

Drying by worming: deciphering how earthworms dry tundra soil

J. Klaminder^{a,*}, L. Hedström^b, H. Jonsson^{a,c}, J. Lee^b, L. Lizana^b

^a Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

^b Integrated Science Lab, Department of Physics, Umeå University, SE-90197 Umeå, Sweden

^c Climate Impacts Research Center, Department of Ecology and Environmental Science, Umeå University, SE-98107 Abisko, Sweden

ARTICLE INFO

Handling Editor: Yvan Capowicz

Keywords:

Drought
Soil-water
Drilosphere
Biopore
Invasive species

ABSTRACT

Deep-burrowing earthworms (anecic and endogeic species) can dry soils by reworking mineral soil layers. Although this ‘drying effect’ has been reported across many ecosystems, including the Fennoscandian tundra, little is known about the driving processes. In this study, we measure plant transpiration in combination with controlled experiments of water holding capacity and evaporation to assess drivers of soil–water losses in tundra soil as the result of endogeic and anecic earthworms. Our experimental system was a common garden experiment with shrub-dominated (heath) and forb-dominated (meadow) vegetation ($N = 48$), where long-term monitoring revealed drier soils due to the addition of earthworms. Although we found that tundra plant transpiration was highest during the peak growing season and that meadow soil had a higher field capacity, our earthworm treatment did not strongly affect these two parameters. Evaporation, on the other hand, was on average 14 % higher in the meadow with earthworms although no such effect was observed in the heath soil. Using a network model of macropore vapor transfer that measures evaporation effects, we found an increase in macropore conductance between the subsoil and the atmosphere and that the vaporization rate in relation to the diffusion rate controls the strength of the evaporation effect. Our findings underscore the need to account for evaporation due to the reworking of pore architectures by soil biota when predicting changes in soil–water availability.

1. Introduction

Earthworms that forage in the mineral soil (endogeic species) or access litter via deep tunnel systems (anecic species) can reduce the soil water content (Ferlian et al., 2020). This ‘drying effect’ has been observed in agricultural, temperate, and boreal ecosystems (Blouin et al., 2007; Ferlian et al., 2020; Liu et al., 2021; Ganault et al., 2024) and, more recently, in the Arctic tundra (Jonsson et al., 2024). While reduced soil moisture due to earthworm activity is reported across many ecosystems, there is an intriguing lack of consensus regarding what process(es) decrease soil water. For example, earthworms may dry soils by increasing plant transpiration rates (Blouin et al., 2007; Xu et al., 2013), increasing evaporation rates (Frelich et al., 2019), reducing the water holding capacity of soils (Blouin et al., 2007), and/or inducing flow paths where vertical flow rates exceed the water sorptivity rate of the macropore (Leue et al., 2015; Jarvis, 2020).

Whereas arctic soils mainly contain litter dwelling (epigeic) earthworms (Wackett et al., 2018), tundra soils mainly contain endogeic and anecic earthworms (Klaminder et al., 2023; Jonsson et al., 2024). Typically, plants respond positively to earthworm’s production of fertile

casts (van Groenigen et al., 2014). For example, litter dwelling earthworms in tundra have been associated with increased belowground plant growth (Blume-Werry et al., 2020). In high latitude ecosystems, plant transpiration constitutes about 16–33 % of the ecosystem’s evapotranspiration (Sabater et al., 2020); hence, it seems plausible that earthworms can induce drier tundra soils by boosting plant transpiration, even though the effect may be small compared to evaporation fluxes. Yet, earthworms may also stimulate evaporation. For example, some epi-endogeic and anecic earthworm species might increase the risk of drought causing negative effect on forest growth as their removal of surface litter increases evaporation (Frelich et al., 2019). In addition, evaporation might increase due to earthworm burrows, acting like chimneys, increasing the diffusion transport of water vapor (Ernst et al., 2009; Ma et al., 2021). This ‘chimney effect’ can be assumed to be substantial in tundra soil where endogeic and anecic earthworms can increase macroporosity by >100 % (Klaminder et al., 2023).

Macropore networks made by endogeic and anecic earthworms not only favor vapor diffusion but also drive vertical soil water transport (Capowicz et al., 2014), which varies between seasons (Blouin et al., 2013) and species ecological strategies (Ernst et al., 2009). For example,

* Corresponding author.

E-mail address: jonatan.klaminder@slu.se (J. Klaminder).

<https://doi.org/10.1016/j.geoderma.2025.117421>

Received 18 March 2025; Received in revised form 9 June 2025; Accepted 29 June 2025

Available online 14 July 2025

0016-7061/© 2025 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

some endogeic species may compact the soil and reduce infiltration and percolation rates, whereas some anecic species de-compact the soil and improve soil drainage (Blanchart et al., 2004). By increasing infiltration, earthworms may reduce surface runoff but also moves the vaporization plane downwards (Jouquet et al., 2008), and positive effects on the soils water budget from increased water inputs and reduced surface evaporation may explain why the soil water content increase due to earthworms in some ecosystems (Ehlers, 1975; Clements et al., 1991; Blouin et al., 2013). However, soils can become drier as drainage along earthworm burrows result in vertical water transport rates that exceed the sorption rate of the soil. This process is also known as ‘none-equilibrium’ flow–i.e., the water holding pores (mesopores) are not in equilibrium with the percolating soil water (Leue et al., 2015; Jarvis, 2020).

Rather than searching for a drying mechanism involving non-equilibrium flow due to earthworm tunnels, Blouin et al. (2007) posited that the drying effect of earthworms is likely caused by the loss of mesopores, which retain water within the soil matrix. In this pioneering study, the authors incubated rice seedlings with an earthworm species (*Millsonia anomala*) known to increase soil compaction. They found that reduced mesopore volume was the key driver behind reduced soil moisture rather than increased evapotranspiration and plant transpiration. Yet, the artificial setting, the agricultural context, and the soil-compacting impact of the studied earthworm species make it difficult to extrapolate this finding to tundra ecosystems. Other studies also show that soil structures made by earthworms can have higher water retention than the bulk soil (Stockdill and Cossens, 1966; Clements et al., 1991; Hallam and Hodson, 2020), indicating that mesopore compaction is unlikely a universal effect of earthworms.

