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Key Points:

- Earthworm presence increased tundra plant biomass, particularly belowground, in both studied vegetation types
- Earthworm effects on the net ecosystem carbon balance differs between vegetation type

Supporting Information:

Supporting Information may be found in the online version of this article.

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Non-Native Earthworms Alter Carbon Sequestration in Arctic Tundra Ecosystems

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Abstract Earthworms, as detritivores, play a significant role in breaking down soil organic carbon (SOC). The introduction of non-native earthworms to arctic ecosystems has, therefore, raised concerns about the potential impact they may have on one of the world's largest SOC reservoirs. Earthworms could also have considerable effects on plant productivity, and the lack of experimental studies quantifying their impact on carbon (C) reservoirs in both soil and plants makes it difficult to predict the effect of earthworms on ecosystem C storage. Here we experimentally tested how earthworms known to be non-native to arctic ecosystems (Aporrectodea spp. and Lumbricus spp.) affect C reservoirs in soil and plants (above and belowground separately) in two common tundra vegetation types (heath and meadow). Earthworms lowered the mean SOC pool and substantially altered SOC quality in meadow soils by increasing the proportion of aromatic-C compounds. Simultaneously, earthworms increased the C pool stored in plant biomass, which counteracted earthworm-induced SOC losses in meadow ecosystems. A positive earthworm effect on belowground biomass in heath soil facilitated a net ecosystem uptake of ~0.84 kg C m^{-2} over the 4-year study period. The higher C uptake into plant biomass in the heath resulted in a notable increase of SOC but lower $\delta^{13}C$ values, likely because of recently captured C being sourced from roots or litter. Our observations of vegetation-specific feedbacks between plants, earthworms, and soils advance our understanding of non-native earthworms' impact on SOC dynamics and C budgets in high-latitude ecosystems.

Plain Language Summary Earthworms are important decomposers of soil organic carbon (SOC). The introduction of non-native earthworms to arctic ecosystems has therefore raised concerns about the potential impact they may have on one of the world's largest SOC reservoirs. Earthworms can also have positive effects on plant productivity and the lack of experimental studies quantifying earthworm impacts on carbon (C) pools in both soil and plants makes it difficult to predict the net effect on ecosystem C storage. Here we experimentally tested how earthworms known to be non-native to arctic ecosystems affect C reservoirs in soil and plants (above and belowground separately) in two common tundra vegetation types (heath and meadow). Earthworms lowered the mean SOC pool in the meadow but increased the C pool stored in plant biomass, which counteracted earthworm-induced SOC losses. We also found a positive earthworm effect on belowground plant biomass in the heath, which contributed to a net ecosystem uptake of C. There was also a higher proportion of recently photosynthesized C in the heath SOC pool with earthworms present. Our observations of vegetation-specific feedbacks between plants, earthworms, and soils advance our understanding of non-native earthworms' impact on SOC dynamics and C budgets in high-latitude ecosystems.

1. Introduction

Arctic ecosystems are large reservoirs of terrestrial carbon (C) and increased emissions of C-based greenhouse gases from the tundra is of great relevance for our planet's climate system (IPCC, 2021). Microbial processes driving soil organic carbon (SOC) mineralization in tundra ecosystems are generally believed to be limited by abiotic constrains such as low temperatures, moisture levels, and substrate quality (Conant et al., 2008; Oberbauer, 2007; Razavi et al., 2017). Yet, emerging evidence suggests that in addition to abiotic constraints, decomposition in tundra soils may also be limited by the absence of large detritivores (Blume-Werry et al., 2023). The theory proposed by Blume-Werry et al. (2023) implies that conditions currently limiting soil organic matter (SOM) decomposition in high latitude ecosystems may be alleviated if large detritivores—such as earthworms—are introduced and establish.

The theory of an "earthworm-limited" turnover of SOC pools in high latitude soils largely stems from observations made in North America. Here, earthworms were eradicated during the last glacial period and an ongoing invasion of earthworm species into previously earthworm-free northern ecosystems is now well-documented (Frelich et al., 2006; Hendrix et al., 2008). A similar northward establishment of non-native earthworm species has also been observed in formerly glaciated areas of the Fennoscandian Arctic (Jerand et al., 2023; Wackett et al., 2018). Nonetheless, it remains unclear to what extent non-native earthworm species currently dispersing into the Fennoscandian Arctic might affect the tundra C balance.

Earthworms can increase C mineralization rates in soils that have previously been free from earthworms. A meta-analysis of both field and laboratory studies strongly suggests that earthworms elevate CO_2 emissions from soils (Lubbers et al., 2013). However, Lubbers et al. (2013) also showed that it is difficult to detect earthworm-mediated SOC losses over longer timescales (>200 days). It has been proposed that earthworms may create persistent forms of SOC through the formation of soil aggregates and/or earthworm-mediated organo-mineral complexes, which provide physical and chemical protection from microbial mineralization (Angst et al., 2024; Bossuyt et al., 2005, 2006). Some studies have also suggested that earthworms may increase long-term soil C sequestration by amplifying SOC stabilization processes to a larger extent than their priming effect on mineralization (Zhang et al., 2013). These contrasting ideas on how earthworms may affect SOC turnover complicates predictions of their impact in the tundra.

It is worth noting that the majority of experimental studies assessing earthworm effects on C dynamics are conducted in systems with only soil and litter butwithout living plants (Lubbers et al., 2013). Plants and their roots play a key role in terrestrial C cycling and excluding feedbacks and interactions between earthworms, plants, and soils makes it difficult to extrapolate earthworm impacts on the ecosystem C balance in natural settings. Earthworm effects on soil nutrient release and ensuing plant uptake might be particularly important, as suggested by a meta-analysis indicating earthworm activities increase plant growth by as much as 25% (van Groenigen et al., 2014). In tundra ecosystems in particular, plant biomass is strongly nutrient (i.e., nitrogen) limited and a potential earthworm fertilization effect from nitrogen rich casts must be considered to understand positive plant growth responses (Blume-Werry et al., 2020).

Plants and their responses to earthworms are not only important for fixing CO_2 but also for regulating C allocation into above- and belowground C pools, for example, via leaf litter, root litter, and exudates. Roots are of particular interest here as rhizodeposition is known to contribute to the build-up of SOC, whereas root exudates may also prime microbial processes and destabilize physical complexes that protect SOC against decomposition (Dijkstra et al., 2021; Fontaine et al., 2007; Keuper et al., 2020). However, root biomass and functions do not respond unidirectionally to earthworm invasions, as previous studies report seemingly contrasting positive (Blume-Werry et al., 2020) and negative growth responses (Cameron et al., 2014; Fisk et al., 2004; Jennings & Watmough, 2016). Furthermore, invasive earthworms can also alter the plant species composition (Craven et al., 2017; Hale et al., 2006; Nuzzo et al., 2009), which may in itself affect the composition and turnover of plant associated C. Given the complexity of earthworm-plant-soil feedback mechanisms, it is important to holistically assess how earthworms affect C reservoirs within whole ecosystem contexts.

Here we assessed soil-plant-worm interactions and their impact on the tundra C balance using a 4-year common garden mesocosm experiment. We added mineral soil dwelling earthworms (Aporrectodea spp. and Lumbricus spp.), henceforth referred to geoengineering earthworms (Wackett et al., 2018), into half the experimental plots containing two common tundra vegetation types: shrub-dominated (heath) tundra and forb-dominated (meadow) tundra. We hypothesized that by stimulating nutrient turnover, the introduction of geoengineering earthworms would: (a) increase plant biomass C pools (above and belowground) and (b) reduce SOC pools in both vegetation types. We tested our hypotheses by deriving an ecosystem C budget, including both SOC and plant C pools, to assess net earthworm effect(s) on the tundra ecosystem. We also measured earthworm impacts on SOC quality using nuclear magnetic resonance (NMR) measurements to test for any concomitant earthworm effects on SOC properties.

