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Non-native species change the tune of tundra soils: Novel access to soundscapes of the Arctic earthworm invasion



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Acoustic indices of soil soundscapes are modulated by earthworm presence.
- Soils containing earthworms are significantly louder than soils without earthworms.
- Soil soundscapes are linked to earthwormmediated reductions of organic soil horizons.
- Acoustic techniques can track invasive earthworms and their re-engineering of soils.



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Soundscapes Earthworm invasion Ecosystem engineer Acoustic monitoring Soil structure Soil fauna Soil organic carbon Ecosystem disturbance Arctic ABSTRACT

Over the last decade, an increasing number of studies have used soundscapes to address diverse ecological questions. Sound represents one of the few sources of information capable of providing in situ insights into processes occurring within opaque soil matrices. To date, the use of soundscapes for soil macrofauna monitoring has been experimentally tested only in controlled laboratory environments. Here we assess the validity of laboratory predictions and explore the use of soil soundscape proxies for monitoring soil macrofauna (i.e., earthworm) activities in an outdoor context. In a common garden experiment in northern Sweden, we constructed outdoor mesocosm plots (N = 36) containing two different Arctic vegetation types (meadow and heath) and introduced earthworms to half of these plots. Earthworms substantially altered the ambient soil soundscape under both vegetation types, as measured by both traditional soundscape indices and frequency band power levels, although their acoustic impacts were expressed differently in heath versus meadow soils. While these findings support the as-of-yet untapped promise of using belowground soundscape analyses to monitor soil ecosystem health, direct acoustic emissions from earthworm activities appear to be an unlikely proxy for tracking worm activities at daily timescales. Instead, earthworms indirectly altered the soil soundscape by 're-engineering' the soil matrix: an effect that was dependent on vegetation type. Our findings suggest that long-term (i.e., seasonal) earthworm activities in natural soil settings can likely be monitored indirectly via their impacts on soundscape measures and acoustic indices. Analyzing soil soundscapes may enable larger-scale monitoring of high-latitude soils and is directly applicable to the specific case of earthworm invasions within Arctic soils, which has recently been identified as a potential

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Received 24 January 2022; Received in revised form 15 April 2022; Accepted 11 May 2022 Available online 24 May 2022 0048-9697/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/). threat to the resilience of high-latitude ecosystems. Soil soundscapes could also offer a novel means to monitor soils and soil-plant-faunal interactions *in situ* across diverse pedogenic, agronomic, and ecological systems.

1. Introduction

Soundscapes provide a rich source of information about landscapes and the myriad ecological processes occurring within them, thereby offering a non-invasive means of addressing ecological questions in otherwise inaccessible environments (Pijanowski et al., 2011; Sueur et al., 2014). The emergence of soundscape ecology and its explosive growth in recent years has resulted in an expanding toolkit of soundscape analysis techniques, permitting their application in increasingly diverse contexts and study systems (Pijanowski et al., 2021). In both terrestrial and underwater studies, soundscapes have been shown to be reliable indicators of biodiversity and species distributions (e.g., Rodriguez et al., 2014; Kaplan et al., 2015), making acoustic tools an appealing alternative to traditional survey methods that are often prohibitively expensive and time-consuming. Previous studies have also established clear connections between the geophysical setting and the soundscape, showing that diverse factors such as human land use, wildfire disturbance, and/or habitat fragmentation can affect soundscape properties (Fuller et al., 2015; Dooley and Brown, 2020; Gasc et al., 2018; Duarte et al., 2021). As soundscape scholarship continues to advance, the development of conceptual frameworks that incorporate acoustic monitoring into broader ecological research contexts is also projected to expand. This process will necessarily involve testing soundscape methodologies in different settings and for novel ecological applications.

Researchers have recently suggested one such novel context in which soundscape analyses could be applied: towards the monitoring of soil fauna and subsurface ecological processes. Acoustic signals could, in theory, supply direct and non-destructive information about macrofauna activity within opaque soil layers (Rillig et al., 2019), and thus may represent a yet untapped source of information about soil ecosystems. Such measurements may be particularly useful for monitoring soil engineering, *i.e.*, the movement, mixing, and/or ingestion soils, which can profoundly alter the physical properties of soils (Wilkinson et al., 2009). Furthermore, soundscapes offer a continuous sample rather than a temporal "snapshot" of the soil system, thereby capturing ongoing changes within dynamic soil communities that are otherwise challenging to detect using manual surveying techniques. Indeed, previous qualitative studies have demonstrated that underground acoustic recordings contain numerous identifiable sound sources, and have demonstrated links between acoustic complexity and taxa richness of soil fauna (Maeder et al., 2019). More promising are the results from a recent laboratory study showing that acoustic emissions (AEs) produced by earthworm movements can be used to track tunnel construction in real-time (Lacoste et al., 2018). These foundational studies illustrate the value of using acoustic analyses for investigations of soils; however, linking soil fauna activity or grain-by-grain soil movements with the production of AEs has yet to be tested experimentally in more complex outdoor environments.

Building upon preliminary research of soil acoustic monitoring, we consider the use of soil soundscapes for the in situ study of earthworms: well-known ecosystem engineers that occupy a functional role as keystone species in soils (e.g., Jouquet et al., 2006; Blouin et al., 2013). Earthworms are considered central to ecosystem functioning and mediate a wide range of soil processes including nutrient cycling and litter decomposition (Dexter, 1991; Wilkinson et al., 2009), making them frequent subjects of agroecological and pedological studies (Blouin et al., 2013). Although earthworms have long been considered to be key bioindicators of soil health (e.g., Blair et al., 1997; Linden et al., 1994) and are often lauded for enhancing plant growth in agricultural systems (e.g., Van Groenigen et al., 2014), there is burgeoning knowledge that soil engineers (i.e., earthworms, ants, termites) can also have profound deleterious effects on soils and ecosystems where they are non-native (Hendrix et al., 2008). One well-known example of this is across the formerly glaciated forest and tundra ecosystems of northern N. America and Northern Europe, which evolved without earthworms until several non-native peregrine species were recently introduced through human activities (Tiunov et al., 2006; Cameron et al., 2007; Hendrix et al., 2008). The ensuing earthworm invasions facilitate a striking array of diverse and often detrimental ecosystem changes by 'side-swiping' the trophic pyramid (Frelich et al., 2019), diminishing floral (Hale et al., 2006; Craven et al., 2017) and faunal biodiversity (Eisenhauer et al., 2007; Maerz et al., 2009; Jochum et al., 2021) and upending the established nutrient cycling regime (Resner et al., 2015; Ferlian et al., 2020).

Given the ongoing expansion of invasive earthworms into previously earthworm-free northern boreal and Arctic soils (Wackett et al., 2018), monitoring the distribution and effects of these soil-dwelling organisms is important for Arctic ecosystem conservation. Besides the potential for triggering the aforementioned ecological cascades, documenting and monitoring earthworm invasions at high latitudes is particularly urgent given that boreal and Arctic soils store a disproportionate amount of soil organic carbon (Hugelius et al., 2014; Jackson et al., 2017), which could greatly impact our planet's climate system if it were to be rapidly mineralized and released as greenhouse gases (Schuur et al., 2015). Notably, earthworms have also been found to increase greenhouse gas emissions (e.g., CO₂ and N₂O) from soils (Lubbers et al., 2013). Despite ever-improving models designed to predict earthworm distributions (e.g., Phillips et al., 2019), critical knowledge gaps persist (Cameron et al., 2018; Guerra et al., 2020): particularly in remote and poorly studied regions like the Arctic. Perhaps even more pressing, non-invasive techniques for monitoring soil fauna in situ remain absent, despite the crucial role soil biota play in regulating carbon cycling and ecosystem functioning at global scales (Wardle et al., 2004, Wall et al., 2008, Bardgett and Van Der Putten, 2014).