Understanding processes involved when earthworms alter the water balance of soils is important given that human land use is currently moving earthworm species into new habitats at a global scale (Hendrix et al., 2008). For example, endogeic and epi-endogeic earthworms are establishing in new environments inside North American forests (Gates, 1982). Here, farmers, gardeners, and fishermen, largely unwittingly, introduced earthworms to previously glaciated landscapes where these organisms were once eradicated during the last glaciation (Cameron et al., 2007; Hendrix et al., 2008; Addison, 2009). Human-mediated introduction of earthworms has also been observed in the Fennoscandian Arctic (Wackett et al., 2018). In this environment, archaeological findings suggest that soils were largely untouched by bioturbation until the first farmers brought soil dwelling earthworms to the landscape (Jerand et al., 2023). In this study, we assess the impacts of these invasive earthworms on the water content of soils in an outdoor experiment with two types of tundra vegetation (heath and meadow). To assess potential drivers of redacted soil water (Klaminder et al., 2023; Jonsson et al., 2024), we measured earthworm impacts on evaporation, plant transpiration, and soil water holding capacity (field capacity). We hypothesized that earthworms i) reduce the field capacity of soils, ii) increase plant transpiration, and iii) increase evaporation. In addition, we used a network model to assess how earthworm activity, specifically its effects on macropore architecture, influences evaporation.

2. Material and methods

2.1. Study system

Measurements were conducted in a common garden experiment with heath tundra (shrub dominated) and meadow tundra (forb and graminoid dominated). The mesocosms ($N = 48$) were constructed in 2013 outside the research station in Abisko (Lat: 68. 356, Long: 18.81591) using monoliths of soils (Leptic Dystric Cambisols) transported from nearby alpine tundra in the Kärkevagge valley (Lat: 68.41, Long: 18.31972). This tundra type does have litter dwelling (epigeic) earthworms, like *Dendrobaena octaedra*, but are free from endogeic and anecic species (Wackett et al., 2018). We did not attempt to remove these

epigeic earthworms. We placed intact vegetation and soil into boxes ($39 \times 50 \times 30$ cm) with drainage holes and embedded the boxes into eight raised sand beds (300 cm \times 160 cm, 40 cm) that were insulated (Fig. S1). Mesocosm surfaces were levelled with the surrounding sand beds to maintain realistic soil temperature fluctuations. The mesocosms were allowed to recover from disturbance between the summer of 2013 and 9 June 2017 when 24.2 g (wet weight) of earthworms were added every year, approximately corresponding to densities of <300 individual m^{-2} . As a comparison, 22 g of earthworms m^{-2} has been reported for adjacent earthworm invasion gradients (Wackett et al., 2018).

To avoid contaminating the controls, we added earthworms to half of the eight sand beds (henceforth referred to as blocks), which resulted in a total of 12 treatments for each vegetation type. About 80 % of the added earthworms were endogeic adult Aporectodea sp. (*Aporrectodea rosea*, *Aporrectodea tuberculata*, and *Aporrectodea trapezoids*) and about 20 % were epi-endogeic (*Lumbricus rubellus*). In 2020, however, about 4 % of the mass also included the anecic species *Lumbricus terrestris*. All these invasive species (i.e., human dispersed), which are found in the Fennoscandian arctic, added up to a mass comparable to invasive earthworms found in adjacent soils (Wackett et al., 2018). We assumed 100 % winter mortality, so we added new earthworms in the spring of 2018, 2019, and 2020. All earthworm-treated mesocosms were found to contain living *Aporrectodea* sp. and *Lumbricus* sp. when the experiments were terminated in September 2020, suggesting that summer survival of the added individuals were high in both vegetation types. 3D x-ray tomography of the mineral soil also revealed that mineral soil dwelling earthworms thrived in both vegetation types (Larsbo et al., 2024). Epigeic earthworms (*Dendrobaena octaedra* Savigny, 1826) that were not introduced but native to the local soil used to construct the mesocosm were found in control plots (1 heath and 3 meadow) but were not observed in the earthworm treatment plots. Both vegetation types were underlain by acidic soils. The average pH_{H_2O} in the O horizon (5 cm, mor-type humus) of the heath was 4.4, and the average pH_{H_2O} in the O horizon of the meadow (3 cm, mor-type humus in control and moder type in treatments) was 5.4. The mineral soil consisted of 27 ± 4 % coarse fragments (>2 mm fraction), 56 ± 5 % sand, 16 ± 3 % silt, and <1 % clay.

2.2. Vegetation community transpiration measurements

We measured plant transpiration using a closed chamber method on three occasions in our mesocosms during the growing season: early growing season (late June), peak growing season (early August), and late growing season (early September). We measured ecosystem H_2O fluxes by closing a transparent plastic chamber (height 90 cm) onto each mesocosm and recorded the change in H_2O concentration within the chamber over two minutes with an infra-red open path gas analyzer (LICOR 7500 open path, LICOR Biosciences). Photosynthetically active radiation (PAR, $mmol\ m^{-2}\ s^{-1}$) was continuously recorded during the measurements. We used two small fans within the chamber to mix the air. The short measurement duration minimized changes in air temperature and humidity within the chamber. We recorded the H_2O flux four times for each mesocosm plot and sampling occasion: one measurement with ambient light conditions, two measurements under reduced PAR levels using varying layers of mesh fabric, and one measurement in complete darkness following the methods for CO_2 flux measurements outlined elsewhere (Sundqvist et al., 2020). For each plot, we fitted linear regressions between measured PAR values and H_2O fluxes. Regressions were used to standardize transpiration measurements to a common light condition (PAR_{600}) for individual mesocosms. This approach followed similar approaches outlined for CO_2 fluxes (Metcalfe and Olofsson, 2015) and allowed us to compare between seasons without having the bias of differences in solar radiation.

2.3. Evaporation and field capacity

Soil cores (Φ 11 cm) were collected from the center of each mesocosm and subjected to 3D x-ray imaging of macropore structures as described in detail in Klaminder et al. (2023). Intact soil cores were placed in plastic cylinders sealed with waterproof aluminum tape and saturated with water by gradually increasing the water table for 48 h. Water-saturated cores were placed in hydraulic contact with artificial sand beds to drain to constant weight under a comparable sand bed drainage as in the outdoor settings (3 kPa). Drained columns were evaporated at 25 °C with air humidity set at 40 %. The mass-loss was recorded for 19 days. At the end of the experiment, the cores were dried at 105 °C. Water held in the upper 0.2 m of the soil after drainage (time zero) was used as a metric for mesopore water holding capacity (henceforth referred to as field capacity). Calculated mass-loss at 25 °C (20 % humidity) during the first 3 weeks was used as a measure of evaporation losses.