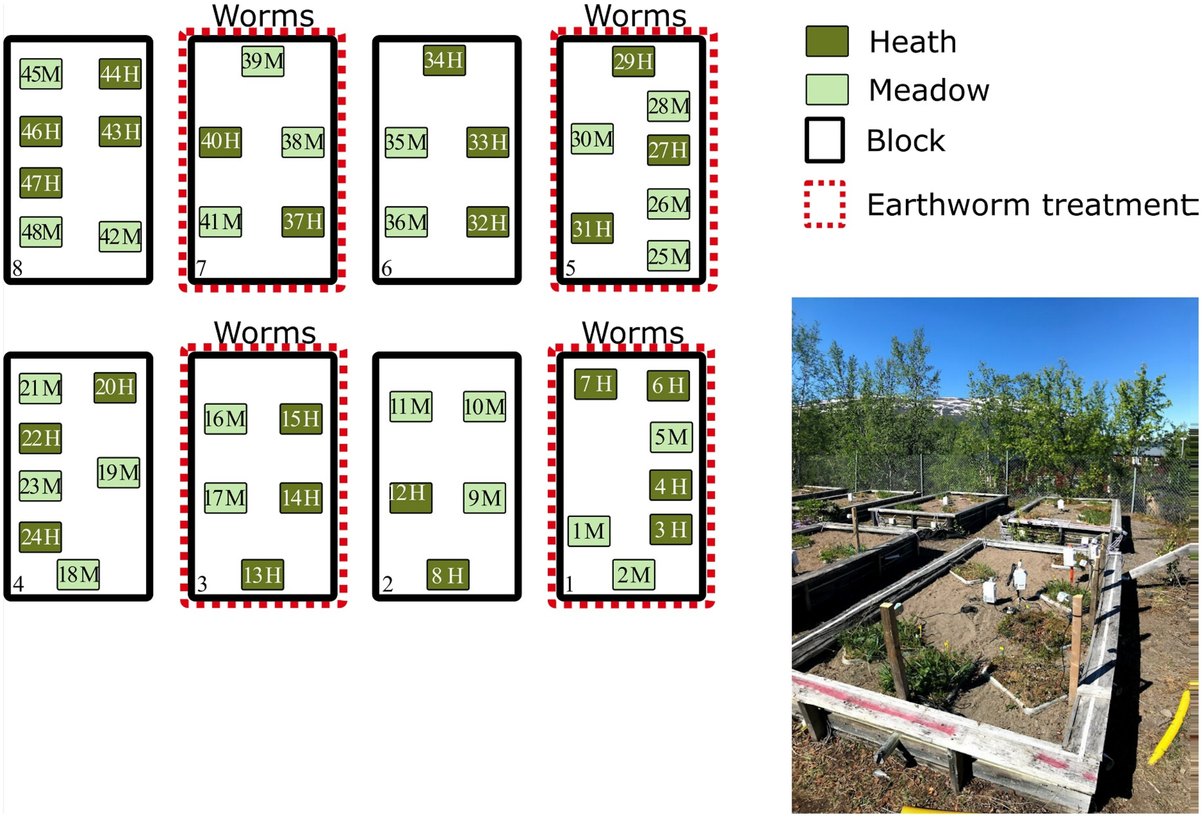

Figure 1. The mesocosm block design where the dark green (heath) and light green (meadow) boxes represent mesocosm plots within the eight blocks of raised sand beds. The blocks with red outlines are the ones with earthworm treatments and the block numbers in the bottom right are used for our applied block designed statistics. The photograph shows the experimental set up, captured 16th of June 2019 by H. Jonsson.

2. Materials and Methods

2.1. Experimental Set-Up

We conducted our study outdoor in the experimental garden at the Abisko Scientific Research Station (68°21′17′′ N; 18°48′54′′E) in northern Sweden. Mean annual temperature at the station is about 0.5°C (1990–2021) and mean annual precipitation is 349 mm (1990–2021). Alpine tundra, sub-Arctic birch forests and sporadic permafrost mires are the dominant vegetation types in the area. We constructed the mesocosms in 2013 ($N = 48$, 39 × 50 cm area and 30 cm deep) using soil and vegetation monoliths transported from nearby alpine tundra in the Kärkevagge valley (68°24′36′′N; 18°19′11′′E) with two vegetation types; heath ($n = 24$) and meadow ($n = 24$). The heath tundra was dominated by evergreen dwarf shrubs (*Vaccinium vitis-idea* L., *Empetrum hermaphroditum* (Hagerup) Böcher), but also consists of graminoids (*Carex bigelowii* Torr. ex Schwein., *Deschampsia flexuosa* (L.) Drejer, *Festuca ovina* L.) and bryophytes (*Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp). The meadow vegetation mainly consists of forbs (*Saussurea alpine (L.) DC., Alchemilla glomerulans* Buser., *Bistortia vivipara* (L.) Delarbre, *Viola biflora* L.), and graminoids (*C. bigelowii, D. flexuosa, F. ovina, Agrostis mertensii* Trinn.). A complete description of the plant species community composition is available in Jonsson et al. (2024).

The mesocosms were installed within eight insulated sand-beds (3 m × 1.6 m × 0.4 m) (see Figure 1) where we leveled out the surrounding sand with the mesocosm soil surface to maintain realistic soil temperature fluctuations. We used impeding Velcro tape on the top of the walls surrounding the sand-beds to prevent earthworms from escaping into the surroundings. The experiment was constructed in 2013 and the vegetation was then allowed to recover for 4 years in the mesocosms prior to exposure to earthworms.

The mesocosms were created from sods of intact vegetation, humus, and mineral soil. They were constructed from till soils with a typical stratigraphy of O, A (in some cases an E horizon was present), and B-horizons in the heath and O, A or Ah, and B in the meadow, where the underlying mineral soils consisted of 27% ± 4% coarse fragments >2 mm (mean ± SD), 56% ± 5% sand, 16% ± 3% silt, and <1% clay. Average O horizon (mor humus) depth was 5 ± 2 cm in heath and 3 ± 2 cm in meadow. The O horizons had >40% SOM content and a pH (in KCl) of 4.1 ± 0.4 in the heath and 5.0 ± 0.2 in the meadow.

In 2017, we started the earthworm treatment by introducing invasive earthworms with a total fresh weight of 24.2 g ± 0.3 (mean ± SE), corresponding to an earthworm density of ∼124 g m^{-2}, into half of the mesocosms (both heath and meadow). The remaining half were maintained as earthworm-free controls. To avoid the risk of having earthworms spreading into the control-mesocosm we contained the earthworm treatment with four of the eight sand beds, hereafter referred to as blocks (see Figure 1). The introduced "geoengineering" earthworms were primarily adults of the endogeic *Aporrectodea sp*. (*Aporrectodea trapezoids* Dugés 1828*, Aporrectodea caliginosa* Savigny 1826*, Aporrectodea rosea* Savigny 1826) (∼80%) and epi-endogeic *Lumbricus rubellus* Hoffmeister, 1843 (∼20%). In 2020, ∼4% of the fresh mass also included the anecic *Lumbricus terrestris* Linnaeus, 1758. Earthworms were introduced at the very center of each mesocosm each year at the beginning of the growing season. While introducing the worms we covered them with a cup until they were no longer visible aboveground (to avoid potential predation during initial establishment). X-ray imaging of soil cores collected at the end of the experiment show that their impacts were widely distributed throughout the whole upper 0.3 m of the earthworm-treated mesocosms (Klaminder et al., 2023).

The total fresh weight of earthworms and the proportion of earthworm functional types (i.e., roughly 4:1 endogeic:epi-endogeic) introduced to the mesocosms mimics the observed earthworm densities and species assemblages found at earthworm invaded sites nearby (Wackett et al., 2018). The mesocosm structure limited the possibility for earthworms to avoid soil frost by migrating downward into deeper soils. We therefore assumed 100% frost mortality and re-introduced earthworms at the beginning of each growing season during the experimental period (2017–2020). At the end of the experiment, living earthworms were present in all mesocosms assigned to the earthworm treatment. We detected litter-dwelling epigeic earthworms (*Dendrobaena octaedra* Savigny, 1826) in four of the control plots (1 heath and 3 meadow) while sampling, which had not been introduced and that were absent from all earthworm treatment plots. These individuals were all juvenile and we only found one in each of the four mesocosms. Because this species is not considered a geoengineering earthworm and may be native to the region (Wackett et al., 2018), we retained these four mesocosms as controls in our analyses.

2.2. Soil Sampling and Analyses

In October 2020 we terminated the experiment and collected soil samples from all 48 mesocosms. We sampled soils in 6 × 6 cm cubes by soil horizon for O (mor type humus), A and E horizons. For the B horizons, we divided the sample in 3 cm depth intervals to capture variations with depth, leading to a total of five to six soil samples per mesocosm. All soil samples ($n = 277$) were brought to the laboratory and dried at 50°C for 10 days. We weighed each sample after drying as an initial determination of soil bulk density, before sorting roots from each sample using an allocated time for sorting that was based on sample volume and soil type (i.e., organic/mineral soil layer). All roots used for analysis were <5 mm diameter and defined as fine roots, as previously defined by Jennings and Watmough (2016). We will refer to this data as belowground biomass C due to the difficulty of excluding C derived from mycorrhiza fungi from root biomass C.