In light of the crucial need for novel tools to track and mitigate the effects of invasive earthworms and considering the promise of soundscape analyses in other ecological contexts, we suggest that soil acoustic monitoring may offer a viable path forward. In order to evaluate the robustness of this approach under realistic conditions, a crucial next step is to determine whether soil acoustic monitoring is possible outside of the laboratory. Here, we test for the first time whether information about earthworm activities is embedded within soil soundscapes recorded in outdoor environments. Specifically, we experimentally tested the following two hypotheses: *H1*) the quantity of AEs reliably indicates levels of earthworm activity; and *H2*) standardized acoustic metrics, such as acoustic indices or measurements of sound attenuation, are correlative with earthworm-driven shifts in Arctic soil morphologies and properties.

2. Methods

2.1. Study site and experimental design

We selected an ongoing mesocosm set-up in the experimental garden at the Abisko Scientific Research Station (68°21'17" N; 18°48'54" E) as the backdrop for our soil soundscapes study. The Abisko Research Station is situated ~200 km above the Arctic circle and is surrounded by sporadic permafrost and tundra (Betula var. tortuosa) with sub-alpine (Betula pubescens) birch forests typical of the Fennoscandian Arctic/alpine zone. Long-term climate monitoring at the station over the 30-year period between 1981 and 2020 indicates mean annual temperature and precipitation to be around 0.3 °C and 335 mm yr⁻¹, respectively. During the last glacial maximum, ice sheets extirpated native earthworms across vast high-latitude regions (Gates, 1982), and earthworms have only recently been re-introduced to these environments by humans (Tiunov et al., 2006; Cameron et al., 2007; Hendrix et al., 2008). Earthworm invasions into the Arctic are believed to be a relatively recent phenomenon. These incipient earthworm invasions are localized in nature and stimulated both by human-mediated introductions, as well as ongoing climate warming that continues to open up new niches (Wackett et al., 2018). The lack of studies from the Arctic makes it difficult to predict at what rates earthworms are expanding into

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the tundra, but studies from northern N. America suggest that earthworm expansions can result in near-total colonization of landscapes over a period of decades to centuries even in areas with relatively low populations densities (Fisichelli et al., 2013).

The outdoor mesocosm experiment contains 48 plots (50 imes 39 imes30 cm) of Arctic tundra vegetation and underlying soil monoliths randomly distributed between eight uniform raised beds, hereafter referred to as blocks (Fig. A1). Both the overlying vegetation and underlying soils (surface humus/O horizon layer plus mineral soil) were sampled from the nearby Kärkevagge valley (68°24'36" N; 18°19'11" E), located ~20 km to the west of Abisko, Sweden. The eight wooden raised beds (300 imes 160×40 cm) and all 48 experimental mesocosm plots were originally established during the fall of 2013 (see Blume-Werry et al., 2020 for details). The mesocosms contain either one of the two tundra vegetation types (*i.e.*, heath or meadow) typical of the Fennoscandian Arctic/alpine region. Heath plots are dominated by dwarf shrubs (i.e., Vaccinium myrtillus, Vaccinium vitis-idaea, Empetrum hermaphroditum), with variable abundances of graminoids (Festuca ovina, Deschampsia flexuosa). The meadow plots are rich in forbs (Saussurea alpina, Bistorta vivipara, Alchemilla glomerulans) and graminoids (Carex bigelowii, F. ovina, D. flexuosa).

As the main treatment effect, half of the mesocosms (*i.e.*, 12 plots from each vegetation type) were inoculated with environmentally relevant densities of earthworms during June 2017. The introduced earthworm populations included several endogeic species such as *Aporrectodea calignosa*, *Aporrectodea tuberculata*, *Aporrectodea trapezoides*, and *Aporrectodea rosea* (16–17 individuals per mesocosm), as well as the epigeic or epi-endogeic (Bottinelli et al., 2020) species *Lumbricus rubellus* (27–29 individuals per mesocosm). The other half of the plots was maintained as controls over the entire 4-year experimental period. The inoculated earthworm communities are typical of the non-native earthworm assemblage found at ongoing earthworm invasion chronosequences in close proximity (<12 km) to the Abisko research station (Wackett et al., 2018). For additional details on the different plant and earthworm mesocosm treatments and/or the effects of earthworms on Fennoscandian Arctic plant communities and soil morphologies, consult Blume-Werry et al. (2020) and Wackett et al. (2018), respectively.

For this soundscape study, we collected acoustic measurements from a selection of 36 mesocosm plots, including 18 with heath vegetation and 18 containing meadow vegetation. Within each vegetation type, nine mesocosms were treated with earthworms and nine remained earthworm free. All acoustic data used in this study were collected during September and October 2020. Excavation of the mesocosms directly after completion of the acoustic recording period revealed no findings of earthworms within control plots, whereas all earthworm treatment plots contained living earthworms.

2.2. Instrumentation

We used 36 Audiomoth acoustic loggers (Hill et al., 2018) to collect audio recordings. These devices were selected for their small size, low cost, and ability to record in rugged weather conditions, making our experimental design easily reproducible across a broad range of environments. Although previous investigations of variability between Audiomoth recorders have found negligible variation among units (Kitzes, 2021), we adapted calibration protocols used in previous studies of terrestrial and underwater sound levels (*e.g.*, Merchant et al., 2015; Gill et al., 2017) to ensure that recordings from different recording units were comparable (See Appendix).

2.3. Acoustic data collection

Recorders were installed in 36 mesocosm plots. To capture belowsurface recordings without altering the structure of the soil matrix, we placed recorders in rhizotron tubes that were inserted 10 cm below the soil surface during mesocosm construction. Rhizotron tubes are commonly used for root studies as well as investigations of earthworms (Cameron et al., 2014; Potvin and Lilleskov, 2017), so other researchers utilizing rhizotrons may easily replicate this technique. All recorders were positioned within rhizotron tubes in an identical manner, with microphones facing upwards. Entrances to the rhizotron tubes were sealed from the ambient environment by placing compacted sand around all sides of the mesocosm blocks, ensuring that at least >5 cm of sand acted as a barrier between the protruding rhizotron tubes and ambient environment. We collected continuous audio recordings (hereafter referred to as soundscape recordings) using a 32 kHz sampling rate and file lengths of 295 s. We collected 37 consecutive hours of acoustic data that were recorded simultaneously in all mesocosms. Table A1 contains a summary of the experimental design and acoustic data used in this study.

2.4. Preprocessing acoustic data

For all analyses, we only used signals between 50 Hz–5 kHz, as most ambient noise was within this range and some recording units produced intermittent self-noise above 6 kHz. One recording unit reported levels that were significantly different from all other recorders used in this study and was therefore excluded from subsequent analyses.

2.5. Acoustic analysis

We used several techniques commonly applied in terrestrial and underwater soundscape analyses to evaluate and identify metrics most useful for measuring soil soundscapes. Below we describe several spectral analyses that are commonly used in underwater and terrestrial acoustic contexts as well as playback experiments and standardized acoustic metrics often used during terrestrial acoustic applications.