2.4. Evaporation model

To assess how earthworms affect a soil's capacity to transport water vapor (by diffusion) to the atmosphere, we created a simplified pore network model (Fig. 1). This model describes the transport of water vapor from the sub-soil via macropores to the atmosphere (see Supporting Information for details). In short, this model allowed us to calculate the expected evaporation of water vapor (E_{loss}) from the upper 0.3 m of the soil in response to an increased macropore conductance between the subsoil and the atmosphere, as earthworms increase macroporosity, continuity of pore system, and tortuosity. We represented the soil-pore network permeating a soil unit as narrow channels (junctions) joined with a node with a volume (the pore). As the study system was situated in the same common garden environment, we assumed that all external environmental conditions driving evaporation (temperature and water pressure) were similar between the treatments and allowed

only the earthworms' reworking of the pore architecture to vary. Therefore, water was vaporized at a similar constant rate (q) in all mesopores within each soil volume (assuming the pores had reached field capacity). The flow between nodes was modelled as outlined in the Supporting Information using the Python module networkX (Batagelj and Brandes, 2005; Hagberg et al., 2008). Modelled evaporation is presented as a function of a dimensionless parameter (K), representing the ratio between the vaporization rate and the diffusion rate (K_d) of water vapor in the macropores. K is expected to vary between soil types (due to differences in meteorological conditions and soil properties). Therefore, by testing whether E_{loss} was sensitive to changes in K , we could evaluate the extent our soil dwelling earthworms affected evaporation depending on the environmental conditions. For example, we evaluated to what extent evaporation was higher in soil systems with strong diffusion gradients (low K) than in soil systems with lower diffusion gradients (high K). Although some network modelling approaches have previously been applied to describe how pores impact the hydraulic properties of soil (Vogel and Roth, 2001; Armatas, 2006), we specifically evaluated how macropore architectures made by earthworms affected evaporation.

2.5. Statistics

We assessed the effects of earthworms and vegetation type on plant transpiration, field capacity, and evaporation with linear mixed-effects models. Earthworm treatment, vegetation type, and their interaction were treated as categorical factors, and the mesocosm blocks were treated as random factors due to the nested experimental design. When we used repeated measures of a variable, we included mesocosm plot as random factor to avoid pseudo replication. The statistical testing was done with the "lme" command from the nlme package (Pinheiro et al., 2022). Heteroscedasticity was tested for each model by checking residuals. In some cases (indicated in the test results), the data were transformed to reach homogeneity of variances. Statistical analyses

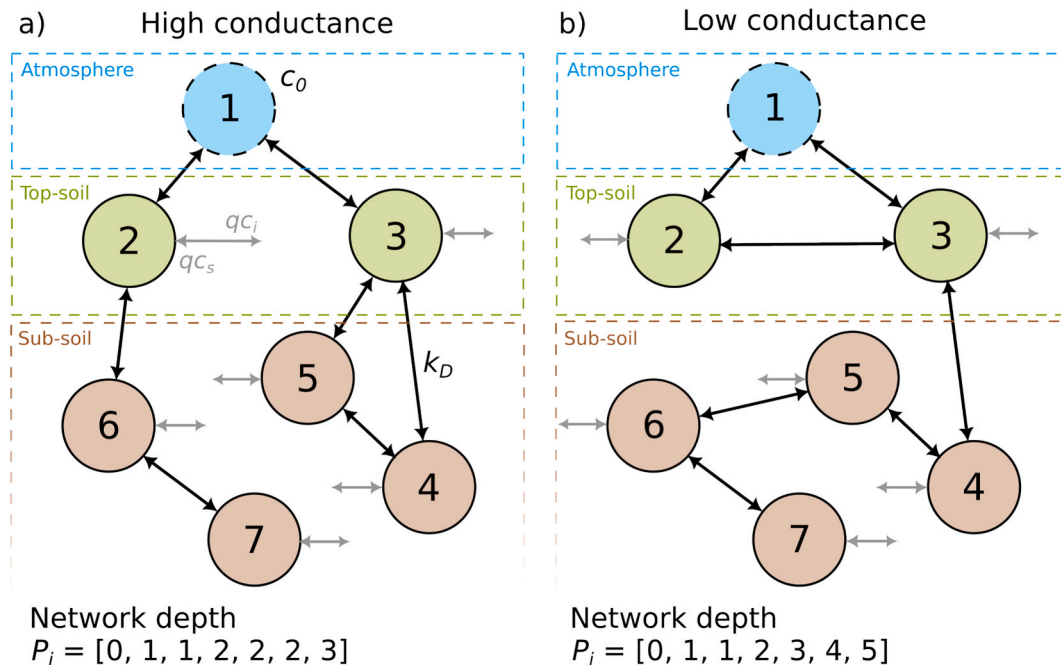


Fig. 1. Illustration of two networks with a) high conductance and b) low conductance where water vapor is absorbed and evaporated in all soil nodes with a rate q (grey arrows) and diffuses between connected nodes with a diffusion rate k_D (black arrows). Node 1 represents the atmosphere and constitutes an evaporation sink from which E_{loss} is calculated. The depth of each node P_i is defined as the minimum number of steps to any source node. Illustration of a soil with high conductance between soil units (topsoil and sub-soil) and the atmosphere. High conductance in this system is generated by more direct vertical links between the atmosphere, topsoil, and subsoil (low tortuosity) than the network illustrated having low conductance between soil units and the atmosphere. The number of links are identical for each network.

were performed in IBM SPSS Statistics V.29 or using the R statistical environment version 4.4.0 (RCoreTeam, 2022).

To compare the effect size for the effects caused by earthworms, we calculated log response ratios (ln(treatment/control)) for our results as well as previous findings from the mesocosm relating to seasonal changes in soil moisture (Jonsson et al., 2024) and macroporosity (Klaminder et al., 2023). Variance around each log-response ratio mean was calculated using the following equation:

$$V = S^2_{pooled} \left(\frac{1}{(n_T(X_T)^2)} + \left(\frac{1}{(n_C(X_C)^2)} \right) \right),$$

where S^2_{pooled} is the pooled standard deviation, X_T the mean of the treatment, n_T the sample size of the treatment, X_C the mean of the control, and n_C the sample size of the control. 95 % confidence intervals for the mean values were calculated assuming normal distribution.