We sieved the remaining root-free soil samples to <2 mm to quantify coarse (>2 mm) and fine (<2 mm) soil mass fractions for each soil sample volume, which we explicitly accounted for in our SOC inventory estimates (Equation 1). Bulk density was determined on each soil "cube" by dividing the dried soil weight by the original sampled soil volume (estimated from cube dimensions) following standard methods. After homogenizing the fine earth (<2 mm) soil fraction we analyzed subsamples ($n = 277$) for SOM content via loss-on-ignition by measuring the mass loss after heating at 550°C for 5 hr (Hoogsteen et al., 2015). We additionally analyzed fine earth (<2 mm) fraction samples from 12 select mesocosms, three from each treatment combination ($n = 93$), for SOC content using an Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany) and quantified $\delta^{13}C$ values using an isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific, Bremen, Germany) (Werner et al., 1999). We used these samples as training data to establish a conversion factor for SOM to C percentage, which we used to interpolate SOC contents for the remaining samples. Our best-fit C conversion factor was 2.4 ($R^2 = 0.98$, $n = 93$). None of the soils contained appreciable inorganic C. Mesocosm SOC inventories were calculated using the expression:

$$\mathrm{SOC}_{\mathrm{inventory}} = \sum_{n=1}^{N} C_{n,\mathrm{fine}} \times \rho_n \times h_n \times (1 - CF_n) \tag{1}$$

where $\mathrm{SOC}_{\mathrm{inventory}}$ is the integrated soil organic C inventory (kg C m^{-2}), $C_{n,\mathrm{fine}}$ is the mass fraction of organic carbon measured on fine fraction (<2 mm) soil splits from the *n*th layer (unitless, or g g^{-1}), ρ_n is the bulk density of the *n*th soil layer (g m^{-3}), h_n is the thickness of the *n*th soil layer (m), CF_n is the mass fraction of coarse fragments (>2 mm) in the *n*th soil layer (unitless, or g g^{-1}), and N is the total number of sampled soil layers or horizons within each mesocosm.

2.3. Above Ground Plant Biomass

We clipped the above ground plant biomass from all mesocosms before terminating the experiment in October 2020. Senesced but standing plant biomass was included in the above ground biomass pool. We immediately froze the plant samples following collection before drying them at 50°C for 7 days. After grinding the above-ground plants and dry root biomass from 12 mesocosms (three of each treatment), we analyzed the samples for C content via mass spectrometry (DeltaV, Thermo Fisher Scientific, Bremen, Germany). We used these training data to establish C conversion factors for dried above ground biomass to C content, which were 50% ± 1.9% and 46% ± 1.9% (mean ± SD) for heath and meadow vegetation, respectively. Similarly, we established C conversion factors for dry root weights to C content, which were determined to be 48% ± 1.5% and 44% ± 1.3% (mean ± SD) for heath and meadow, respectively.

2.4. NMR Analyses of SOM Quality

We used NMR spectroscopy to study earthworm effects on SOM quality within the upper O/A-horizons. Whenever an organic (O) horizon was present, we collected a homogenized subsample from this horizon. In cases where the uppermost soil horizon was classified as an A horizon (10 earthworm-treated plots and two control treatments, all under meadow vegetation) we used this instead. O horizons were defined by ≥40% SOM content due to the high observed SOC:SOM conversion factor of 2.4 for our soils, which motivated a slight increase of the 35% SOM limit from USDA soil taxonomy (Soil Survey Staff, 1999) given that USDA soil survey criteria typically assumes the conventional conversion factor of 1.7 (Pribyl, 2010). The samples were not washed nor treated in any other way before analysis.

We began by milling an aliquot of dried soil from each topsoil layer (O or A horizon). We then weighed each 4 mm ZrO_2 rotor and KEL-F cap before compacting a dried and milled soil sample from each O (or A) horizon into the rotor, sealing the tube with the KEL-F cap, and re-weighing the sealed sample. This resulted in approximately ∼100 mg of soil from each sample. We made all the NMR measurements using ^{13}C Cross-Polarization Magic Angle Spinning (CP-MAS) on a Bruker 500 MHz Avance III spectrometer. The CP-MAS spectra were acquired at a spin rate of 10 kHz, using a 1.5 ms contact time with ^{13}C at 60 kHz and a ^{1}H ramp of 45–90 kHz to sweep both +1 and −1 sidebands and achieve stable polarization transfer. We applied SPINAL64 ^{1}H decoupling at 83 kHz during acquisition followed by a 2 s relaxation delay. The number of scans, and therefore experimental time, differed depending on previous measurements of SOM content: 4,000 scans (for SOM contents between 60% and 89%), 8,000 scans (SOM 40%–59%), and 16,000 scans (SOM <40%). We processed the acquired data using Topspin (version 3.6.2) software. Functional groups were assigned to the following seven chemical shift regions in the NMR spectra (Smernik & Baldock, 2005): carbonyl C (190–160 ppm), O-aromatic C (160–140 ppm), aromatic C (140–112 ppm), di-O-alkyl C (112–93 ppm), O-alkyl C (93–60 ppm), methoxy/N-alkyl C (60–50 ppm), and alkyl C (50–0 ppm). From these assignments, we computed relative contributions to the total NMR spectral area from 190 to 0 ppm for each topsoil sample.

2.5. Supporting Field Study

In addition to the mesocosm sampling, we performed a field study at three sites in alpine/sub-arctic Sweden where non-native earthworm species were initially introduced by human activities and are now spreading into adjacent birch forests. The purpose of this survey was to evaluate the realism of the mesocosm experiment and assess whether similar earthworm effects on δ^{13}C and root biomass merged under complex field conditions. We conducted earthworm population surveys and collected soil samples as described and presented in Text S1 in Supporting Information S1. Details and descriptions of Torne Hamn (N 68°25,888′E 018°36,968′), Njunjes (N

66°57,617′E 017°27,034′) and Solberg (N 65°44,842′E 015°21,299′) sites are reported in Table S3 in Supporting Information S1.

2.6. Statistics

All statistics and data visualizations were conducted in the R statistical environment using R version 4.2.2 and R studio version 2022.07.2 + 576 (R Core Team, 2022) and the data we used is available in Jonsson et al. (2024). We used linear mixed effect (LME) models to test earthworm and vegetation effects on C pools, NMR functional group compositions, and above- and belowground plant biomass stocks. Each model was investigated for heteroscedasticity and homoscedasticity by checking model residuals. For aboveground and belowground biomass C (see Table 1) the response variable was transformed to achieve normality. We used vegetation type, earthworm treatment and their interaction as fixed factors and mesocosm block as a random factor in our models to account for spatial differences in the experiment. To assess potential within-block spatial effects, we examined model residuals across plots within each block. These analyses did not indicate a systematic spatial pattern within blocks, suggesting that the random block effect adequately accounted for spatial variation. We computed statistical models using the lme() command from the nlme package (Pinheiro et al., 2022). All visualisations were made with the ggplot2 package (Wickham, 2016), and we report all C pools as the mean kg C m^{-2} ± standard error.

Table 1
Linear Mixed Effect Models Output Analyzing the Effects of Earthworm Treatment, Vegetation Type, and Their Interaction on Tundra C Pools

Variable	Fixed factor	numDF, denDF	F	p
SOC	Vegetation type	1, 38	7.10	0.011
	Earthworm	1, 6	0.18	0.69
	Interaction	1, 38	4.34	0.044
BGB C[a]	Vegetation type	1, 38	67.41	<0.0001
	Earthworm	1, 6	9.08	0.024
	Interaction	1, 38	1.81	0.19
AGB C[b]	Vegetation type	1, 38	52.35	<0.0001
	Earthworm	1, 6	1.74	0.24
	Interaction	1, 38	0.54	0.46
Total C	Vegetation type	1, 38	0.39	0.54
	Earthworm	1, 6	1.07	0.34
	Interaction	1, 38	4.79	0.035

[a]Cubic root transformed. [b]Log transformed.

We tested the effects of earthworms and soil depth (continuous data) on the raw soil data for bulk density, carbon concentration, root biomass and soil $\delta^{13}C$ isotope ratios using LME models. For these analyses, the full initial model used for each response variable was as follows:

$$\text{Response variable} \approx \text{depth} + \text{depth}^2 + \text{earthworm treatment} + (\text{depth} \times \text{earthworm treatment}) + \left(\text{depth}^2 \times \text{earthworm treatment}\right) + (1|\,\text{block/plot})$$

We also included mesocosm block and plot as nested random factors in the models, and performed model selection with likelihood ratio testing using ANOVA.