2.6. Acoustic emission measurement

To test our first hypothesis, we quantified acoustic emissions (AEs), i.e., short peaks in amplitude produced by acoustic signals generated as earthworms create soil tunnels (Lacoste et al., 2018) or move within existing burrows. We employed a threshold detection approach, resembling the method used by Lacoste et al. (2018), which was modified for application in noisy outdoor environments. To account for changing levels of background noise, we applied adaptive thresholding by selecting five-minute windows of pre-processed audio data, applying Tukey running median smoothing to the time signal, and calculating the AE threshold as the median signal mean plus four standard deviations. We quantified the number of energy peaks exceeding this threshold for 5 min of audio data from every hour of data collection. To evaluate whether acoustic signatures emanating from earthworm geo-engineering correlated with earthworm presence, we used a mixed model (i.e., lme4 (Bates et al., 2007)) within the R statistical environmental (R Core Team, 2020) with number of AEs as the response variable, vegetation, and earthworm treatment as fixed effects, and mesocosm number, block number, and time (i.e., hour) as random effects.

2.7. Spectral analyses

To visualize below-surface sound levels and assess temporal trends in soundscapes, we first calculated long-term spectral averages for each mesocosm using 5 Hz/30 s bins following the approach described by Wiggins et al. (2010). To quantify variation in sound levels at different frequencies, we calculated the power spectral density (PSD) for each mesocosm using Welch's method (Welch, 1967) with a hamming window with zero overlap and 1 Hz/5 min bins. This produced one-sided PSD distributions for every 5 min sound file. For each sound file, we then calculated the sound pressure level (SPL) for 500-Hz bands between 0 and 5 kHz by summing the PSD values across each frequency band before converting to dB (sensu Daly and White, 2021). When calculating SPL in the 0-500 Hz band we excluded values below 50 Hz. Band analysis of SPL reduced the dimensionality of the data, while still permitting distinction between power present at frequencies below 2 kHz, which typically comprises geophony and/or anthropogenic noise, and power present at higher frequencies, which often includes biological noise, e.g., signals from birds or insects (Pijanowski et al., 2011). To determine if vegetation or worm presence affects the power level

at different frequencies, we averaged SPLs from the first 5 min of every hour of data collection (N = 37) to find mean SPL band values for each mesocosm and used a linear mixed model with SPL values as a response variable and included vegetation type, worm treatment, and frequency band as fixed effects. To account for slight differences in mesocosm positioning we included mesocosm number, block number, and time as random effects.

To evaluate the variation in power at different frequencies, we calculated the empirical probability density (EPD; Parks et al., 2009; Merchant et al., 2013) from the PSD estimates obtained in the previous step. The EPD reflects the distribution of power levels measured in each frequency bin throughout the recording period and thus describes the likelihood of the ambient noise level occurring at a particular value for a given frequency. EPD can identify variation in power levels at particular frequencies, making it a useful tool for identifying intermittent signals that consistently occur within the same frequency range. For example, high EPD values at certain frequencies could indicate the presence of vocalizing animals and/ or recurring anthropogenic noise. To investigate differences in ambient power levels among different vegetation types and worm treatments, we calculated the mean EPD for each vegetation-worm treatment combination and identified the 1st, 5th, 50th, 95th, and 99% percentiles (Curtis et al., 1999) for each group. Percentiles are the power level at which a certain proportion of samples fall below that value, and within this context they provide approximate estimates of the noise floor, median noise levels, and upper boundary of noise within each individual mesocosm. All spectral analyses were implemented using the Matlab IoSR toolbox (Hummersone, 2021) and all statistical analyses were conducted in R (R Core Team, 2020) using the lme4 package (Bates et al., 2007).

2.8. Soil sampling and laboratory measurements of soil properties

We collected soil samples (N = 36; n = 245) laterally by horizon and depth interval from each of the 36 mesocosm plots to analyze basic soil physiochemical properties in the lab. After completing the acoustic recordings, we removed the mesocosm plots from each block and opened up one side of the polypropylene box to expose the vertical soil profile. We photographed each profile and observed visual differences in soil morphology between the worm and vegetation treatments (Fig. A2). We described the genetic soil horizons within each profile based on visual assessment of morphological characteristics. Visual inspection was validated by a quantitative approach in which we cut cubes of known width out from the organic (O) and mineral topsoil (A) and subsoil (B) horizons identified in each mesocosm (N = 36). Cubic samples (n = 245) also permitted back-calculation of the net volume of each sample for subsequent measurements of soil properties.

We transported samples back to the laboratory and dried them at 50 °C for 10 days until they achieved a constant weight. We measured the mineral matter content of each individual sample (n = 245) using a standardized loss-on-ignition protocol (Soil Survey Staff, 2014). To obtain precise measurements of soil bulk density (ρ_b), we cut cubes of known dimensions out from different horizons/depth intervals along the exposed soil profiles to quantify the volume of soil sampled from each layer (as outlined above). We then removed roots by hand and passed the samples through a 2 mm sieve to remove coarse fragments (>2 mm), and then weighed each sample to obtain ρ_b values for the <2 mm fraction of interest. We validated our initial genetic horizon designations against our quantitative mineral matter (MM) measures, using the USDA taxonomic criterion to designate topsoils as either A (higher in mineral matter) or O (decomposing organic matter with <40 wt% mineral mass) horizon samples. The porosity (%) of each sample was calculated using the ρ_b measurements and average particle density of soil components relative to the volume of soil samples (Blake, 1965). See the Appendix for additional details on soil measurements and ensuing calculations related to soil properties.

For the 36 mesocosms, we calculated profile-integrated (*I*) values of MM (%) content for the upper 10 cm of the soil column using the expression:

$$I = \frac{\sum_{n=1}^{N} \rho_b * \Delta h_n * M M_{n, < 2mm}}{\sum_{n=1}^{N} \rho_b * \Delta h_n} \tag{1}$$

where *N* represents the number of soil horizons/samples within the upper 10 cm, the subscript *n* indicates the *n*th soil layer, ρ_b is bulk density (g/cm³), Δh_n indicates the thickness of horizon/layer *n*, and $MM_{n,<2mm}$ represents the MM content (in wt%) of the *n*th soil layer. We used a simplified expression to calculate profile-integrated values of ρ_b and soil porosity (%), as this simply involved a summation of the weighted (based on layer thickness) bulk density or porosity values down to 10 cm soil depth. We excluded all soil measurements from samples collected below 10 cm depth because we assumed that subsoils would have minimal influence on soundscape properties, given that the rhizotron tubes (and thus the recording units collecting acoustic data) were buried at 10 cm depth.

To quantify the amount of earthworm soil engineering that had occurred during the experiment, we used the values of MM, ρ_b , and porosity (%) collected from each sample (n = 245) to calculate the range (*i.e.*, maximum variation, or V_{max}) of each soil property within each mesocosm (N = 36) using the expression below:

$$MM V_{max,N} = MM_{max,0-10cm} - MM_{min,0-10cm}$$
(2)

where *MM* V_{max,N} represents the range or maximum variation in MM content (%) within the upper 10 cm of soil within mesocosm *N*, *MM*_{max,0-10cm} denotes the maximum MM (%) value for samples collected from 0 to 10 cm depth, and *MM*_{min,0-10cm} represents the minimum MM (%) value for soils within the upper 10 cm of the soil profile. This analysis permitted an objective assessment of the effects of earthworm engineering, as earthworms are known to increase vertical mixing rates and translocate soil materials within the depth profile, which could impact the degree to which soil properties differ between upper and lower soil layers. Specifically, in line with the conceptual framework proposed by Jouquet et al. (2006), we hypothesized that earthworm activities would homogenize the upper soil profile, and thereby decrease the range (*i.e.*, lower the V_{max}) for MM, ρ_b , and soil porosity within earthworm-occupied mesocosm plots.