3. Results

3.1. Soil moisture and field capacity

At the time of sampling, the soil moisture content was on average lower in the heath ($0.28 \text{ m}^3 \text{ m}^{-3}$) than in the meadow ($0.32 \text{ m}^3 \text{ m}^{-3}$) tundra (Fig. 2a) (Table 1). The earthworm-treated mesocosms were on average drier per soil volume than the control ($F_{1,6} = 7.13$) ($P = 0.035$). We observed no apparent interaction between the earthworm treatment and the two vegetation types (Veg \times Treatment) ($P > 0.8$). Here, the water content of the earthworm treatment was about 9 % lower than in the control tundra in both vegetation types. When saturated to field

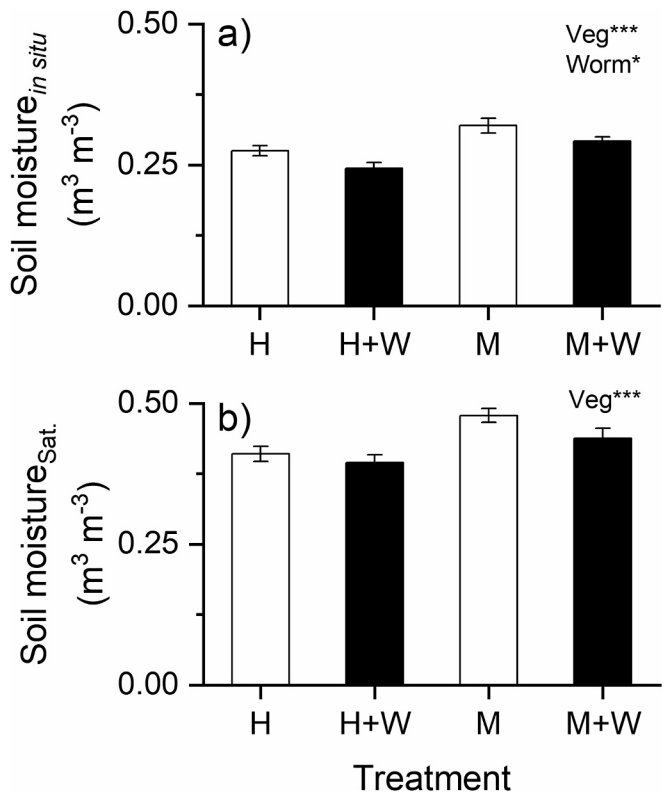


Fig. 2. (a) Soil moisture at the time of sampling (in situ) in the heath (H) and meadow (M) where control soil without added earthworms is shown with white bars and soil with added worms (+W) are shown with black bars. Effects of vegetation (Veg) and treatments (Worms) are shown in the upper right corner. (b) Soil moisture at saturation for the two tundra vegetation types. Labels, colors, and symbols are the same as for the upper panel. Notes. *** $P < 0.001$ and * $P < 0.05$.

Table 1

Linear mixed effect model outputs analyzing the effects of earthworm treatment, vegetation type on the measured soil water content (in situ), and field capacity. Also shown are effects on soil moisture due to plant transpiration and evaporation. Plant transpiration was measured in 2020 and standardized to a fixed solar radiation input (PAR_{600}) during three seasons (spring, summer, and autumn) and the effect of seasons was included in the model for this factor.

Variable	Fixed factor	numDF	denDF	F	p
Soil moisture (in situ) $\text{m}^3 \text{ m}^{-3}$	Treatment (T)	1	6	7.128	0.035
	Vegetation type (V)	1	40	21.097	<0.001
	T \times V	1	40	0.048	0.827
Field capacity $\text{m}^3 \text{ m}^{-3}$	Treatment	1	6	1.765	0.229
	Vegetation type	1	40	15.441	<0.001
	T \times V	1	40	3.010	0.091
Evaporation $\text{L m}^{-2} \text{ Day}^{-1}$	Treatment	1	6	0.511	0.50
	Vegetation type	1	38	38.959	<0.001
	Hours (H)	1	188	319.095	<0.001
	T \times V	1	38	4.595	0.038
	T \times H	1	188	0.367	0.55
	V \times H	1	188	0.225	0.64
	T \times V \times H	1	188	0.623	0.43
Transpiration (PAR_{600}) $\text{mmol mol}^{-1} \text{ s}^{-1} \text{ m}^{-2}$	Treatment	1	6	0.331	0.59
	Vegetation type	1	38	0.029	0.87
	Season (S)	1	524	22.047	<0.001
	T \times V	1	38	0.818	0.37
	T \times S	1	524	2.517	0.11
	V \times S	1	524	10.018	0.0016
	T \times V \times S	1	524	2.251	0.13

capacity, the soil from the meadow still contained a higher soil moisture content than the heath ($F_{1,6} = 15.44$) ($P < 0.001$), but the previous observed differences due to earthworm treatments disappeared (Fig. 2b). That is, we did not observe any main effects or interaction effects ($P > 0.09$) in earthworm treatment on the water holding capacity of soils.

3.2. Plant transpiration

Measured plant transpiration in the studied tundra types increased linearly with increasing light exposure, reaching about $0.2 \text{ mmol/mol m}^{-2} \text{ s}^{-1}$ around 1000 PAR (Fig. 3). Transpiration normalized to PAR_{600} depending on the season ($F_{5, 524} = 22.047$) ($P < 0.001$), with a lower flux in autumn than in spring or summer (Table 1). Interestingly, there were seasonal differences between the two vegetation types. The evergreen-dominated heath had higher transpiration in the late growing season than the forb-dominated meadow tundra (Season \times Veg) ($F_{5, 524} = 10.018$) ($P < 0.001$). We found no main or interaction effect on plant transpiration from our earthworm treatment.

3.3. Evaporation and model predictions

Evaporation from the incubated soil cores decreased over time before reaching stable evaporation around $0.7 \text{ L m}^2 \text{ day}^{-1}$ for the control heath and around $0.9 \text{ L m}^2 \text{ day}^{-1}$ for the control meadow (Fig. 4) (Table 1). Both the decrease over time ($F_{1,188} = 319.09$) ($P < 0.0001$) and the higher evaporation rate for the meadow ($F_{1,38} = 38.95$) ($P < 0.0001$) were statistically significant. Interestingly, there was a higher evaporation rate from the meadow soil containing earthworms (Veg \times Treatment) ($F_{1,38} = 319.09$) ($P < 0.038$). Evaporation from earthworm-treated meadow stabilized around $1 \text{ L m}^2 \text{ day}^{-1}$, and the average

