Title: The sound of restored soil: Measuring soil biodiversity in a forest restoration chronosequence with ecoacoustics

Running Head: Soil ecoacoustics in forest restoration

Jake M. Robinson[1*], Martin F. Breed[1], and Carlos Abrahams[2,3]

[1]College of Science and Engineering, Flinders University, Bedford Park, SA 5042, Australia

[2]Biosciences Department, School of Science and Technology, Clifton Campus, Nottingham Trent University, Nottingham, NG11 8NS, UK

[3] Baker Consultants Ltd, Cromford, Derbyshire, DE4 5JJ, UK

***Correspondence:** Jake Robinson jake.robinson@flinders.edu.au

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ORCIDs:

JMR: 0000-0001-8108-3271

MFB: 0000-0001-7810-9696

CA: 0000-0003-0301-5585

Abstract | Forest restoration requires monitoring to assess changes in above- and below-ground communities, which is challenging due to practical and resource limitations. With emerging sound recording technologies, ecological acoustic survey methods—also known as 'ecoacoustics'—are increasingly available. These provide a rapid, effective, and non-intrusive means of monitoring biodiversity. Above-ground ecoacoustics is increasingly widespread, but soil ecoacoustics has yet to be utilised in restoration despite its demonstrable effectiveness at detecting meso- and macrofauna acoustic signals. This study applied ecoacoustic tools and indices (Acoustic Complexity Index, Normalised Difference Soundscape Index, and Bioacoustic Index) to measure above- and below-ground biodiversity in a forest restoration chronosequence. We hypothesised that higher acoustic complexity, diversity and high-frequency to low-frequency ratio would be detected in restored forest plots. We collected n = 198 below-ground samples and n = 180 ambient and controlled samples from three recently degraded (within 10 years) and three restored (30-51 years ago) deciduous forest plots across three monthly visits. We used passive acoustic monitoring to record above-ground biological sounds and a below-ground sampling device and sound-attenuation chamber to record soil communities. We found that restored plot acoustic complexity and diversity were higher in the sound-attenuation chamber soil but not *in situ* or above-ground samples. Moreover, we found that restored plots had a significantly greater high-frequency to low-frequency ratio for soil, but no such association for above-ground samples. Our results suggest that ecoacoustics has the potential to monitor below-ground biodiversity, adding to the restoration ecologist's toolkit and supporting global ecosystem recovery.

Keywords: Ecosystem restoration; Ecoacoustics; Bioacoustics; Restoration Ecology; Innovation; UN Decade of Ecosystem Restoration

Implications for Practice

- This is the first known study to assess the sounds of soil biodiversity in a forest restoration context, paving the way for more comprehensive studies and practical applications to support global ecosystem recovery.
- Soil ecoacoustics has the potential to support restoration ecology/biodiversity assessments, providing a minimally intrusive, cost-effective and rapid surveying tool. The methods are also relatively simple to learn and apply.
- Ecoacoustics can contribute toward overcoming the profound challenge of quantifying the effectiveness (i.e., success) of forest restoration interventions in reinstating target species, functions and so-called ‘services’ and reducing disturbance.

Introduction

In the absence of large-scale ecosystem restoration and effective monitoring strategies, 95% of the Earth's land is projected to be degraded by 2050 (Yu et al. 2020). This includes forests—ecosystems that comprise a combination of species, geology and climatic processes in which trees are the dominant vegetation type (Kimmins 2004; Glatthorn et al. 2021; Seidl and Turner 2022). The integrity of forest ecosystems depends on a rich tapestry of biodiversity (Müller 2000; Watson et al. 2018). Microscopic organisms or 'microbiota' provide forest trees with nutrients and the ability to communicate via mycorrhizae (Simard 2018; Robinson et al. 2021), and soil meso- and macrofauna contribute to soil formation and energy flows (Le Bayon et al. 2021). The strength and complexity of the relationships between organisms confer resilience to forest ecosystems. Without this complexity, the integrity of forests diminishes, and their capacity to respond to environmental stressors, such as extreme heat caused by climate change, is inhibited (Messier et al. 2019; Pardos et al. 2021). Deforestation—the purposeful clearing of forested land—now occurs at a rapid pace globally. Indeed, the tropics alone lost 12.2 million ha of tree coverage in 2020, an area three times the size of the Netherlands (Sama 2021; Gola et al. 2022). Deforestation contributes to global species extinctions, which are currently occurring at 1,000 times higher than the natural background rate (De Vos 2015). Deforestation also reduces key functional elements (so-called 'ecosystem services') that benefit humans, such as stormwater management, climate regulation, sustainable resources and recreational amenities (Li et al. 2007; Taye et al. 2021). Therefore, effective forest restoration strategies are vital to biodiversity and human wellbeing.

Forest restoration is often conceptualised as intervening to convert a degraded forest starting point to an endpoint that is an idealised natural forest, whilst recognising that restoring functions is a priority (Stantfurt et al. 2014). However, a profound challenge in this process is quantifying the effectiveness (i.e. success) of forest restoration interventions in reinstating target species, functions and 'services' (Camarretta et al. 2020), and reducing further disturbance. Indeed, ecosystem restoration can be viewed as a continuum of stages from planning to implementation to monitoring (Robinson et al. 2022). The monitoring stage plays a crucial role in quantifying the effectiveness of restoration interventions by measuring recovery and potential ongoing disturbance (de Almeida et al. 2020). Primary observations and derived measurements of changes in biodiversity status are considered fundamental to monitoring the effectiveness of restoration strategies (Breed et al. 2019; Hansen et al. 2021). This is exemplified by GEO BON Essential Biodiversity Variables (EBVs), which provide the first level of abstraction between low-level observations and high-level indicators of biodiversity (Kissling et al. 2018). However, acquiring these EBVs, which include genetic composition, species populations, species traits, community composition, ecosystem functioning and ecosystem structure (O'Connor et al. 2020), via traditional survey methods can be time and resource-intensive and potentially intrusive (Gollan et al. 2013; Beng et al. 2020; Hoban et al. 2022).