To evaluate the effects of earthworm communities on soils, we applied eight separate linear mixed models with the following unique response variables: thickness of the O and A soil horizons, profile-integrated values for MM, ρ_b , and soil porosity (derived from Eq. (1)), and the calculated ranges (*i.e.*, V_{max}) of MM, ρ_b , and soil porosity (derived from Eq. (2)). In each model, we used worm treatment and vegetation type as fixed effects and block number as a random effect. For each model, we iteratively determined whether or not to include an interaction term between worm treatment and vegetation type by using the Akaike Information Criterion for model comparison, in order to optimize model fit while retaining the maximum available degrees of freedom. To account for the non-Gaussian distribution of O horizon thickness measurements, we transformed all O horizon thickness values using the expression $\log_{10} (x + d) - c$, where $c = \log_{10} dc$ $(\min(x)), \min(x) =$ the lowest non-zero *x* integer, and *d* = inverse log₁₀ (c), which preserves both zeros and the original distribution of values within the dataset (Hale et al., 2005a). All other soil properties of interest displayed normal distributions, so transformations were not necessary.

2.9. Relationship between soil properties and soil soundscapes

To investigate the relationship between soil soundscapes and soil characteristics, we first selected three frequency bands of interest to include in our analysis: 50–500 Hz, 1.5–2 kHz, and 3.5–4 kHz. These low, medium, and high frequency bands are expected to contain signals produced by geophysical, anthropogenic, and biological sources, respectively. We used a multivariate regression approach with SPL values for each frequency band as response variables and thicknesses of the O and A horizons – as well as profile-integrated (see Eq. (1)) bulk density (ρ_b), porosity (P_o), and mineral mass (*MM*) values – as the explanatory variables. To evaluate the effects of soil biota and vegetation on soil properties, we conducted a secondary analysis using a series of regression models. For each of these models, we used one of the aforementioned soil measurements as a response variable and included vegetation type and worm treatment as explanatory variables. Additionally, to further explore the connection between sound attenuation and soil properties, we conducted a small number of playback tests using known source signals (see Appendix for details on the playback experiments and results).

2.10. Acoustic indices

We measured six standardized acoustic indices that are commonly used to analyze terrestrial soundscapes, following the recommended guidelines from Bradfer-Lawrence et al. (2019). These indices included the Acoustic Complexity Index (ACI; Pieretti et al., 2011), which quantifies the change in power within each frequency band between adjacent time samples; Acoustic entropy (H; Sueur et al., 2008), which represents the information entropy (Shannon, 1948) in the spectrum of an acoustic signal and ranges between 0 for a pure tonal signal and 1 for random noise; Acoustic Evenness (AEven; Villanueva-Rivera et al., 2011), which measures how evenly power is distributed across frequencies; the Acoustic Diversity Index (ADI; Villanueva-Rivera et al., 2011), which uses the Shannon Diversity Index (Shannon, 1948) to assess variation across frequency bands; the Bioacoustic Index (BIO; Boelman et al., 2007), a measure of the number of occupied frequency bands above 2 kHz and the intensity of power in these bands; and lastly, the Normalized Difference Soundscape Index (NDSI, Kasten et al., 2012), which evaluates relative differences in power between 1 and 2 kHz and power above 2 kHz. Because acoustic indices are not influenced by small differences in microphone sensitivity, we calculated all indices from acoustic data that had not been adjusted using correction coefficients. We used the first 5 min recorded at the beginning of every hour to calculate indices using the R packages seewave and sound ecology (Sueur et al., 2008; Villanueva-Rivera et al., 2018). We evaluated differences in acoustic indices among different vegetation types and worm treatments using separate linear mixed models (lme4) with vegetation and worm treatment as fixed effects and mesocosm number, block number, and time as random effects.

3. Results

3.1. Earthworm impacts on ambient belowground soundscapes

Most of the power in our soil recordings occurred below 2 kHz (Fig. 1; Fig. A3). Ambient sound levels were significantly higher in low frequency bands for all mesocosms, regardless of vegetation type or worm treatment (Fig. 1; Fig. A3). Signals in this range included noise from wind and/or distant anthropogenic noise (*e.g.*, vehicle traffic and trains passing on a distant railway), which penetrated through the soil matrix down to at least the sampling depth recorded here (10 cm). We also observed occasional noise from wind above 2 kHz, as well as a small number of bird calls that were visible in spectrograms between 5 and 10 kHz.

3.2. Hypotheses testing

In contrast to our first hypothesis (*H1*), we found no effects on acoustic emissions in response to the earthworm treatment (Fig. A4). Although we did detect higher numbers of AEs in mesocosms containing earthworms, this difference was not statistically significant (LMM: worms: t = -0.2, p = 0.85, vegetation: t = -0.32, p = 0.75, worms * vegetation: t = 1.7, p = 0.1; Fig. A4). In line with our second hypothesis, soils containing earthworms had louder below-surface soundscapes than soils without worms (Fig. 1a, b), although this difference was only significant for mesocosms with meadow vegetation (LMM: worms: t = 0.42, p = 0.68, vegetation: t = 0.56, p = 0.59, worms * vegetation: t = 2.4, p = 0.016, frequency: t = -26.12, p < 0.0001). Empirical probability density plots showed that the highest levels of variability in PSD levels were below 1 kHz (Fig. A5). We also observed a slight increase in PSD variability between 2 and 3.5 kHz in mesocosms containing earthworm communities.

Three of the six acoustic indices we measured showed significant differences among soils due to earthworm treatments (Figs. 2a–c, A6). The bioacoustic (BIO) and acoustic complexity indices (ACI) were significantly higher in soils under heath vegetation, though for both metrics this



Fig. 1. Ambient subsurface noise levels throughout the recording period, represented as a) median power spectral density (PSD) for each of the vegetationearthworm treatment groups; and b) sound pressure level (SPL) within 500-Hz bands for the four vegetation-treatment groups.

effect was reduced when worms were present (LMM: ACI: vegetation: t = -4.24, <0.001; worms: t = -0.19, p = 0.86; interaction: t = 12.3, p < 0.001; BIO: vegetation: t = -4.2, p < 0.001; worms: t = -1.95, p = 0.09; interaction: t = 3.44, p < 0.001). The normalized difference soundscape index (NDSI) was higher in soils that contained worms, but this difference was only significant under meadow vegetation (LMM: vegetation: t = 0.78, p = 0.43; worms: t = 1.86, p = 0.11; interaction: t = 1.93, p = 0.05). Acoustic evenness (AEven), acoustic entropy (H), and the acoustic diversity index (ADI) did not vary significantly among treatments (LMM – p > 0.05).

We found that the bulk density, porosity, and mineral mass of soils were positively correlated with subsurface noise levels (Table 1). For example, PSD levels in the low, medium, and high frequency bands were significantly higher in more dense, porous, and/or mineral-rich soils (Table 1). Moreover, sound levels in the mid- and high-frequency bands were positively correlated with thicker A horizons (Table 1). The observed earthworm loudening effect coincided with a significant reduction in O horizon thickness (Fig. 3a) and concomitant expansion of the A horizon (Fig. 3b), which was particularly pronounced under meadow vegetation (Figs. 3a, b, A6). Earthworms significantly decreased the range (i.e., V_{max}) in porosity and bulk density values within the upper 10 cm of soil under both vegetation types (Fig. 3c, d; Table 2). Heath soils had a significantly larger difference in MM content between the upper and lower soil layers than meadow soils, and earthworm presence amplified this effect by further diminishing the MM V_{max} of meadow soils (Fig. 3e; Table 2). While earthworms significantly affected the range (i.e., Vmax) of these soil properties of interest, they did not significantly affect the profile-integrated bulk density, porosity, or mineral mass values: although we note that meadow soils containing



Fig. 2. Acoustic indices measured from soil soundscapes, including the: a) normalized difference soundscape index, or NDSI; b) acoustic complexity index, or ACI; and c) bioacoustic index, or BIO. Significant differences are denoted by * (P < 0.05) and *** (P < 0.001).

earthworms did have higher bulk density values than all other soils. In addition, heath soils had significantly lower net bulk density and higher net porosity and mineral content than meadow soils, irrespective of earthworm

Table 1

Results table from multiple regression models evaluating the relationship between soil physical characteristics and sound pressure levels (SPL) in low (50–500 Hz), mid (1.5-2 kHz) and high (3.5-4 kHz) frequency bands.