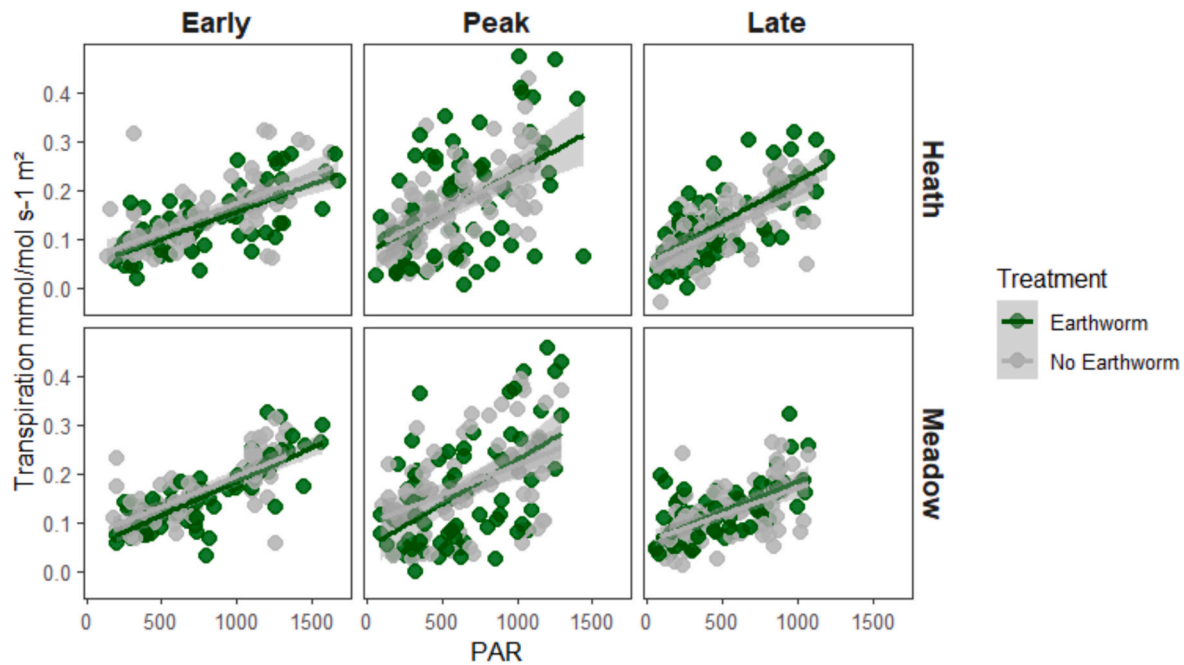


Fig. 3. Increased evasion of water vapor as a function of increased photosynthetic active radiation (PAR) used to estimate effects on plant transpiration by vegetation type (Heath and Meadow) and season (early, peak, and late growing season). Earthworm-treated plots are indicated with green (darker) and the control treatment (no worms) with grey (lighter). 95 % confidence intervals of the regressions for the two treatments are shown with shading. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

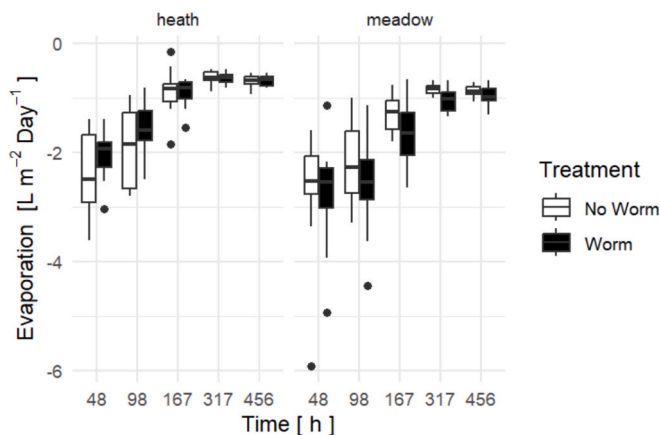


Fig. 4. Evaporation ($\text{L m}^{-2} \text{ day}^{-1}$) measured between periods during our 456 h-long experiment with intact soil cores from a) heath soils with no effect on evaporation from the earthworm treatment (black box) and b) meadow soils with an average 14 % increase in evaporation from the earthworm treatment. Note that evaporation is expressed as a negative flux where lower values indicate greater (increased) evaporation. Also observe that earthworms-effects on evaporation was only significant for the meadow. Data are presented as box plots with the box indicating 25 % and 75 % of the data range. Whiskers indicate the 1 % and 99 % not including outliers (black diamond symbol). Color of the boxplots indicate control (white) and earthworm treatments (black).

evaporation flux for the experimental period was 14 % higher in this tundra than in the control. There was no other interaction effect observed in the experiment ($P > 0.43$).

That earthworms increased evaporation motivated us to model impacts from increased macropore conductance on evaporation (E_{loss}). The macropore conductance is stimulated not only by earthworm burrows but also by the soil drying per se as more air-filled pores implies improved conditions for vapor exchange between pores. Our network model suggested that evaporation increases linearly, but not

proportionally, with increased soil macropore conductance (Fig. 5). Here, the relative effect of conductance on evaporation decreases with increasing K -values (i.e., the ratio between the vaporization rate and the vapor diffusion rate). Our model explains the 14 % higher evaporation rate in earthworm-treated meadows with these K -values as the

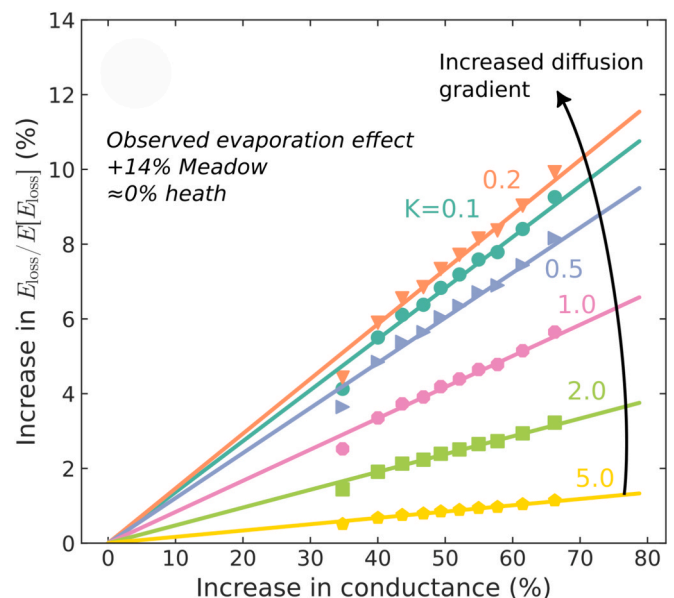


Fig. 5. The relative change in evaporation (E_{loss}) versus relative change in network conductance for a soil system where the vaporization rate in the macropores remains constant, but where increased earthworm burrows increase the conductance between sub-soil and topsoil layers (x-axis). The results are presented for six K values (water vaporization rate/water gas diffusion rate). Arrows indicate how the function between evaporation and macropore conductance varies as the diffusion gradient increases (increased diffusion rates). Measured changes in evaporation due to earthworms in the two tundra types (meadow and heath) are inserted as reference.

earthworms had to improve macroporosity to a much higher degree. While the predicted numbers should be treated with caution, given the simplicity of the model approach and considering that K -values are dynamic variables in soils, our model made one important prediction: soils subjected to a massive increase in macropore conductance due to earthworm burrows may experience a minute increase in evaporation if the diffusion rate is too low in relation to the vaporization rate (i.e., if K -values ≥ 5).