3. Results

3.1. Carbon Pools

Tundra heath stored more C in plant biomass, both above- and belowground, than did the meadow treatments (Figure 2). Aboveground heath vegetation contained 0.12 ± 0.01 kg C m^{-2}, whereas aboveground meadow vegetation stored about a third of that (0.04 ± 0.02 kg C m^{-2}). Similarly, root biomass C was almost three times greater under heath (0.52 ± 0.03 kg C m^{-2}) than meadow (0.18 ± 0.01 kg C m^{-2}) vegetation. Conversely, the SOC pool (from 0 to 20 cm) was 20% greater in the meadow (7.1 ± 0.2 kg C m^{-2}) than in the heath (5.9 ± 0.3 ecosystem kg C m^{-2}). Taken together, there was no significant difference in the total C pool (sum of above- and belowground biomass C and SOC pool) between the two vegetation types ($p = 0.054$, Table 1) under worm-free conditions.

Earthworms significantly increased belowground biomass C by ~43% in both vegetation types (earthworm effect; $F_{1,6} = 9.08$, $p = 0.024$). Belowground biomass C in the heath increased by 0.22 kg C m^{-2} due to the earthworm treatment whereas this increase was lower (0.08 kg C m^{-2}) under meadow vegetation (Figure 2). We found no evidence that earthworm presence affected above ground biomass (earthworm effect, $p = 0.2$) in either of the vegetation types (earthworm × vegetation, $p = 0.5$).

Earthworms and vegetation type had divergent effects with respect to SOC pools. The earthworm-vegetation interaction had a negative effect of—0.41 kg C m^{-2} (corresponding to a –6% net change) in the meadow. Conversely, we observed a positive interaction effect in the heath, where average SOC pools increased by + 0.61 kg C m^{-2} (corresponding to a +10% net change) (earthworm × vegetation, $p = 0.044$; Figure 2; Table 1). The

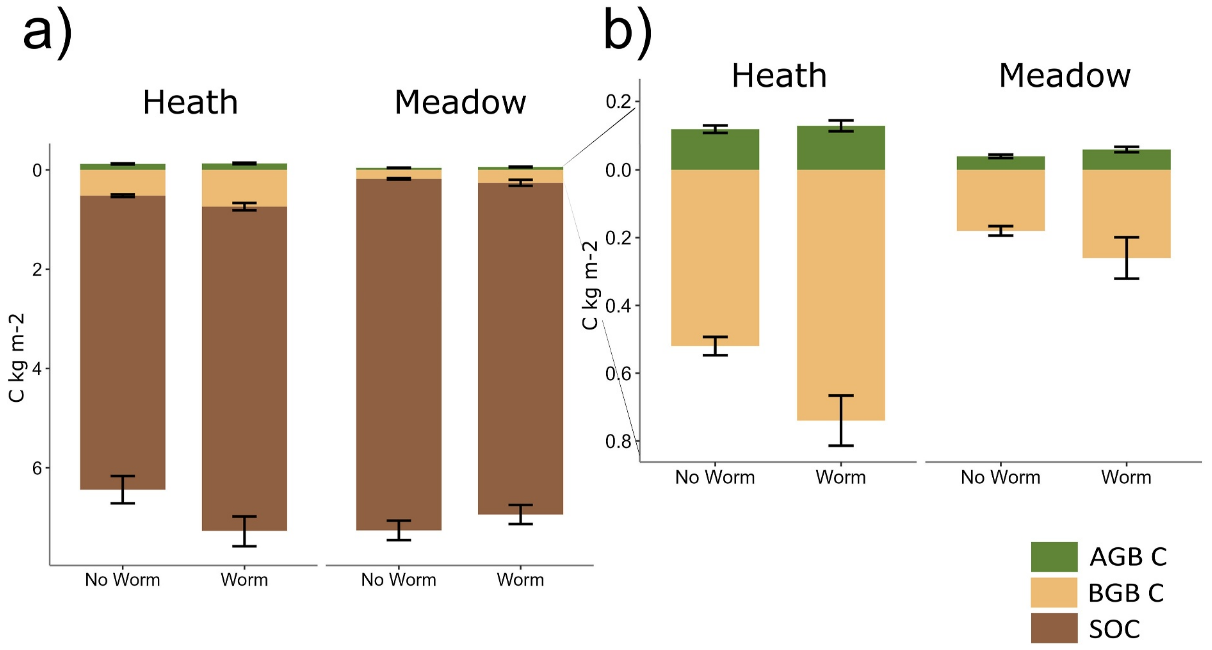

Figure 2. Earthworm effects on net carbon stocks in tundra heath and meadow ecosystems (a) separated by carbon reservoir; aboveground plant biomass C (AGB C) in green, belowground plant biomass C (BGB C) in yellow, and soil organic C (SOC) in brown. (b) Close-up inset panel zooming in to highlight earthworm and vegetation effects on plant biomass C pools. Bars denote the mean values and error bars represent standard errors. Supporting statistics are available in Table 1.

net change in ecosystem C storage (including both plant biomass and SOC pools) in response to earthworm presence also varied with vegetation type (earthworm × vegetation, $F_{1,38} = 4.79$, $p = 0.035$; Figure 2). In the heath, the total ecosystem C pool was +0.84 kg C m^{-2} greater (+13%) with earthworms relative to the control plots. In contrast, the meadow ecosystem shifted toward a lower net C stock by –0.3 kg C m^{-2} (–4%) in the presence of earthworms.

3.2. Earthworm Effects on the Vertical Distribution of SOC and Belowground Biomass

We observed no earthworm effect on the vertical distribution of SOC concentrations (%) in the tundra heath (Table S2a in Supporting Information S1). In the meadow, earthworms had a reducing main effect on the SOC profile ($\beta = -0.38$, $p < 0.02$) but also a significant interaction with depth ($\beta = +0.03$, $p < 0.02$) indicating that most of the earthworm induced losses of SOC in meadow were in the upper soil (Figure 3a, Table S2b in Supporting Information S1). Despite no significant differences in SOC concentrations by depth, the δ^{13}C isotopic signal of the SOC fraction in heath soils decreased with depth in the presence of earthworms ($\beta = -0.11$, $p < 0.001$), whereas this δ^{13}C earthworm effect was not present in the meadow (Figures 3c and 3d). Although earthworms increased total root biomass in both vegetation types, there was only an effect on root biomass as a function of depth in the heath vegetation. There was also a significant interaction effect of earthworm treatment and depth on root biomass ($\beta = +0.04$, $p = 0.04$, Figure 3e), indicating that earthworms increased root biomasses primarily in the deeper soil layers. There was no significant earthworm effect on soil density as a function of depth in either vegetation type (Figure 3d, Tables S2a–S2h in Supporting Information S1).

3.3. Soil Organic Carbon Quality

SOC in meadow plots had a higher proportion of O-aromatic C, aromatic C, methoxy/N-alkyl-C, and carbonyl-C in comparison to heath (Figure 4). In contrast, SOC in heath soil had a higher abundance of di-O-alkyl C and alkyl C. Earthworm presence reduced the abundance of O-aromatic C compounds in heath by 5% relative to the controls (F1, 6 = 7.3, $p = 0.04$). In contrast, earthworms increased the proportion of O-aromatic C compounds by 20% (E × V interaction effect F1, 38 = 16.6, $p = 0.01$) in meadow soils. In the meadow we also observed an 11% increase in aromatic C compounds (E × V, F1, 38 = 6.2, $p = 0.02$) and a 7% decline in alkyl C compounds (E × V, F1, 38 = 5.2, $p = 0.03$) with the earthworm treatment.