Response variable	Fixed effect	Estimate	SE	t	р
SPL low frequency	Intercept	-460.94	113.0	-3.47	< 0.01
	A horizon thickness	0.23	0.19	1.22	0.23
	O horizon thickness	0.56	0.39	1.44	0.16
	Bulk density	181.16	55.78	3.25	< 0.01
	Porosity	4.04	1.31	3.07	< 0.01
	Percent mineral mass	0.52	0.14	3.82	< 0.001
SPL mid frequency	Intercept	-360.44	113.13	-3.19	< 0.001
	A horizon thickness	0.32	0.16	2.02	0.05
	O horizon thickness	0.29	0.33	0.90	0.38
	Bulk density	132.2	47.44	2.78	< 0.01
	Porosity	2.95	1.11	2.63	0.01
	Percent mineral mass	0.44	0.12	3.80	< 0.001
SPL high frequency	Intercept	-306.33	95.36	-3.2	< 0.01
	A horizon thickness	0.34	0.14	2.45	0.02
	O horizon thickness	0.14	0.28	0.51	0.62
	Bulk density		39.99	2.66	0.01
	Porosity	2.36	0.94	2.50	0.02
	Percent mineral mass	0.42	0.01	4.19	< 0.001

P-values of 0.05 or less were considered to be statistically significant.

presence/absence (Table A2). A conceptual diagram summarizing the effects of vegetation and earthworm activity on soil properties and subsurface soundscapes is presented in Fig. 4.

4. Discussion

4.1. Relationship between earthworm activity and acoustic emissions (AEs) in soils

Sounds within soils have been suggested to contain information of crucial importance for the next generation of soil monitoring programs (Rillig et al., 2019), but until now these theoretical suggestions have yet to be rigorously tested in the field. While acoustic emissions (AEs) have been shown to work as a proxy for detecting earthworm burrowing under simplified laboratory conditions (Lacoste et al., 2018), we found no evidence for the use of AEs as a proxy for tracking earthworm activities in situ. That is, in contrast to our first hypothesis, we found no significant difference (P >0.05) in AEs emanating from soils containing earthworms relative to those emitted from control plots. We note that a directional hypothesis could in theory be motivated, considering the previous findings by Lacoste et al. (2018). Under these criteria, we would then find that AEs were significantly higher (P < 0.1) in the earthworm treatments under meadow vegetation. However, because we conducted the first non-laboratory study of this kind and lacked true justification for a one-tailed test, we conclude that our first hypothesis was not supported by our experiment.

We did, however, detect numerous acoustic signals within the soil as well as continuous background noise in all recordings. Although we cannot fully



Fig. 3. The effects of vegetation and earthworm geo-engineering on soil morphology and select physiochemical properties, including: a) O horizon thickness; b) A horizon thickness; c) the range (V_{max}) in soil porosity; d) the range (V_{max}) in bulk density; and e) the range (V_{max}) in percent mineral mass. The V_{max} values indicate the difference between the maximum and minimum values of the measured soil characteristic within the upper 10 cm of the soil column; lower V_{max} values thus signify increased homogenization of the soil profiles (see Eq. (2) in text). Significant differences are indicated with * (P < 0.05), ** (P < 0.01), *** (P < 0.001), and **** (P < 0.001).

resolve all factors contributing to soil noise, we can point towards several likely sources. In our study, soil soundscapes mainly included geophony – *i.e.*, sounds from the natural environment – and anthrophony – *i.e.*, human-generated noise – that could have contributed to impulsive acoustic signals detected within the recordings. Within all mesocosms, wind and occasional

cars passing by on a distant roadway produced relatively constant noise below 1 kHz, which likely masked any low amplitude signals that might have been generated by soil biota. Wind noise may include the sounds of vegetation moving above the surface, as well as subsurface wind-induced root movement: both of which may generate the AEs detected by our sensors

Table 2

Results table from linear mixed models evaluating the effects of vegetation and earthworms on soil morphological (i.e., horizon thickness) and physiochemical properties.

Response variable	Fixed effect	Estimate	SE	t	р
O horizon thickness (cm) ^a	Intercept	0.60	0.04	15.07	< 0.0001
	Worm treatment	-0.01	0.06	-0.12	0.906
	Vegetation	-0.15	0.06	-2.76	0.010
	Interaction ^b	-0.39	0.08	-4.97	< 0.0001
A horizon thickness (cm)	Intercept	2.13	0.91	2.35	0.026
	Worm treatment	3.77	1.17	3.22	0.018
	Vegetation	2.20	0.76	2.90	0.007
B horizon thickness (cm)	Intercept	10.13	1.06	9.60	< 0.0001
	Worm treatment	-2.03	1.36	-1.49	0.187
	Vegetation	1.11	0.89	1.25	0.222
Porosity (%) range	Intercept	36.33	2.40	15.13	< 0.0001
	Worm treatment	-7.59	2.77	-2.74	0.034
	Vegetation	-0.81	2.77	-0.29	0.771
Bulk density (g cm $^{-3}$) range	Intercept	0.99	0.06	15.53	< 0.0001
	Worm treatment	-0.22	0.07	-2.98	0.025
	Vegetation	-0.01	0.07	-0.18	0.856
Mineral mass (%) range	Intercept	64.18	3.34	19.21	< 0.0001
	Worm treatment	0.01	4.73	0.002	0.998
	Vegetation	-10.47	4.73	-2.22	0.036
	Interaction	-24.23	6.68	-3.63	<0.001

P-values of 0.05 or less were considered to be statistically significant.

^a O horizon thicknesses were log transformed (*b*) using the expression $b = \log_{10} (x + d) - c$ where $c = \log_{10} (\min(x))$, $\min(x) =$ the lowest non-zero *x* integer, and d = inverse log₁₀ (*c*).

^b Interaction terms were removed and models re-run with only main effects (*i.e.*, worm + vegetation) for all models where no interaction term is listed in the results table above.



Fig. 4. Conceptual diagram highlighting the sources of ambient sound (anthrophony – black arrows; geophony – blue arrows; biophony – orange arrows) and their differential attenuation through Arctic soils under different vegetation types and with/without earthworm communities. The thickness of the arrows correlates to the degree of matrix attenuation by soils, with thinner arrows (quieter soil soundscape) representing greater attenuation and thicker arrows (louder soil soundscape) denoting less attenuation of ambient sounds. The porosity V_{max} depth profiles for each vegetation and treatment type are shown next to the soil profiles depicting representative soil horizons, which have been scaled to their average thickness for each treatment (down to 10 cm depth). Genetic soil horizons are denoted by small letters (O, A, B) in the upper right corner of the shaded (white/grey) boxes. a) Highly porous heath soils without earthworms (far left) have a large range (*i.e.*, V_{max}) in porosity values, whereas b) heath soils containing earthworms have a significantly lower V_{max} porosity. c) Meadow soils without earthworms are less porous than heath soils in general, but have a high V_{max} porosity, while d) meadow soils with earthworms (far right side of figure) have lower net and V_{max} porosity. Meadow soils with earthworms are also significantly louder overall than meadow soils where earthworms are absent. All soundscapes were recorded continuously using Audiomoth acoustic devices embedded inside rhizotron tubes that were buried at 10 cm soil depth for all treatments.

and may vary with vegetation type, as the differences in heath and meadow plant morphology are likely to transmit distinct structural sounds into the subsurface. Gusts of wind and noise from trains passing on a distant railway also created occasional bursts of broadband noise, which appear as vertical streaks in the spectrograms depicted in Fig. A3.