3.4. Effect sizes

Seasonal reductions in soil moisture due to earthworms were generally larger for the meadow soil than the heath soil, but both vegetation types showed negative response ratios for all three studied seasons (Fig. 6). Response ratios for transpiration, field capacity, and evaporation were generally smaller than the observed reductions in soil moisture. However, the response ratio observed for macroporosity was substantially larger than that seen for soil moisture and evaporation, where the latter agreed with our network-model predictions – i.e., large increases in macroporosity result in smaller effects on evaporation.

4. Discussion

Endogeic and anecic earthworms reduced soil moisture in our experiment, a finding supported both by short-term ‘snapshot’ measurements (Jonsson et al., 2024) and long-term logger measurements (Klaminder et al., 2023) from the very same studied system. This result is also in line with previous studies showing that endogeic and anecic species reduce the water content of soil (Blouin et al., 2007; Ferlian et al., 2020; Liu et al., 2021; Ganault et al., 2024). Reduced soil moisture was recorded already at the end of the first summer of our experiment (Klaminder et al., 2023). As a comparison, field studies from Canadian

forests did not observe reduced soil moisture during the first seasons following invasion (Thouvenot et al., 2024).

But what process(es) caused the drying effect of earthworms in our treatment? The soil dwelling earthworms used in our experiment did not substantially increase plant transpiration, making increased transpiration an unlikely driver of reduced soil water. That is, although our applied method was sensitive enough to detect seasonal differences in plant transpiration between the vegetation types, we found that our treatments had no impact. Similarly, we observed differences in field capacity depending on vegetation types, but the average reduction in field capacity observed for treatments with earthworms was not statistically significant compared with the control and smaller than the observed reduction in soil moisture. Instead, our experiment revealed increased evaporation from the meadow with earthworms. This result supports hypothesis 3: evaporation is stimulated by earthworm activities. In other words, the impact of earthworms on evaporation appeared as one important driver of diminishing soil water in our earthworm-treated soil.

Despite a massive increase in macroporosity in the heath (on average 293 %), we observed only detectable evaporation effects for the meadow, where the impact on macroporosity was more modest (on average 70 %). Our network model predictions can assist when trying to understand the drivers behind these contrasting responses. Our macropore network model suggested that to achieve an increase in evaporation at the lower tens of percentage scale—a proportional change corresponding to the evaporation effect observed in earthworm-treated meadow soil—the relative increase in pore network conductance must be much greater. Macropore conductance does not generate a proportional increase in evaporation, a finding that suggests massive changes in macropore conductance can occur with only modest or negligible changes in evaporation as in the case for the heath. According to our model, minute effects of increased conductance occur in soils with higher K -values ($K \geq 5$), and the strongest proportional evaporation response to earthworm-enhancing macropore conductance is found in soils with higher diffusion gradients, where vapor diffusion rates are comparable to, or exceed, vaporization rates ($K \leq 1$). In other words, the model predicts that presence of moisture-containing organic matter at the soil surface, which reduces the strength of the atmosphere-sub-soil diffusion gradient, decreases evaporation effects from earthworm burrows. In the heath, the O horizon was on average 2-cm thicker and the moss cover was twice as extensive as in the meadow (Jonsson et al., 2024) and moisture held in these organic compartments likely caused a lower diffusion gradient (higher K) in the heath than in the meadow. Vapor diffusion in the meadow may also have been further stimulated by increased litter removal by earthworms, which was more pronounced in the meadow (Blume-Werry et al., 2020). Importantly, the higher near-soil surfaces burrow activity (i.e., soil ingestion rates) in the meadow compared to the heath, observed via x-ray imaging of the cores (Larsbo et al., 2024), may have also stimulated evaporation in the meadow as this activity likely generated more near-surface pores linking the soil to the atmosphere.

As shown in our model, earthworm impacts on evaporation are affected by vaporization and diffusion rates, indicating that our observed effects are not directly applicable to other ecosystems without considering differences in soil structures and meteorological conditions. Moreover, our modelling also suggests that there is, at least theoretically, one additional condition where increased conductance in macropores made by earthworms matters little for evaporation rates: systems with very strong diffusion gradients between the soil and atmosphere as these conditions result in vapor diffusion rates widely exceeding vaporization rates ($K < 0.2$). In these systems, water vapor will diffuse to the atmosphere despite pore architectures with low conductance.

The field measurements reported by Jonsson et al. (2024) clearly show that the strongest in situ ‘drying effect’ of earthworms is in meadow soil, a finding in line with our observation of an earthworm-induced boost in evaporation in this tundra type. Nevertheless, the

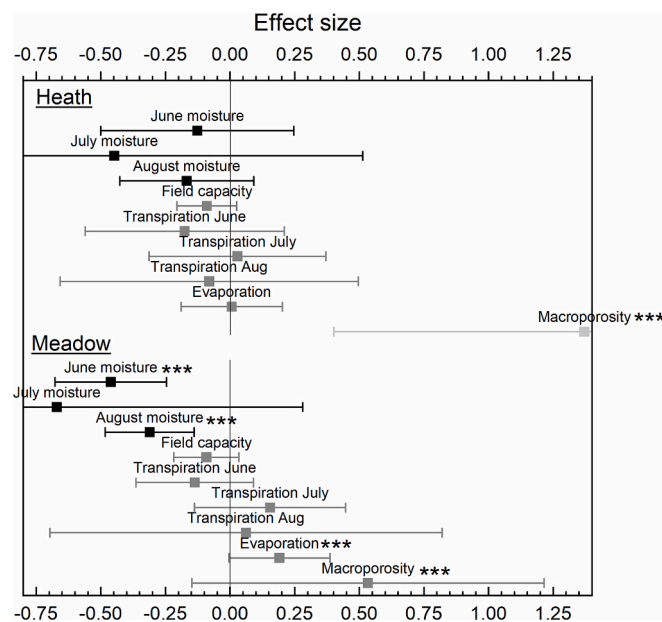


Fig. 6. Response ratio ($\ln(\text{treatment/control})$) for the measured soil water content for three months (June, July, and August) in our study system (black square), which has previously been published by Jonsson et al. (2024). Data are presented separately for heath soil (upper panel) and the meadow tundra (lower panel). Also shown are the response ratio for field capacity, plant transpiration, and evaporation (grey squares) as well as for macroporosity published in Klaminder et al. (2023). Zero line (no response) is shown with a dashed line. Note. Error bars represent the standard error of the mean estimates and *** indicates significant effects suggested by the statistical approaches applied in the original analysis.