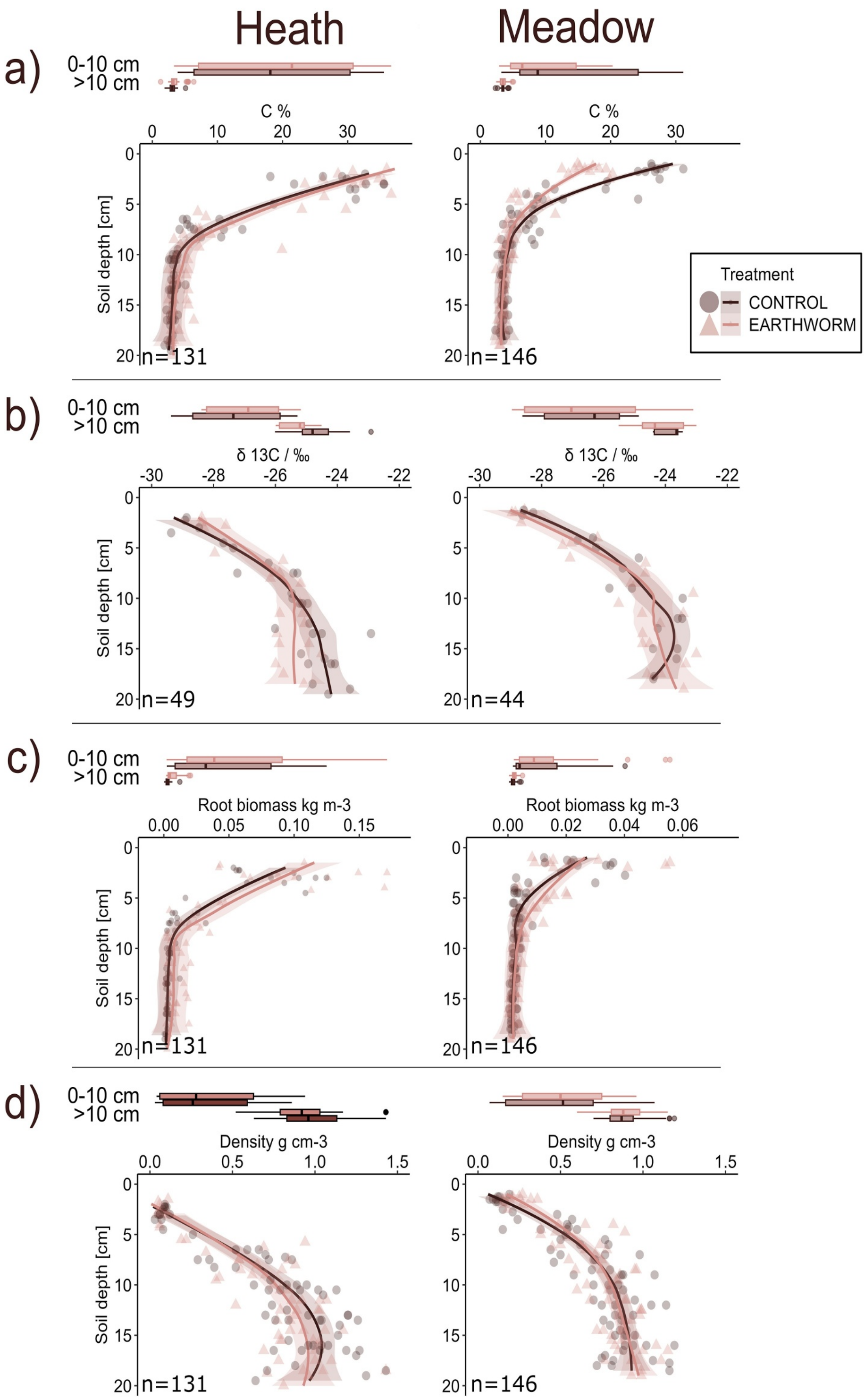

Figure 3. Earthworm treatment effects on the vertical depth profiles of (a) soil C concentration, (b) δ^{13}C values, (c) root biomass, and (d) bulk density in tundra heath and meadow vegetation with (triangles) and without (circles) earthworms. Points depict each soil or root sample, and lines are the running average, with standard errors shown as shaded fields. The overhead boxplots display the distribution of samples split by treatment and by two depth intervals: 0–10 cm and >10 cm. The boxes indicate the lower and upper quartiles, and the line denotes the median. The whiskers indicate minimum and maximum values. Smooth lines show the running average with 95% confidence interval shaded. Linear mixed effect model outputs from all eight depth profiles are available in Tables S2a–S2h in Supporting Information S1.

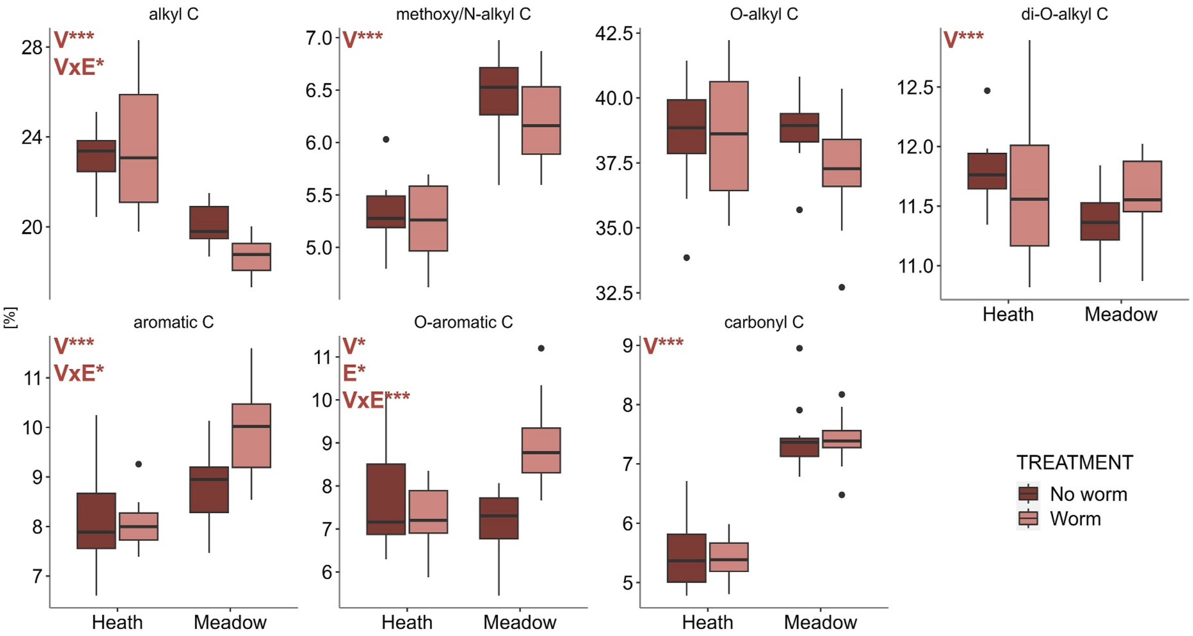

Figure 4. Earthworm and vegetation effects on the relative abundance of SOC functional types inferred from solid-state ^{13}C nuclear magnetic resonance spectroscopy of the O/A horizons of tundra heath and meadow soils. Bold letters indicate the significant variable that was tested (V = vegetation type, E = earthworm treatment, V × E their interaction) and asterisks denote the level of significance ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$). The full outputs from linear mixed effect models are listed in Table S1 in Supporting Information S1.

4. Discussion

4.1. Earthworms as Catalysts for Plant Growth

We hypothesized that the introduction of non-native, geoengineering earthworm species to tundra ecosystems would increase the plant biomass C reservoir. Although we did not detect any effects of earthworms on aboveground biomass, we found that earthworms had a positive effect on C stored in belowground biomass. Remarkably, the observed response in root growth was nearly double the documented earthworm effects on agricultural crop growth (van Groenigen et al., 2014). The stronger response for tundra plant growth compared to agricultural crops agrees with the observations of Mudrák and Frouz (2018), who showed that earthworm effects on plant productivity are typically more pronounced in less developed soils relative to soils that already have established detritivore populations. A stronger plant growth response to earthworms in tundra relative to agricultural soils may also be expected given that Blume-Werry et al. (2020) noted that earthworm casts in tundra have plant-available ammonium concentrations more than a magnitude higher than those typically observed in agricultural ecosystem. We cannot fully exclude the possibility that the added earthworms and their necromass provided an external source of nitrogen in our mesocosm experiment. However, an isotope labeling experiment conducted as part of the same mesocosm experiment demonstrated that a majority of the plant assimilated N came from ^{15}N labeled litter that was supplied at the start of the growing season (Blume-Werry et al., 2020). The findings of Blume-werry et al. (2020) indicate that faster plant N cycling in our study system stemmed primarily from accelerated SOM mineralization in the earthworm plots. Given the harsh climate in arctic ecosystems, we may also expect higher earthworm mortality rates during fall and winter months under field conditions, so some minor N supplied from earthworm necromass may be representative in these environments.