The earthworm densities within our mesocosm treatments are typical of earthworm invaded soils in adjacent (~10 km) sub-alpine Arctic birch forests (Wackett et al., 2018), as well as within invaded North American hardwood (Hale et al., 2005a; Suarez et al., 2006) and boreal (Eisenhauer et al., 2007) forests. Therefore, we expect our results to be representative of a broad range of environments with ongoing and incipient earthworm invasions. We cannot exclude the possibility that where higher earthworm abundances (*i.e.*, upwards of 300 m⁻²) occur in agricultural soils (e.g., Simonsen et al., 2010; Bertrand et al., 2015) and/or other soil environments. their vigorous mixing and burrowing may generate AEs that are detectable above ambient environmental noise. Alternatively, the low temperatures (mean 5 °C) at the time of sampling during late fall (Sept-Oct) could also mean that earthworm activities were diminished during the recording period. Finally, it is possible that our recording devices and configuration were simply not sufficiently sensitive to detect earthworm movements: earthworm-induced AEs may not be loud enough to pass through rhizotron tubes, for example. In all likelihood, it is some combination of these factors. We also cannot rule out the possibility that earthworm movements in soil still create signals that are audible to other soil biota, given that soundscapes

are inherently subjective and dependent on the receiver's perception. For example, some nematode species have been shown to detect low amplitude vibrations at low frequencies (*e.g.*, Holbrook and Mortimer, 2018). Thus, we cannot exclude the possibility that earthworms both contribute to and perceive acoustic signals that went undetected in our study.

4.2. Relationship between soil soundscapes and soil morphology

While our first hypothesis appears invalid (unless a directional hypothesis is applied), our second hypothesis, suggesting that acoustic measurements collected from soil soundscapes can be used to detect earthworm presence, was well supported by our findings. This is, to our knowledge, the first empirical evidence highlighting that earthworms alter the soundscapes of soils in outdoor environments. The observed differences in subsurface acoustic environments appear linked to earthworm-induced changes in soil characteristics, suggesting that earthworms engineer not only their physiochemical environment but also their acoustic surroundings. This novel finding also emphasizes that monitoring subsurface soundscapes may function as a non-destructive proxy for soil macrofauna activity. Importantly, the soundscape functions as an indirect proxy in this context, rather than relying on AEs directly linked to earthworm burrowing. Because the timeline of our experiment is well constrained, we can infer that earthworm activities accumulated over four years (or less) are enough to significantly alter the soundscape of Arctic soils, perhaps through the creation of tunnels and macropores that allow for ambient noise to more easily penetrate soils or from AEs produced as tunnels and macropores collapse. As mentioned above, earthworm invasions into formerly glaciated forests have been shown to dramatically affect soil morphology – *e.g.*, O and A horizon thicknesses – within several growing seasons (Hale et al., 2005b; Lyttle et al., 2015; Frelich et al., 2019; Ferlian et al., 2020 for review), with these effects compounding as the duration of invasion increases. This would suggest that soundscape analyses can likely be used to detect earthworm arrivals and their ensuing impacts on formerly glaciated forest soils and ecosystems over annual time scales under field conditions.

Earthworm effects on soil soundscapes were also dependent on vegetation type, which should be taken into consideration when using soundscapes for biomonitoring purposes. Earthworms almost entirely eliminated the O horizon (humus) in meadow - but not heath - soils (Fig. 3a), demonstrating that the degree to which earthworms alter soil structure and biogeochemistry is mediated by vegetation (Fig. 3; Table 2). This key difference appears to explain why both heath and meadow soils with worms were louder, but meadow soils with worms exhibited more pronounced differences in noise levels (Fig. 1). It is possible that the earthworm-mediated reduction in O horizon thickness (Fig. 3a) could have slightly altered the distance between the ground surface and rhizotron tubes (buried at 10 cm depth) over the experimental period. However, based on estimated annual earthworm casting rates from around Europe (Feller et al., 2003), it is unlikely that a pronounced change in depth would have occurred over only 4 years. Previous studies have suggested that heath and meadow vegetation have distinct root growth phenology (Schwieger et al., 2018) and that earthworms differentially affect fine-root phenology under these two vegetation types (Blume-Werry et al., 2020). Roots may affect underground sound propagation, and earthworm impacts on root systems may contribute to the observed interaction effect between our earthworm treatment and vegetation type.

The notion that surface sounds experience less attenuation when passing through bioturbated meadow soils was also supported by a small playback experiment (see Appendix). Interestingly, because earthworminduced changes to the soil matrix allowed more aboveground noise to permeate meadow soils, *in situ* acoustic detection of sounds from soil biota (*i.e.*, AEs) may in turn be made more challenging by their presence. This changing matrix effect may also help explain why the data presented by Lacoste et al. (2018) indicates that the linkage between acoustic emissions and earthworm burrowing faded after ten days.

Utilizing acoustic indices offered further insights into the coupled processes through which vegetation and earthworm presence can filter ambient environmental sounds in soils. Our finding that the normalized difference soundscape index (NDSI) was higher in meadow soils containing earthworms (Fig. 2a) indicates that frequency bands above 2 kHz consistently contained more power than lower frequency bands, in agreement with the results shown in Fig. 1. Our finding that the acoustic complexity index (ACI) was higher in heath soils indicates that signals above 2 kHz exhibited more temporal variability in heath plots (Fig. 2b), perhaps because high frequency signals can transmit more easily through highly porous heath soils (Table A2). We also observed higher ACI levels in meadow soils with earthworms, further supporting the notion that soil structure influences acoustic transmission at higher frequencies. Similarly, the bioacoustic index (BIO) was higher in heath soils (Fig. 2c), indicating that these soundscapes had more variation at frequencies above 2 kHz and permitted less transmission of low frequency signals than meadow soils. This effect was reduced in heath soils with worms, meaning that intermittent signals above 2 kHz were less common in these soils. Together, these results collectively suggest that earthworms may modify the composition and intensity of soil sounds by changing soil structure; for example, by altering the interactions between organic and mineral matter and/or modifying the spatial distributions and dimensions of soil pore networks.

4.3. Ecological significance

Our results suggest that non-destructive acoustic monitoring can detect the 'geo-engineering' activities of earthworms, which is a consequence of the complex interactions between earthworm bioturbation, the structural properties of soils, and vegetation. Soundscape analyses may, therefore, enable belowground tracking of earthworm activities or complement existing monitoring programs in a wide variety of environments. Monitoring earthworm presence and activity is important from a food-security perspective, as improved earthworm health can increase crop production by up to 25% (Van Groenigen et al., 2014). Across formerly glaciated landscapes, detecting and monitoring earthworms through time is becoming increasingly critical from a conservation perspective, given the profound (and often deleterious) effects of earthworm invasions into northern forest ecosystems (Craven et al., 2017; Wackett et al., 2018; Frelich et al., 2019). Our findings suggest that soil chemical and/or morphological transformations can likely be detected through relative differences in soundscapes on daily, seasonal, or annual timescales. This would indicate that soundscapes hold great potential for long-term monitoring programs of earthworm invasions over larger spatial and temporal scales.