heath soil also experienced a reduction in soil water per soil volume at the end of the vegetation season (i.e., when we sampled the soil). In addition, the effect observed for evaporation in the meadow was on average too small to explain the *in situ* reduction in the soil water content. This larger than expected effect in combination with an earthworm effect on the water content of heath soil indicates that we may have missed processes affecting the water balance of soils. Although the effect on field capacity was not statistically significant, soils with earthworms typically had a lower water holding capacity and it seems plausible that our applied methods were not sensitive enough to detect small reductions in response to this treatment. Especially considering that the field capacity reduction would be statistically significant if assuming a one-tailed test, but the lack of previous earthworm studies on tundra soil, makes us hesitate to adopt this directional statistical approach. Yet, it seems plausible that part of the observed earthworm induced soil drying was caused by mesopore compaction. Field capacity has previously been used to assess impacts of earthworms on water storage of soils (Blouin et al., 2007), but it is important to highlight that this measure does not necessarily reflect the soils' ability to store water if percolation rates exceed the sorptivity of water-holding mesopores (Leue et al., 2015). This kind of non-equilibrium water flow, which occurs in macropores made by earthworms, is a recognized feature (Jarvis, 2020). Although dye and packed soil column experiments have provided qualitative evidence for non-equilibrium flow, quantifying the net impact of this flow type *in situ* over several seasons is a challenge. Yet, given the substantial increase in macroporosity caused by earthworm in the heath, it seems reasonable to assume that the lower soil water content in heath in the fall was caused by earthworm-induced non-equilibrium flow and/or a small reduction in mesopore volume. In other words, the impact of earthworms on soil water is more complex than solely being the result of stimulated evaporation. That is, macropores created by the earthworms stimulate both soil water vapor emissions as well as causing reduced retention of percolating soil water, where the importance of each process depends on vegetation type.

5. Conclusions

We conclude that endogeic and anecic earthworms can decrease the water content of tundra soils. One important process behind this effect is that these earthworms create soil structures that stimulate water vapor emissions from the soil to the atmosphere. Our findings underscore the need to recognize actions of soil biota when predicting future changes in the water balance of soils. To date, impacts from soil fauna entering high latitude soils due to human-mediated dispersal or a general 'biological awakening' has mainly been discussed from a perspective of decomposition processes (Blume-Werry et al., 2023). Less attention has been given to soil fauna impacts on soil moisture. Our study indicates that earthworms established in high latitude soils may not only increase evaporation but also—at least for the heath soil—enhance the vertical transport of soil water to deeper layers by reducing the retention of percolating water in surface soil. It seems important to assess eventual cascading effects from these changed water fluxes. For example, microbial communities in deeper soil layers at high latitudes are largely limited by allochthonous inputs of carbon, nitrogen, and oxygen (Mack et al., 2004; Capek et al., 2015; Keiluweit et al., 2016; Keuper et al., 2020), making increased deeper drainage of limiting nutrients or increased oxygen diffusion a plausible boosting factor for the turnover of deep soil organic matter. Predicting how burrowing soil fauna may alleviate conditions for microbial processes offers a scientific challenge. Yet, our findings highlight the need to account for the mechanism(s) where burrowing soil fauna reshape soils when making sound predictions of future environmental changes in high latitude ecosystems.

CRedit authorship contribution statement

J. Klaminder: Writing – original draft, Funding acquisition, Writing

– review & editing, Supervision, Conceptualization. L. Hedström: Formal analysis. H. Jonsson: Formal analysis, Data curation. J. Lee: Conceptualization. L. Lizana: Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jonatan Klaminder reports financial support was provided by Swedish Research Council. Jonatan Klaminder reports financial support was provided by Swedish Research Council Formas. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Financial support was provided for this research from The Swedish Research Council (2017-04548) and Formas (2018-01312) and the Kempe Foundation (Icelab multidisciplinary postdocs). We thank the Swedish Polar Research Secretariat for the support of the work done at the Abisko Scientific Research Station and CIRC for assisting with field equipment.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2025.117421>.

Data availability

Data will be made available on request.

References

- Addison, J., 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. In: *Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems*, pp. 59–79.
- Armatas, G.S., 2006. Determination of the effects of the pore size distribution and pore connectivity distribution on the pore tortuosity and diffusive transport in model porous networks. *Chem. Eng. Sci.* 61, 4662–4675.
- Batagelj, V., Brandes, U., 2005. Efficient generation of large random networks. *Phys. Rev. E* 71, 036113.
- Blanchart, E., Albrecht, A., Brown, G., Decaens, T., Duboiset, A., Lavelle, P., Mariani, L., Roose, E., 2004. Effects of tropical endogeic earthworms on soil erosion. *Agric. Ecosyst. Environ.* 104, 303–315.
- Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. *Eur. J. Soil Sci.* 64, 161–182.
- Blouin, M., Lavelle, P., Laffray, D., 2007. Drought stress in rice (*Oryza sativa* L.) is enhanced in the presence of the compacting earthworm *Millsonia anomala*. *Environ. Exp. Bot.* 60, 352–359.
- 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, 1979–1990.
- Blume-Werry, G., Krab, E.J., Olofsson, J., Sundqvist, M.K., Väisänen, M., Klaminder, J., 2020. Invasive earthworms unlock arctic plant nitrogen limitation. *Nat. Commun.* 11, 1766.
- Cameron, E.K., Bayne, E.M., Clapperton, M.J., 2007. Human-facilitated invasion of exotic earthworms into northern boreal forests. *Ecoscience* 14, 482–490.
- Capek, P., Diáková, K., Dickopp, J.-E., Bárta, J., Wild, B., Schnecker, J., Alves, R.J.E., Aiglsdorfer, S., Guggenberger, G., Gentsch, N., 2015. The effect of warming on the vulnerability of subducted organic carbon in arctic soils. *Soil Biol. Biochem.* 90, 19–29.
- Capowiez, Y., Sammartino, S., Michel, E., 2014. Burrow systems of endogeic earthworms: effects of earthworm abundance and consequences for soil water infiltration. *Pedobiologia* 57, 303–309.
- Clements, R., Murray, P., Sturdy, R., 1991. The impact of 20 years' absence of earthworms and three levels of N fertilizer on a grassland soil environment. *Agric. Ecosyst. Environ.* 36, 75–85.
- Ehlers, W., 1975. Observations on earthworm channels and infiltration on tilled and untilled loess soil. *Soil Sci.* 119, 242–249.