One possible explanation for the lack of an effect aboveground is that herbivores (voles and lemmings) were found to graze more intensively on tundra plants growing in earthworm-affected soils over the course of our experiment, in part due to their higher nitrogen content and palatability (Jonsson et al., 2023). We posit that significant biomass removal via preferential grazing of tundra vegetation in earthworm-invaded plots may have counteracted any underlying increases in aboveground plant growth. The study by Jonsson et al. (2023) also found that earthworms increased the abundance of graminoid plant species in both vegetation types without significant effects on other plant functional groups. We therefore surmise that shifting plant community compositions toward an increase in graminoids likely drove the increase in belowground biomass we observed, rather than being a direct plastic response of the preexisting plants. Previous research on tundra plant biomass allocation in response to environmental changes, such as warming, suggests that biomass allocation remains largely unaffected unless there is a concomitant change in plant community structure (Blume-Werry et al., 2018). Earthworm-induced shifts in plant community structures may thus be important determinants of C allocation patterns in future tundra ecosystems.

4.2. Earthworm-Plant Interactions Affect SOC in the Tundra

We hypothesized that the introduction of non-native, geoengineering earthworm species to tundra ecosystems would reduce the SOC reservoir, as expected when a new detritivore alleviates functional constraints on decomposition (Blume-Werry et al., 2023). Our results emphasize the key role of ecosystem type in controlling the direction and magnitude of earthworm effects on SOC in tundra: earthworms reduced SOC pools in meadow ecosystems, but increased SOC pools in heath (Figure 2). Although root biomass increased in both vegetation types when earthworms were present, the numerical increase of belowground biomass C due to earthworms was more than the double in heath compared to the meadow. Given the substantial increase in root biomass in earthworm-affected heath soils, we suspect that the main driver behind the earthworm-mediated increase in SOC pools under heath vegetation, was elevated root-derived C inputs. We highlight three observations supporting our assertion that augmented root-derived C inputs, rather than increases in SOC persistence, is the mechanism that best explains the earthworm-mediated SOC increase in heath tundra soils.

First, earthworm presence increased root biomass, and they did so more strongly in heath vegetation (Figure 2). It thus follows that root-derived C inputs may have increased proportionally more in the heath ecosystem where we also observe an increase in SOC. Second, the lower $\delta^{13}C$ signature of SOC in earthworm-affected heath soil depth profiles indicates infusions of recently fixed carbon into deeper soil layers, which supports the notion of increased root-derived C entering the SOC pool. Third, we did not detect any major chemical alteration of SOC functional types in the heath that would suggest that earthworms generated more persistent SOC forms (Figure 4). Earthworms did appear to increase the proportion of O-aromatic C structures—which source from recalcitrant lignin and tannin products (Kögel-Knabner, 2002)—but this was only true under meadow vegetation. Conversely, earthworm effects on SOC quality were negligible in heath.

Plant community allocation to roots and the vertical distribution of roots has long been suggested to determine the vertical distribution of SOC at global scales (Jobbágy & Jackson, 2000). Roots are important C contributors to the SOC pool (Dijkstra et al., 2021) and the earthworm-mediated increase in root biomass makes a case for potential increases to high latitude SOC pools following earthworm establishment. Additionally, earthworms can incorporate root litter into macro- and (even more likely) micro-aggregates, thereby stabilizing root-derived C and making it more resistant to decomposition (Fahey et al., 2021; Sánchez-de León et al., 2014). Earthworms have also been shown to more effectively stabilize root-derived SOM relative to leaf-derived SOM, which may further contribute to elevated root-derived C stocks in earthworm-affected soils (Angst et al., 2020). Although our data cannot reveal the long-term stability of the newly formed SOC observed here, it does indicate that over the multi-year timescale of our experiment, we find no indications that root exudates have a priming effect on the heath SOC reservoir.

In the tundra meadow, earthworms both reduced SOC pools as we hypothesized but also altered SOC properties in the O horizon. We observed that earthworms reduced the proportion of alkyl C forms (such as leaf surface waxes and leaf cutin) relative to the controls. This change coincided with a shift toward a greater proportion of degraded SOM dominated by lignin and tannin-derived structures (aromatic and O-aromatic SOC). The observed changes in SOC quality indicate more extensive earthworm-mediated decomposition in meadow soils, which support our findings of a decreasing SOC reservoir in the presence of earthworms for this specific tundra system. Stronger decomposition effects in the meadow could be explained by the more nutrient (nitrogen) rich litter and higher pH in meadow soils, since plants in this tundra vegetation type typically have a higher nitrogen content (Blume-Werry et al., 2020; Jonsson et al., 2023). The lower impact of earthworms on SOC properties in the heath O horizon remains uncertain but could be explained by their deeper burrowing pattern in this vegetation type relative to the meadow. That is, x-ray imaging of heath soils from the same mesocosm experiment indicate that the main zone of earthworm activity is beneath the O horizon in the heath soils whereas earthworms are active closer to the surface in the meadow (Klaminder et al., 2023). Although low litter quality could be one explanation for low

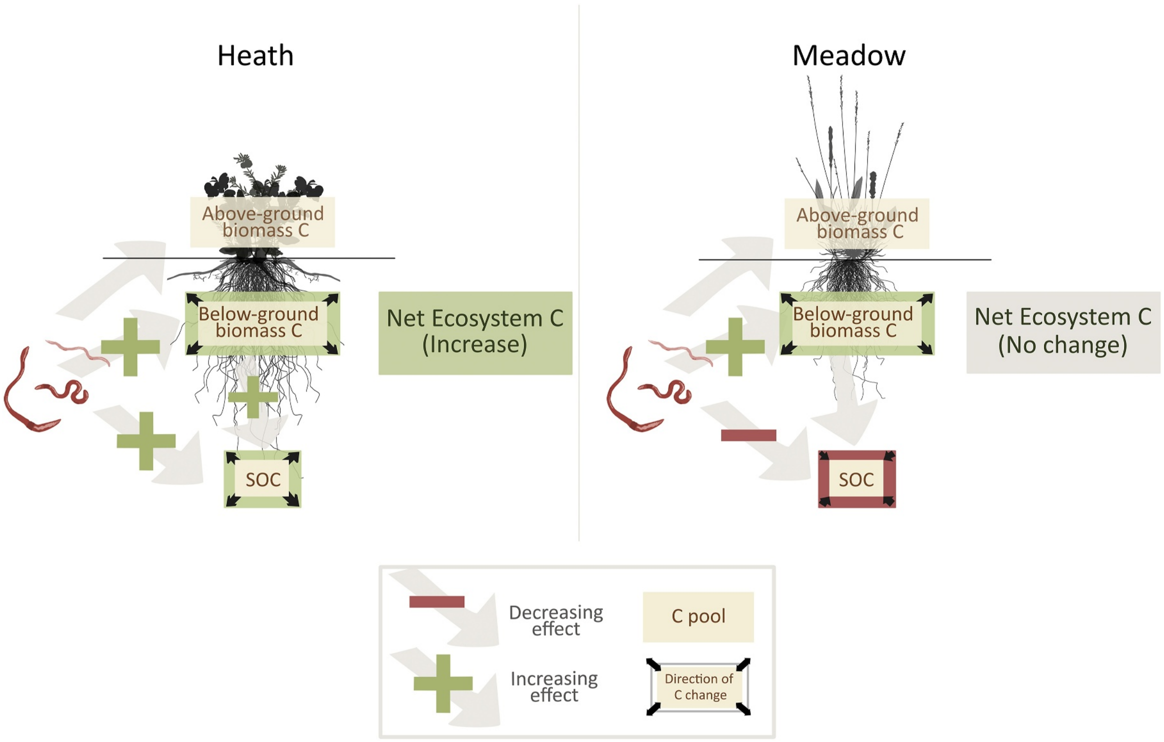

Figure 5. Conceptual figure highlighting the relative earthworm effects on above- and belowground plant biomass C, soil organic C, and the net ecosystem C pools in tundra heath and meadow. Boxes represent the C pools of interest (as well as their relative sizes and changes), whereas arrows indicate the earthworm-induced increase (green), decrease (red), or negligible effect (gray) on the various C reservoirs.

earthworm activity in heath soil O horizons, their lower water content could also deter worms from entering and/or contribute to slower microbial processing of earthworm casts in these layers (Klaminder et al., 2023; Oberbauer, 2007).

4.3. Implications for C Sequestration in Ecosystems Invaded by Earthworms

The net effects of earthworms on whole ecosystem C storage have rarely been comprehensively explored. Instead, earthworm effects on below- and aboveground C reservoirs are often assessed in isolation, and worm impacts on plant C reservoirs have usually been inferred from proxies such as plant cover (%) and/or community composition. In instances where both plant biomass and SOC pools have been assessed for in tandem, only one plant compartment (e.g., root biomass) was considered (Jennings & Watmough, 2016). In our full system assessment, we demonstrate that geoengineering earthworms have divergent effects on ecosystem C budgets depending on vegetation type (Figure 5). In the meadow, SOC losses were offset by increased C storage in plant biomass, leading to no significant net change in ecosystem C storage. We emphasize that this finding could have been (mis)interpreted as a negative earthworm effect on meadow ecosystem C if we had not tracked associated changes in both the above and belowground plant biomass.