Perhaps more importantly, soil soundscapes offer a new potential means for studying critical but methodologically challenging soil parameters, such as the size, distribution, anisotropy, and connectivity of the soil pore network. As highlighted in a recent review (Baveye, 2021), there remains a near complete 'bypass' of the study of soil pores and their myriad properties and configurations, despite their widely recognized importance in soil functioning. At least part of this research 'bypass' stems from the methodological challenges associated with studying soils – and more specifically soil pores – *in situ:* an ongoing problem that soundscape analyses are poised to help address. By monitoring soil processes and their ecological communities *in situ,* soundscapes may also expand our capacity to explore dynamic plantsoil-macrofaunal interactions, which are often difficult to observe or disentangle when soils and their associated biota are extracted from the field and studied in isolation using conventional laboratory methods.

Our results suggest that earthworms modify soils in a way that reconstructs their own acoustic environment. Given that some nematode species have been found to sense acoustic signals through their skin (Iliff et al., 2021), while other earthworm species (Diplocardia mississippiensis) react strongly to sounds generated by digging by predators (Catania, 2008), it may be possible that earthworms might benefit from making soils louder (i.e., easier to hear predators coming). Interestingly, owing to these same earthworm-driven changes to the soundscape, in situ detections of AEs from soil biota may in turn be made more challenging by their presence. This apparent coupling between earthworm activities and changing matrix effects may explain why the data presented by Lacoste et al. (2018) suggest the linkage between AEs and burrowing faded over a weekly time-scale. Future soundscape studies may aim to more directly test these exciting hypotheses, along with other outstanding questions about the myriad interactions between soils, plants, and fauna: all of which will benefit from the ability to non-destructively monitor belowground communities and processes through time.

5. Conclusion

Our results suggest that direct monitoring of earthworm activities in soils through the detection of AEs - as previously indicated by controlled laboratory studies - is challenging. However, we found that Arctic soil soundscapes are shaped by interactions between plants and soil biota, and that earthworm actions can be sensed indirectly using acoustic methods due to their structural and/or physiochemical alterations of the soil matrix. Earthworms seemingly make Arctic soils louder, which may further complicate the in situ detection of AEs sourcing from earthworm activities in outdoor contexts. Although it remains to be seen whether such effects are transient and/or may differ in settings with distinct ambient soundscapes, this study provides the first empirical evidence that soil soundscapes reflect earthworm-induced changes to soil properties. Lastly, these findings suggest that soil soundscapes may offer an effective and inexpensive means for monitoring earthworm invasions and their concomitant effects on soil properties over large spatial and temporal scales. Our findings highlight the untapped promise of using soil soundscapes as a non-destructive

belowground monitoring tool, with potential applications across a diverse range of pedogenic, agronomic, and ecological systems.

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CRediT authorship contribution statement

S.C. K, J.K.W., J.K., A.A.W, K.Y., and T.C. conceived and planned the experiments. A.A. W, H.J., J.K., and S.C.K. carried out the experiments. All authors contributed to the interpretation of the results. S.C.K. took the lead in writing the manuscript and all authors

Appendix A

Microphone calibration

participated in writing, reviewing, and editing the text. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

Declaration of competing interest

The authors declare that they have no financial interests or personal relationships that influenced the work reported here.

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To calibrate recorders, we measured the amplitude and frequency responses of microphones by conducting a series of playback tests in a sealed laboratory space containing sound-absorbing panels to reduce reflection. The playback signal included four computer-generated wav files of pure sinusoidal tones at 440 Hz, 1 kHz, 2 kHz, and 5 kHz, as well as two broadband signals that we measured as having an amplitude between 70 and 75 dB at a distance of 1 m from the JBL Flip 5 speaker using an NM102 Sound level meter (A weighting, peak response). All playback sounds had a duration of 5 s, 16-bit resolution, 44.1 kHz sampling rate, and were normalized to ensure that signals had equal amplitude. All recorders were programmed to record at a sampling rate of 32 kHz and gain levels were set to high (i.e., 32 dB; Hill et al., 2019), and the recording units were arranged adjacent to one another on a flat surface with microphones facing upwards. We then positioned a JBL Flip 5 Bluetooth speaker 1 m above the recording units and played the calibration signals to all recorders simultaneously. The amplitude of the playback signals was measured as between 70 and 75 dB 1 m from the speaker using an NM102 Sound level meter (A weighting, peak response). To quantify variation in sensitivity among recorders, we first used Raven Pro 1.6 (Cornell Center for Conservation Bioacoustics) to select five consecutive 1 s segments of each playback signal. We then calculated the root mean squared (RMS) of sound pressure levels for each audio segment and derived the median RMS for each calibration signal on each recording unit, as well as the mean RMS for each calibration signal across the 36 recording units. We observed that variations among RMS measurements for each playback signal were negligible within recording units, but in some cases varied between units. To eliminate this error, we used mean RMS values for each calibration signal as a reference and calculated correction coefficients that permitted each recorder to report identical measured RMS values for each calibration signal. We calculated the mean correction coefficient for each recording unit and multiplied all recorded time signals by this value for all subsequent acoustic processing and measurements (mean \pm SE of correction coefficients (N = 36): 1.07 \pm 0.042). To further ensure that no underlying similarities were present among recorders used in the same treatment groups, we evaluated differences between recording units using a linear mixed model with uncorrected RMS as a response variable and soil type (heath vs. meadow) and treatment (worms vs. no worms) as fixed effects, and playback signal type as a random effect. We found no evidence for significant differences among recorders used within the same soil type or treatment groups (LMM: soil: t = -1.35, p = 0.18, treatment: t = -1.07, p = 0.28, interaction: t = 0.72, p = 0.47). All RMS calculations were made in MATLAB 2021a (MathWorks Inc., Natick, MA).

Soil sampling and determination of soil properties

After drying soil samples in the laboratory, we weighed each sample as an initial measurement of soil bulk density (ρ_b). We then lightly crushed the samples and picked roots from each, then sieved the soil samples to <2 mm to quantify their coarse fragment (>2 mm) contents and re-weighed the <2 mm sieved fractions to obtain ρ_b values for the <2 mm fraction. Masses of coarse fragments (>2 mm) were determined after sieving and root picking, and we used a smoothing approach to infer average coarse fragment content (value of 11.1 ± 0.7 wt% for topsoil, *i.e.*, O and A horizons) above the installed microphones. Coarse fragment contents were subsequently subtracted from each soil sample mass to estimate the bulk density of the <2 mm fraction (ρ_b).

To validate our initial horizon designations made by visual inspection, we referred to USDA taxonomic criterion, which determines horizons using quantitative mineral matter (MM) measures. In this classification scheme, organic (O) horizons must contain <40 wt% MM, but in our data the transition into mineral soil occurred at 44 wt% MM. Mineral soil with a MM content between 44 and 90 wt% was classified as an A horizon. Samples with MM contents <10.5 wt% MM were classified as B horizons.

The porosity (%) of each sample was calculated using the following expression:

$$P_{o} = \left[1 - \frac{\rho_{b}}{\rho_{s}}\right] \times 100$$

where P_o is soil porosity (%), ρ_b is the final corrected value for fine-earth fraction (<2 mm) bulk density (g/cm³), and ρ_s represents the average particle density (g/cm³): assuming a ρ_s of 0.9 g/cm³ for pure soil organic matter (SOM) and 2.65 g/cm³ for inorganic (mineral) soil components. Using these constants, we calculated unique particle densities for each soil sample based on their SOM (g/g) and mineral (g/g) contents, which we routed into the expression above.