- Ernst, G., Felten, D., Vohland, M., Emmerling, C., 2009. Impact of ecologically different earthworm species on soil water characteristics. *Eur. J. Soil Biol.* 45, 207–213.
- Ferlian, O., Thakur, M.P., Castañeda González, A., San Emeterio, L.M., Marr, S., da Silva Rocha, B., Eisenhauer, N., 2020. Soil chemistry turned upside down: a meta-analysis of invasive earthworm effects on soil chemical properties. *Ecology* 101, e02936.
- Frelich, L.E., Blossey, B., Cameron, E.K., Dávalos, A., Eisenhauer, N., Fahey, T., Ferlian, O., Groffman, P.M., Larson, E., Loss, S.R., Maerz, J.C., Nuzzo, V., Yoo, K., Reich, P.B., 2019. Side-swiped: ecological cascades emanating from earthworm invasions. *Front. Ecol. Environ.* 17, 502–510.
- Ganault, P., Nahmani, J., Capowiez, Y., Fromin, N., Shihan, A., Bertrand, I., Buatois, B., Milcu, A., 2024. Earthworms and plants can decrease soil greenhouse gas emissions by modulating soil moisture fluctuations and soil macroporosity in a mesocosm experiment. *PLoS One* 19, e0289859.
- Gates, G., 1982. Farewell to North American megadriles. *Megadrilogica* 4, 12–77.
- Hagberg, A., Swart, P., Chult, D.S., 2008. Exploring network structure, dynamics, and function using NetworkX. Los Alamos National Lab. (LANL), Los Alamos, NM (United States).
- Hallam, J., Hodson, M.E., 2020. Impact of different earthworm ecotypes on water stable aggregates and soil water holding capacity. *Biol. Fertil. Soils* 56, 607–617.
- Hendrix, P.F., Callahan, 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. *Annu. Rev. Ecol. Syst.* 39, 593–613.
- Jarvis, N., 2020. A review of non-equilibrium water flow and solute transport in soil macropores: principles, controlling factors and consequences for water quality. *Eur. J. Soil Sci.* 71, 279–302.
- Jerand, P., Klaminder, J., Linderholm, J., 2023. The legacy of ecological imperialism in the Scandes: earthworms and their implications for arctic research. *Arct. Antarct. Alp. Res.* 55, 2274650.
- Jonsson, H., Olofsson, J., Blume-Werry, G., Klaminder, J., 2024. Cascading effects of earthworm invasion increase graminoid density and rodent grazing intensities. *Ecology* 105, e4212.
- Jouquet, P., Podwojewski, P., Bottinelli, N., Mathieu, J., Ricoy, M., Orange, D., Tran, T. D., Valentin, C., 2008. Above-ground earthworm casts affect water runoff and soil erosion in Northern Vietnam. *Catena* 74, 13–21.
- Keiluweit, M., Nico, P.S., Kleber, M., Fendorf, S., 2016. Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? *Biogeochemistry* 127, 157–171.
- Keuper, F., Wild, B., Kumm, M., Beer, C., Blume-Werry, G., Fontaine, S., Gavazov, K., Gentsch, N., Guggenberger, G., Hugelius, G., 2020. Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nat. Geosci.* 13, 560–565.
- 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. *Sci. Total Environ.* 859, 160125.
- Larsbo, M., Koestel, J., Krab, E.J., Klaminder, J., 2024. Quantifying earthworm soil ingestion from changes in vertical bulk density profiles. *Eur. J. Soil Biol.* 120, 103574.
- Leue, M., Gerke, H.H., Godow, S.C., 2015. Droplet infiltration and organic matter composition of intact crack and biopore surfaces from clay-illuvial horizons. *J. Plant Nutr. Soil Sci.* 178, 250–260.
- Liu, T., Cheng, J., Li, X.D., Shao, M., Jiang, C., Huang, B., Zhu, X.C., Huang, S.H., Huang, Y.L., 2021. Effects of earthworm (*Amyntas aspergillum*) activities and cast mulching on soil evaporation. *Catena* 200, 105104.
- Ma, L., Shao, M.a., Fan, J., Wang, J., Li, Y., 2021. Effects of earthworm (*Metaphire guillelmi*) density on soil macropore and soil water content in typical Anthrosol soil. *Agric. Ecosyst. Environ.* 311, 107338.
- Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R., Chapin, F.S., 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431, 440–443.
- Metcalfe, D.B., Olofsson, J., 2015. Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO₂ exchange during the peak of the growing season. *Oikos* 124, 1632–1638.
- RCoreTeam, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Sabater, A.M., Ward, H.C., Hill, T.C., Gornall, J.L., Wade, T.J., Evans, J.G., Prieto-Blanco, A., Disney, M., Phoenix, G.K., Williams, M., 2020. Transpiration from subarctic deciduous woodlands: environmental controls and contribution to ecosystem evapotranspiration. *Ecohydrology* 13, e2190.
- Stockdill, S., Cossens, G., 1966. The role of earthworms in pasture production and moisture conservation. In: *Proceedings of the New Zealand Grassland Association*, pp. 168–183.
- Sundqvist, M.K., Sanders, N.J., Dorrepaal, E., Lindén, E., Metcalfe, D.B., Newman, G.S., Olofsson, J., Wardle, D.A., Classen, A.T., 2020. Responses of tundra plant community carbon flux to experimental warming, dominant species removal and elevation. *Funct. Ecol.* 34, 1497–1506.
- Thouvenot, L., Ferlian, O., Horn, L., Jochum, M., Eisenhauer, N., 2024. Effects of earthworm invasion on soil properties and plant diversity after two years of field experiment. *NeoBiota* 94, 31–56.
- 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. *Sci. Rep.* 4, 7.
- Vogel, H.J., Roth, K., 2001. Quantitative morphology and network representation of soil pore structure. *Adv. Water Resour.* 24, 233–242.
- Wackett, A.A., Yoo, K., Olofsson, J., Klaminder, J., 2018. Human-mediated introduction of geoeengineering earthworms in the Fennoscandian arctic. *Biol. Invasions* 20, 1377–1386.
- Xu, D., Li, Y., Fan, X., Guan, Y., Fang, H., Zhao, X., 2013. Influence of earthworm *Eisenia fetida* on *Iris pseudacorus*'s photosynthetic characteristics, evapotranspiration losses and purifying capacity in constructed wetland systems. *Water Sci. Technol.* 68, 335–341.