We note that earthworms may have long term effects on both SOC turnover and plant C allocation that are not captured in our experimental set up. Previous experiments assessing earthworm effects on permafrost soils show that additions of only earthworms or only litter accelerated C mineralization, contributing to losses from the SOC pool (Frouz & Cajthaml, 2023). However, combining both litter and earthworm additions increased organic matter stabilization in mineral soils, particularly within microaggregates and silt/clay fractions (Frouz & Cajthaml, 2023). These findings would suggest that if earthworm effects on plant biomass eventually stagnate with time, the net earthworm effect on the ecosystem C balance may change. Furthermore, the feeding and casting activities of geoengineering earthworms could shift SOC fractions from predominantly particulate organic C toward a larger fraction of mineral associated organic C forms. Over longer timescales, this could lead to a net increase in SOC stocks due to longer SOC residence times (Angst et al., 2024). We therefore call for further exploration of earthworm-plant-SOC interactions over long timescales to better elucidate potential time-dependent impacts and feedbacks on ecosystem C.

In the heath, earthworms stimulated an increase in both SOC and plant-C pools, corresponding to a net ecosystem uptake of ~0.84 kg C m^2 over 4 years. When divided over a 4-year study period this corresponds to an average annual flux of 0.21 kg C m^2 yr^{-1}, which is more than 10 times higher than the estimated mean net ecosystem C uptake (0.02 kg m^2 yr^{-1}, 1990–2009) for european arctic tundra ecosystems (McGuire et al., 2012). The inferred worm-induced increase in annual C uptake in the heath ecosystem is also 4 times greater than the estimated increase in C uptake (~0.05 kg m^2 yr^{-1}) following long-term (19-year) experimental warming of +1.5°C in a similar sub-arctic heath ecosystem (Ylänne et al., 2015). These comparisons suggest that the impact of arctic wʻoʼrming may *per se* be on par with, or even exceed, the effects of relevant warming scenarios in some tundra ecosystems. We do note that the current scale of earthworm invasion in the Arctic remains minute relative to the land area affected by climate change, but with a warmer and wetter arctic climate and continued human mediated dispersal of earthworms this may change in the future.

Our results highlight that earthworm effects on C sequestration are strongly dependent on the ecosystem they invade and how belowground C inputs respond to their presences. Our findings also highlight that to fully capture earthworm impacts on SOC dynamics, we must recognize their indirect effects on plants and their roots, which can increase C inputs and/or SOC persistence. We remain cautious about extrapolating our findings to other vegetation and soil types, because earthworm effects can vary significantly depending on specific interactions between the different ecosystems and earthworm community structures (Ross et al., 2021). Nonetheless, we note that our field study (see Supplementary Information, Text S2) indicates that our results are also representative for sub-alpine arctic birch forests. In short, soil cores taken along three earthworm invasion gradients in sub-alpine birch forest, reveal that earthworm invasions have a positive effect on root biomass and generate decreasing $\delta^{13}C$ with increasing soil depth, mimicking the results from our mesocosm experiments. These findings tentatively suggest that the earthworm-mediated increase in the delivery of recently fixed C to depth (via roots and/or physical mixing) may be relevant beyond the two vegetation examined in our mesocosm experiment.

5. Conclusion

Our results highlight that earthworm effects on C sequestration are strongly dependent on both the ecosystem and the belowground plant responses. We show that geoengineering earthworms increased root biomass of both tundra heath and meadow vegetation but had contrasting effects on SOC pools depending on vegetation type. In the meadow, earthworms caused SOC losses that were offset by increased plant biomass, resulting in no net change to the C ecosystem balance. In contrast, we observed a substantial net C sequestration effect when earthworms were introduced to the heath system. Our findings thereby offer empirical support for the counter-intuitive idea that introductions of a detritivore that feeds directly on SOM can facilitate C sequestration at an ecosystem level.

The scientific debate around earthworms' effects on ecosystem C has primarily focused on the fate of SOC, whereas cascading earthworm effects on plant growth, belowground in particular, has received far less attention. Our study suggests that plant-soil-earthworm interactions need to be incorporated into this discussion. Although our findings demonstrate the direct earthworm impacts on SOC, they also simultaneously emphasize that the influence of earthworms on root growth and biomass can be equally if not more important for determining the net earthworm effect on ecosystem C. These intertwined effects are essential to accurately forecast how the ongoing and incipientspread of invasive earthworms will influence the C balance of northern ecosystems.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad, https://doi.org/10.5061/dryad.n5tb2rc47.

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References

Angst, G., Angst, Š., Frouz, J., Peterse, F., & Nierop, K. G. J. (2020). Preferential degradation of leaf- vs. root-derived organic carbon in earthworm-affected soil. *Geoderma*, *372*, 114391. https://doi.org/10.1016/j.geoderma.2020.114391

Angst, G., Potapov, A., Joly, F.-X., Angst, Š., Frouz, J., Ganault, P., & Eisenhauer, N. (2024). Conceptualizing soil fauna effects on labile and stabilized soil organic matter. *Nature Communications*, *15*(1), 5005. https://doi.org/10.1038/s41467-024-49240-x

Blume-Werry, G., Klaminder, J., Krab, E. J., & Monteux, S. (2023). Ideas and perspectives: Alleviation of functional limitations by soil organisms is key to climate feedbacks from arctic soils. *Biogeosciences*, *20*(10), 1979–1990. https://doi.org/10.5194/bg-20-1979-2023

Blume-Werry, G., Krab, E. J., Olofsson, J., Sundqvist, M. K., Väisänen, M., & Klaminder, J. (2020). Invasive earthworms unlock arctic plant nitrogen limitation. *Nature Communications*, *11*(1), 1766. https://doi.org/10.1038/s41467-020-15568-3

Blume-Werry, G., Lindén, E., Andresen, L., Classen, A. T., Sanders, N. J., von Oppen, J., & Sundqvist, M. K. (2018). Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra. *Journal of Vegetation Science*, *29*(2), 226–235. https://doi.org/10.1111/jvs.12605

Bossuyt, H., Six, J., & Hendrix, P. (2005). Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology and Biochemistry*, *37*(2), 251–258. https://doi.org/10.1016/j.soilbio.2004.07.035

Bossuyt, H., Six, J., & Hendrix, P. F. (2006). Interactive effects of functionally different earthworm species on aggregation and incorporation and decomposition of newly added residue carbon. *Geoderma*, *130*(1), 14–25. https://doi.org/10.1016/j.geoderma.2005.01.005

Cameron, E. K., Cahill, J. F., Jr., & Bayne, E. M. (2014). Root foraging influences plant growth responses to earthworm foraging. *PLoS One*, *9*(9), e108873. https://doi.org/10.1371/journal.pone.0108873

Conant, R. T., Drijber, R. A., Haddix, M. L., Parton, W. J., Paul, E. A., Plante, A. F., et al. (2008). Sensitivity of organic matter decomposition to warming varies with its quality. *Global Change Biology*, *14*(4), 868–877. https://doi.org/10.1111/j.1365-2486.2008.01541.x

Craven, D., Thakur, M. P., Cameron, E. K., Frelich, L. E., Beauséjour, R., Blair, R. B., et al. (2017). The unseen invaders: Introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis). *Global Change Biology*, *23*(3), 1065–1074. https://doi.org/10.1111/gcb.13446

Dijkstra, F. A., Zhu, B., & Cheng, W. (2021). Root effects on soil organic carbon: A double-edged sword. *New Phytologist*, *230*(1), 60–65. https://doi.org/10.1111/nph.17082

Fahey, T., Bohlen, P., Feldpausch, T. R., Fisk, M., Goebel, M., Groffman, P. M., et al. (2021). Tracing carbon flow through a sugar maple forest and its soil components: Role of invasive earthworms. *Plant and Soil*, *464*(1), 517–537. https://doi.org/10.1007/s11104-021-04971-4

Fisk, M. C., Fahey, T. J., Groffman, P. M., & Bohlen, P. J. (2004). Earthworm invasion, fine-root distributions, and soil respiration in north temperate forests. *Ecosystems*, *7*(1), 55–62. https://doi.org/10.1007/s10021-003-0130-3

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, *450*(7167), 277–280. https://doi.org/10.1038/nature06275

