata* or *L. terrestris*, respectively, and functionally classified as endogeic and anecic. Total earthworm density and dry biomass for the 24 quadrats were 125 ± 63/m² and 12.6 ± 8.0 g/m², respectively, which are typical of North American forests (Addison 2009; Sackett *et al.* 2013). The community was dominated by endogeic *Aporrectodea* spp. in density and by anecic *L. terrestris* in biomass (Figure 2).
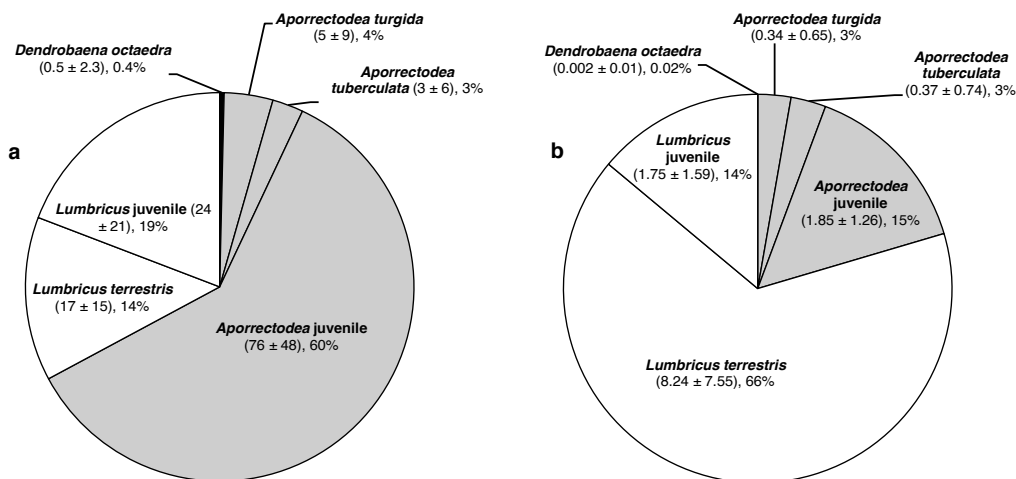

FIGURE 2. a. Density (mean n/m² ± SD and % of total) and b. dry biomass (mean g/m² ± SD) of earthworm communities from 24 plots in a central Great Lakes forest, Ontario, Canada, October 2019. Shaded area shows earthworm functional group including epigeic (black for *D. octaedra*, not visible in b), endogeic (grey), and anecic (white).

Seeds were collected from 37 adult *L. terrestris* and 234 other earthworms. Total recovered seed density was $2125 \pm 827/m^2$ from the top 0–10 cm of soil, $46 \pm 36/m^2$ from earthworms, and $2171 \pm 828/m^2$ in total. Per plot, significantly more of the recovered seeds were found in the soil ($97.6 \pm 2.0\%$) than in earthworms (i.e., seeds in earthworms at the time of collection that were egested afterwards; $2.4 \pm 2.0\%$; paired $t_{23} = 12.29$, $P < 0.001$). The egested seed pool was split evenly between earthworm species groups with no statistically significant difference found between the number of seeds collected from adult *L. terrestris* and other earthworms (paired $t_{23} = 0.33$, $P = 0.75$).

Individual earthworms egested an average of 0.4 ± 0.5 seeds/earthworm (range 0–5). However, individual adult *L. terrestris* egested a significantly higher mean number of seeds per earthworm (1.62 ± 0.35) than other species (0.35 ± 0.58; Welch's test, $F_{1,19.68} = 11.67$, $P = 0.003$; $n = 17$ adult *L. terrestris* containers, $n = 24$ other earthworm containers). Therefore, the contribution of adult *L. terrestris* to the egested seed pool (~50%) was disproportionately high for their density (17% of earthworms) and more proportionate to their biomass (66% of earthworms by weight). There was a positive correlation between earthworm density and earthworm biomass but no other statistically significant correlations were found between the other variables (Table 1).

Discussion

Ours is the first study to directly quantify seeds actively passing through earthworms in the field. A small previously unrecognized portion of the forest soil seed bank is found in earthworms (2.4% of collected seeds per plot, 46 ± 36 seeds/m^2). This portion consists of seeds that have been removed from the total pool of available seeds via ingestion minus those lost to digestion. Assuming that the seeds we collected in the laboratory would normally have been egested back into the soil several hours after ingestion (Hartenstein and Amico 1983), they would have returned to the soil seed pool. Thus, over time, an increasing portion of the seed bank would be composed of seeds egested by earthworms. Earthworms may also re-ingest seeds previously egested by themselves or other earthworms, although there is evidence that they will preferentially avoid these previously egested seeds (McTavish and Murphy 2019).