Playback experiment

As a separate experiment, we investigated the effects of vegetation and earthworms on sound attenuation in soil using a series of calibrated playback tests. To account for differing levels of attenuation at different frequencies, the playback signal included three 5 s synthetic tones at 440 Hz, 1 kHz, and 10 kHz,

formatted identically to those used for microphone calibration. We buried recorders (N = 7) at 10 cm depth below the soil surface in seven mesocosms that captured the full range of vegetation types and worm treatments (Table 1). For each playback, we suspended a JBL Flip 5 Bluetooth speaker 1 m above the center of the focal mesocosm and used an iPhone SE to play the tonal signals at 50% of max speaker volume. To evaluate the effects of soil moisture on sound transmission, we then used an automated watering system to add 2 L of water (corresponding to 10 mm of precipitation) to each mesocosm over the course of 1 min, allowed 1 min for infiltration, and then conducted a second playback using the same protocol. We repeated these steps for all seven mesocosms. All playback experiments occurred after the soundscape data collection period had ended. Mesocosms were sampled in random order to reduce potential biases caused by changes in ambient wind conditions, temperature, *etc.*

We followed the steps used for microphone calibration to select five 0.25 s segments of each playback signal and calculate RMS for each audio clip. For each recording unit, we used RMS values measured from 440 Hz, 1 kHz, and 10 kHz signals during playbacks as a reference to calculate sound pressure level (SPL) during playbacks as $20 * log10(RMS_{playback}/RMS_{ref})$. We computed this separately for every 0.25 s audio clip and then calculated the mean SPL for each unique playback signal on every recording unit. We evaluated the effects of different vegetation types and worm treatments on sound transmission in soil using a multivariate regression with SPL values for 440 Hz, 1 kHz, and 10 kHz playback signals as response variables and vegetation, worm treatment, and order as explanatory variables. To evaluate the effects of moisture on sound transmission, we used a separate mixed model for each vegetation earthworm treatment combination and included SPL values as a response variable, order (before *vs.* after watering) as a fixed effect, and playback frequency as a random effect.

We found that tundra soils with earthworms had significantly higher attenuation of 440 Hz tones and significantly lower attenuation of 1 kHz tones (440 Hz playback: worm treatment: t = -3.04, p = 0.013; vegetation: t = 0.85, p = 0.42; order: t = 0.57, p = 0.58; 1 kHz playback: worm treatment: t = 2.60, p = 0.027; vegetation: t = -0.26, p = 0.8; order: t = 0.30, p = 0.77; Fig. A6a, b). However, transmission of 10 kHz signals appeared to be unaffected by earthworm presence (10 kHz playback: worm treatment: t = -0.36, p = 0.72; vegetation: t = -0.75, p = 0.47; order: t = 0.48, p = 0.65; Fig. A6c) and we found no evidence that vegetation type affects sound transmission, regardless of signal frequency. We found no effect of differences in moisture levels on sound transmission, regardless of vegetation type or earthworm presence (LMM: heath control: t(8) = 0.78, p = 0.46; heath with worms: t(8) = 0.97, p = 0.36; meadow control: t(2) = -8.3, p = 0.5; meadow with worms: t(8) = 0.41, p = 0.97).

The results of our playback experiment partially support our primary findings from the ambient soundscape. We found that received levels of playback sounds were higher in soils with worms, suggesting that above-surface signals experience less attenuation when passing through bioturbated soils. As in our other soundscape analyses, we also observed that differences in sound levels were most noticeable in frequencies above 1 kHz. Interestingly, we found no significant effects of vegetation type, moisture levels, and/or interaction effects between vegetation type and earthworm presence, which differs markedly from our long-term recordings of the ambient Abisko soundscape. However, our playback measurements may have been limited by microphone sensitivity, spatial constraints, and/or sample size, so we cannot exclude the possibility that these effects went undetected.





Fig. A1. Common garden experimental design. a) Arrangement of mesocosm plots in the common garden experiment conducted at the Abisko Scientific Research Station. Original figure is modified from Blume-Werry et al. (2020), b) photo of experimental garden showing blocks containing mesocosms.





Fig. A2. Soil cross-sections collected from mesocosm plots after the experiment was complete. Thin white lines denoted the divisions between genetic soil horizons.



Fig. A3. Long term spectral averages from recordings collected in soils containing a) heath vegetation, b) heath vegetation with earthworms, c) meadow vegetation, and d) meadow vegetation with earthworms. Each plot shows the average power in 5 Hz/30 s bins from a single mesocosm. Color scale represents relative intensity of each bin. Intermittent bursts of wind and noise from trains passing created broadband noise that appears as vertical streaks in the plots.



Fig. A4. a) Total number of acoustic emissions (AEs) detected within each mesocosm during experiment, b) number of AEs detected within mesocosms during five-minute periods sampled every hour. Lines represent mean values among mesocosms with same vegetation and earthworm treatment and shading represents standard error. The recording period began at 00 h.



Fig. A5. Empirical probability density for a) control heath plots, b) heath plots treated with worms, c) control meadow plots, and d) meadow plots treated with worms. Shading represents the probability that power spectral density values fall within a given range based on data collected throughout the experiment. Lines represent empirical probability density levels for 1st, 5th, 50th, 95th, and 99th percentiles.



Fig. A6. Acoustic indices measured from soil soundscapes, including a) acoustic evenness, b) acoustic diversity index, and c) acoustic entropy. The following indices did not vary significantly among soils with different vegetation types and/or worm treatments (LMM: AEven: vegetation: t = -0.34, p = 0.73, worms: t = -1.18, p = 0.27, interaction: 0.09; ADI: vegetation: t = -0.73, p = 0.46; worms: t = 0.85, p = 0.39, interaction: t = -0.43, p = 0.66; H: vegetation: t = -1.2, p = 0.23; worms: t = 1.79, p = 0.12; interaction: t = 1.42, p = 0.16).



Fig. A7. Measured sound pressure levels (SPLs) from recorders (N = 7) buried at 10 cm depth during playbacks of tones at a) 440 Hz, b), 1 kHz, and c) 10 kHz. Blue and green shading indicates whether measurements were taken before (blue) or after (green) water was added to the soils to simulate a 10 mm rainfall event. The 440 Hz tones were significantly attenuated in soils containing worms, while the 1 kHz tones were significantly louder in soils containing worms.

Table A1

Summary of data collected for this study. The numbers in brackets indicate the number of experimental replicates within each treatment group.

Data collected	Vegetation	Treatment
Soundscape recordings from rhizotron tubes	Heath $(N = 18)$	Earthworms $(N = 9)$
		Control ($N = 9$)
	Meadow ($N = 18$)	Earthworms ($N = 9$)
		Control $(N = 9)$
Playback recordings from buried audiomoths	Heath $(N = 4)$	Earthworms $(N = 2)$
		Control $(N = 2)$
	Meadow $(N = 3)$	Earthworms $(N = 2)$
		Control $(N = 1)$

Table A2

Other results from linear mixed models evaluating the effects of vegetation and earthworms on physical (porosity, bulk density) and chemical (mineral mass) properties.

Response variable	Fixed effect	Estimate	SE	t	р
Net porosity (%) ^a	Intercept	82.75	1.68	49.27	< 0.0001
	Worm treatment	-0.55	1.94	-0.28	0.786
	Vegetation	-8.71	1.94	-4.49	0.0001
Net bulk density (g cm $^{-3}$)	Intercept	0.39	0.04	9.12	< 0.0001
	Worm treatment	0.02	0.05	0.34	0.746
	Vegetation	0.22	0.05	4.50	0.0001
Net mineral mass (%)	Intercept	77.65	2.32	33.47	< 0.0001
	Worm treatment	-1.69	2.68	-0.63	0.552
	Vegetation	8.02	2.68	2.99	0.006

^a Interaction terms were removed and models re-run with only main effects (*i.e.*,

worm + vegetation) for all models where no interaction term is listed in the results table above.

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