Frelich, L. E., Hale, C. M., Scheu, S., Holdsworth, A. R., Heneghan, L., Bohlen, P. J., & Reich, P. B. (2006). Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, *8*(6), 1235–1245. https://doi.org/10.1007/s10530-006-9019-3

Frouz, J., & Cajthaml, T. (2023). Do earthworm and litter inputs promote decomposition or stabilization of cryoturnated organic matter from melted permafrost? *European Journal of Soil Biology*, *119*, 103568. https://doi.org/10.1016/j.ejsobi.2023.103568

Hale, C. M., Frelich, L. E., & Reich, P. B. (2006). Changes in hardwood forest understory plant communities in response to European earthworm invasions. *Ecology*, *87*(7), 1637–1649. https://doi.org/10.1890/0012-9658(2006)87[1637:CIHFUP]2.0.CO;2

Hendrix, P. F., Callaham, M. A., Drake, J. M., Huang, C. Y., James, S. W., Snyder, B. A., & Zhang, W. X. (2008). Pandora's box contained bait: The global problem of introduced earthworms. *Annual Review of Ecology Evolution and Systematics*, *39*(1), 593–613. https://doi.org/10.1146/annurev.ecolsys.39.110707.173426

Hoogsteen, M. J. J., Lantinga, E. A., Bakker, E. J., Groot, J. C. J., & Tittonell, P. A. (2015). Estimating soil organic carbon through loss on ignition: Effects of ignition conditions and structural water loss. *European Journal of Soil Science*, *66*(2), 320–328. https://doi.org/10.1111/ejss.12224

IPCC. (2021). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/9781009157896

Jennings, B. W., & Watmough, S. A. (2016). The impact of invasive earthworms on soil respiration and soil carbon within temperate hardwood forests. *Ecosystems*, *19*(5), 942–954. https://doi.org/10.1007/s10021-016-9977-y

Jerand, P., Klaminder, J., & Linderholm, J. (2023). The legacy of ecological imperialism in the Scandes: Earthworms and their implications for Arctic research. *Arctic, Antarctic, and Alpine Research*, *55*(1), 2274650. https://doi.org/10.1080/15230430.2023.2274650

Jobbágy, E. G., & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its climate and vegetation. *Ecological Applications*, *10*(2), 423–436. https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Jonsson, H., Blume-Werry, G., Wackett, A. A., Olofsson, J., Arvidsson, E., Sparrman, T., & Klaminder, J. (2024). Data of how non-native earthworms alter carbon sequestration in sub-arctic tundra ecosystems [Dataset]. *Dryad*. https://doi.org/10.5061/dryad.n5tb2rc47

Jonsson, H., Olofsson, J., Blume-Werry, G., & Klaminder, J. (2023). Cascading effects of earthworm invasion increase graminoid density and rodent grazing intensities. *Ecology*, *105*(2). https://doi.org/10.1002/ecy.4212

Keuper, F., Wild, B., Kummu, M., Beer, C., Blume-Werry, G., Fontaine, S., et al. (2020). Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nature Geoscience*, *13*(8), 560–565. https://doi.org/10.1038/s41561-020-0607-0

Klaminder, J., Krab, E. J., Larsbo, M., Jonsson, H., Fransson, J., & Koestel, J. (2023). Holes in the tundra: Invasive earthworms alter soil structure and moisture in tundra soils. *Science of the Total Environment*, *859*, 160125. https://doi.org/10.1016/j.scitotenv.2022.160125

Kögel-Knabner, I. (2002). The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biology and Biochemistry*, *34*(2), 139–162. https://doi.org/10.1016/S0038-0717(01)00158-4

Lubbers, I. M., van Groenigen, K. J., Fonte, S. J., Six, J., Brussaard, L., & van Groenigen, J. W. (2013). Greenhouse-gas emissions from soils increased by earthworms. *Nature Climate Change*, *3*(3), 187–194. https://doi.org/10.1038/nclimate1692

McGuire, A. D., Christensen, T. R., Hayes, D., Heroult, A., Euskirchen, E., Kimball, J. S., et al. (2012). An assessment of the carbon balance of Arctic tundra: Comparisons among observations, process models, and atmospheric inversions. *Biogeosciences*, *9*(8), 3185–3204. https://doi.org/10.5194/bg-9-3185-2012

Mudrák, O., & Frouz, J. (2018). Earthworms increase plant biomass more in soil with no earthworm legacy than in earthworm-mediated soil, and favour late successional species in competition. *Functional Ecology*, *32*(3), 626–635. https://doi.org/10.1111/1365-2435.12999

Nuzzo, V., Maerz, J. C., & Blossey, B. (2009). Earthworm invasion as the driving force behind plant invasion and community change in Northeastern North American Forests. *Conservation Biology*, *23*(4), 966–974. https://doi.org/10.1111/j.1523-1739.2009.01168.x

Oberbauer, S. F., Tweedie, C. E., Welker, J. M., Fahnestock, J. T., Henry, G. H. R., Webber, P. J., et al. (2007). Tundra CO2 fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecological Monographs*, *77*(2), 221–238. https://doi.org/10.1890/06-0649

Pinheiro, J. B. D., DebRoy, S., Sarkar, D., & R. Core Team. (2022). nlme: Linear and nonlinear mixed effects models.

Pribyl, D. W. (2010). A critical review of the conventional SOC to SOM conversion factor. *Geoderma*, *156*(3–4), 75–83. https://doi.org/10.1016/j.geoderma.2010.02.003

Razavi, B. S., Liu, S., & Kuzyakov, Y. (2017). Hot experience for cold-adapted microorganisms: Temperature sensitivity of soil enzymes. *Soil Biology and Biochemistry*, *105*, 236–243. https://doi.org/10.1016/j.soilbio.2016.11.026

R Core Team. (2022). R: A language and environment for statistical computing. (Version 4.2.2 (2022-10-31 ucrt) 'Innocent and Trusting') [Computer software]. *R Foundation for Statistical Computing*. Retrieved from https://www.R-project.org/

Ross, D. S., Knowles, M. E., Juillerat, J. I., Görres, J. H., Cogbill, C. V., Wilmot, S., & D'Agati, K. (2021). Interaction of land use history, earthworms, soil chemistry and tree species on soil carbon distribution in managed forests in Vermont, USA. *Forest Ecology and Management*, *489*, 119049. https://doi.org/10.1016/j.foreco.2021.119049

Sánchez-de León, Y., Lugo-Pérez, J., Wise, D. H., Jastrow, J. D., & González-Meler, M. A. (2014). Aggregate formation and carbon sequestration by earthworms in soil from a temperate forest exposed to elevated atmospheric CO_2: A microcosm experiment. *Soil Biology and Biochemistry*, *68*, 223–230. https://doi.org/10.1016/j.soilbio.2013.09.023

Smernik, R. J., & Baldock, J. A. (2005). Does solid-state 15N NMR spectroscopy detect all soil organic nitrogen? *Biogeochemistry*, *75*(3), 507–528. https://doi.org/10.1007/s10533-005-2857-8

Soil Survey Staff. (1999). *Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys* (2nd ed.). Natural Resources Conservation Service. U.S. Department of Agriculture.

van Groenigen, J. W., Lubbers, I. M., Vos, H. M. J., Brown, G. G., De Deyn, G. B., & van Groenigen, K. J. (2014). Earthworms increase plant production: A meta-analysis. *Scientific Reports*, *4*(1), 6365. https://doi.org/10.1038/srep06365

Wackett, A. A., Yoo, K., Olofsson, J., & Klaminder, J. (2018). Human-mediated introduction of geoengineering earthworms in the Fennoscandian arctic. *Biological Invasions*, *20*(6), 1377–1386. https://doi.org/10.1007/s10530-017-1642-7

Werner, R., Bruch, B., & Brand, W. (1999). ConFlo III - An interface for high precision delta(13)C and delta(15)N analysis with an extended dynamic range. *Rapid Communications in Mass Spectrometry*, *13*(13), 1237–1241. https://doi.org/10.1002/(SICI)1097-0231(19990715)13:13<1237::AID-RCM633>3.0.CO;2-C

Wickham, H. (2016). *ggplot2: Elegant Graphics for data analysis*. Springer-Verlag.

Ylänne, H., Stark, S., & Tolvanen, A. (2015). Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: Evidence from 19 years of warming and simulated herbivory in the subarctic tundra. *Global Change Biology*, *21*(10), 3696–3711. https://doi.org/10.1111/gcb.12964

Zhang, W., Hendrix, P. F., Dame, L. E., Burke, R. A., Wu, J., Neher, D. A., et al. (2013). Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nature Communications*, *4*(1), 2576. https://doi.org/10.1038/ncomms3576