Many of the egested seeds we collected would not normally have been counted, except for those that might have been deposited in and quantified from aboveground casts (e.g., Decaëns *et al.* 2003). Although measuring seed densities from surface casts remains useful to assess the impact of earthworms on seedbank dynamics, it does not capture the transient pool of seeds found within earthworms and does not account for seeds egested below ground. Large-bodied anecic earthworms such as *L. terrestris* are often considered the primary contributors to seed predation because of their size (Asshoff *et al.* 2010). Although we did find that *L. terrestris* egested more seeds per individual than smaller earthworms, the latter occurred at higher densities overall and egested just as many seeds in total. The influence of mineral soil-dwelling endogeic earthworms may be even greater than observed because of the tendency of mustard extraction to marginally under-sample these taxa (Lawrence and Bowers 2002). Given the predominantly belowground feeding behaviour of many of the earthworms that egested seeds, these findings also reinforce the relatively unique ability of earthworms to access seeds both below and above ground (Thompson 1987).

Our findings also contribute to better understanding of the overall ecological importance of earthworm–seed interactions. Individual earthworms contained an average of 0.4 ± 0.5 seeds (range 0–5) when they were collected. Although this may seem small, the cumulative number of seeds that may pass through earthworm communities with densities of up to several hundred individuals/m^2 (Addison 2009; Sackett *et al.* 2013) could be considerable, particularly as we found no relation between earthworm density and the number of seeds per earthworm (Table 1). In addition, given the rapid transit time of seeds moving through earthworms (in the order of several hours; Hartenstein

TABLE 1. Correlation between earthworm density, earthworm biomass, seeds per earthworm, and density of plant seeds in soil from 24 quadrats in a central Great Lakes forest, Ontario, Canada. Cells contain the correlation coefficient and corresponding P values (in bold if significant at $\alpha = 0.05$).

	Earthworm density, no./m^2	Earthworm biomass, g/m^2	No. seeds/earthworm
Earthworm biomass, g/m^2	**0.58** **($P = 0.003$)**	—	—
No. seeds/earthworm	−0.13* ($P = 0.55$)	0.22* ($P = 0.22$)	—
Soil seeds, no./m^2	0.09 ($P = 0.67$)	0.14* ($P = 0.51$)	0.02* ($P = 0.91$)

*Correlations for variables lacking bivariate normality were calculated using Spearman's correlation.

and Amico 1983), a large number of seeds could be ingested and egested over a year. Notably, our instantaneous measure of 46 earthworm seeds/m^2 was only slightly smaller than the annual estimate of 60–100 germinable seeds/m^2 found in earthworm casts in a Dutch grassland (Willems and Huijsmans 1994), again suggesting how studies of only surface-egested seeds might underestimate the pool of seeds egested by all earthworm taxa throughout the soil profile.

It is important to note that this proof-of-concept study focussed on one sampling effort in a single forest and was intended to see if seeds egested by field-collected earthworms could be quantified. It was not designed to provide a full accounting of the soil seed bank *per se*, although we hope that this approach may be used in such future studies. Given our assumption that most unburied and earthworm-buried seed would be found in the top 10 cm of soil (Willems and Huijsmans 1994; Regnier *et al.* 2008; Cassin and Kotanen 2016; McTavish and Murphy 2021) and to simplify the laborious seed extraction process, we did not sample the deeper soil profile. In addition, although we initially attempted to sample earthworm casts for seeds, wet field conditions and degraded casts collected later in the fall made it difficult to reliably distinguish between casts and surface soil. Overall, we expect that these limitations may have omitted seeds deeply buried by earthworms (Regnier *et al*. 2008; McTavish and Murphy 2021) and deposited in casts (Willems and Huijsmans 1994), thereby producing an underestimate of the size of the earthworm seed pool and the contributions of deep-burrowing, surface-casting *L. terrestris*.

It is also unknown whether bringing the earthworms into the laboratory may have altered rates of seed digestion/egestion compared with field conditions; although temperature can affect processes, such as soil consumption (Curry and Schmidt 2007), we do not think the conditions compromised the egestion estimates. Conditions in the field would naturally fluctuate over time, and earthworm seed egestion has already been observed to be unaffected by other variables such as seed density and previous seed egestion (McTavish and Murphy 2019). We recommend that future studies attempt a more complete seed bank accounting including identification of the seed species present (e.g., from the vegetation present on site or a seed emergence assay), viability testing of recovered seeds, and analysis of a deeper soil profile and surface earthworm casts sampled across multiple locations and time points.

Conclusions

The results of our study show the dynamic nature of the soil seed bank and the often-unseen biotic interactions that help shape it (Chambers and MacMahon 1994). Specifically, our study identifies a previously overlooked pool of soil seeds found within earthworms in small but potentially ecologically significant numbers. Although field studies of earthworm–seed interactions are scarce, our findings are consistent with emerging evidence that the primary ecological significance of these interactions is not strictly associated with the magnitude of seed removal (Cassin and Kotanen 2016; McTavish and Murphy 2020), but rather with more subtle processes such as seed burial (Zaller and Saxler 2007) and spatial aggregation (Milcu *et al.* 2006; McTavish and Murphy 2021). We therefore encourage further consideration of this small but potentially ecologically significant pool of seeds in the soil seed bank that are egested by earthworms and propose the adoption of methods to study this interaction at a larger scale and in a broader range of habitats.

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