Due to these constraints, forest restoration data are often limited to visible macro-organisms, particularly the trees and other floral and faunal assemblages above-ground (Stoddard et al. 2011; Williams-Linera et al. 2021). Moreover, ecological data are often ambiguous and, therefore, incompatible with further research (Zipkin et al. 2021). With the advent of new sound recording technologies, ecological acoustic survey methods, also known as 'ecoacoustics', are becoming increasingly available (Abrahams and Geary 2020; Abrahams et al. 2021; Müller et al. 2022). They can provide effective and non-invasive approaches to gathering biodiversity data—e.g. on target species, assemblages and environmental variables essential to restoration monitoring (Teixeira et al. 2019; Stowell and Sueur 2020). In recent years, ecoacoustics has been applied to monitor elusive species in several environmental contexts—particularly in conservation biology (Teixeira et al. 2019; Stowell and Sueur 2020). For instance, passive acoustic monitoring (often shortened to 'PAM'), which involves deploying autonomous acoustic sensors, has been used to collect recordings of biological sounds (known as 'biophony') from bats (Hintze et al. 2021; López-Baucells et al. 2021), birds (Abrahams 2019; Abrahams and Geary 2021), and invertebrates (Harvey et al. 2011; van der Mescht et al. 2021; Mankin et al. 2022) in terrestrial environments; and cetaceans (Jones et al. 2020; Guidi et al. 2021), amphibians (Gan et al. 2020), crustaceans (Kühn et al. 2022), and fish (Popper and Hawkins 2019) in aquatic environments. Indeed, ecoacoustics has emerged as an efficient tool to measure and monitor biodiversity and has the potential to enhance the toolbox of restoration ecologists. Moreover, the same audio recording devices can detect anthropogenic noise (known as 'anthrophony') (de Framond and Brumm 2022). Anthrophony may contribute to ecosystem degradation by adversely affecting animal fitness, health (De Jong et al. 2018; Kleist et al. 2018) and behaviour (Tidau and Briffa 2019; Hastie et al. 2021), and the composition and functionality of microbial communities (Robinson et al. 2021). Therefore, ecoacoustics could provide important measurements across the degradation-restoration continuum.

Despite the potential of ecoacoustics to contribute to forest restoration monitoring, few studies have deployed this technology to assess above-ground faunal soundscapes in a forest restoration context (Turner et al. 2018; Vega-Hidalgo et al. 2021). Moreover, to our knowledge, no studies have applied ecoacoustics to measure or monitor below-ground biodiversity in a restoration context. This is despite its demonstrable effectiveness at detecting soil meso- and macrofauna acoustic signals in other settings, such as agriculture (Maeder et al. 2019), silviculture (Maeder et al. 2022), and in controlled chambers (Lacoste et al. 2018). Here we apply novel ecoacoustics devices to measure above- and below-ground biodiversity in a forest restoration chronosequence (a set of ecological sites that share similar attributes but represent different times since restoration), using a range of acoustic indices to analyse the recordings, including the Acoustic Complexity Index (ACI) (Pieretti et al. 2011), Normalised Difference Soundscape Index (NDSI) (Kasten et al. 2012), and Bioacoustic Index (BI) (Boelman et al. 2007). As faunal species richness, abundance, biomass and functional diversity are known to increase with restoration age (Derhé et al. 2016), we expected acoustic diversity to increase accordingly. Specifically, our study aimed to test the following hypotheses:

(a) Acoustic complexity/diversity will be higher in restored plots (30-50 years since restoration), compared with degraded plots (0-10 years since clearing without any active restoration intervention), in both soil and ambient recordings.

(b) The high-frequency to low-frequency ratio (an amended version of the Bioacoustic Index) will be higher in restored plots than in degraded plots. This would indicate lower noise disturbance in the restored plots, based on the assumption that high-frequency sounds are more representative of biophony than low-frequency anthrophony resulting from mechanical noise and ground vibrations.

(c) Soil acoustic diversity will positively correlate with invertebrate abundance and richness, with higher scores in the restored plots.

Materials and Methods

Study location: Greno Woods is a large forest (169 ha) near Sheffield in South Yorkshire, UK (Fig. 1). The forest comprises several restoration age classes. Due to comparator site availability constraints, samples were collected from two age classes: 0-10 years since deforestation and no active restoration interventions since (referred to in this study as 'degraded') representing recent degradation; and 31-50 years since restoration (referred to in this study as 'restored'). We identified three spatially-independent replicate plots for sampling each age class (0A, 0B, 0C, and 30A, 30B, 30C; Fig. 1 and Fig. 2A, B). The habitat classification of all restored sampling plots was semi-natural broadleaved woodland of the W16 National Vegetation Classification (Rodwell 2006). The degraded plots were dominated by bracken *Pteridium aquilinum*, with occasional silver birch *Betula pendula* saplings. The restored plots were dominated by English oak *Quercus robur,* sessile oak *Q. petraea*, silver birch and rowan *Sorbus aucuparia,* with a well-developed understory of bilberry *Vaccinium myrtillus,* bramble *Rubus fruticosus agg.*, holly *Ilex aquifolium*, and bracken.

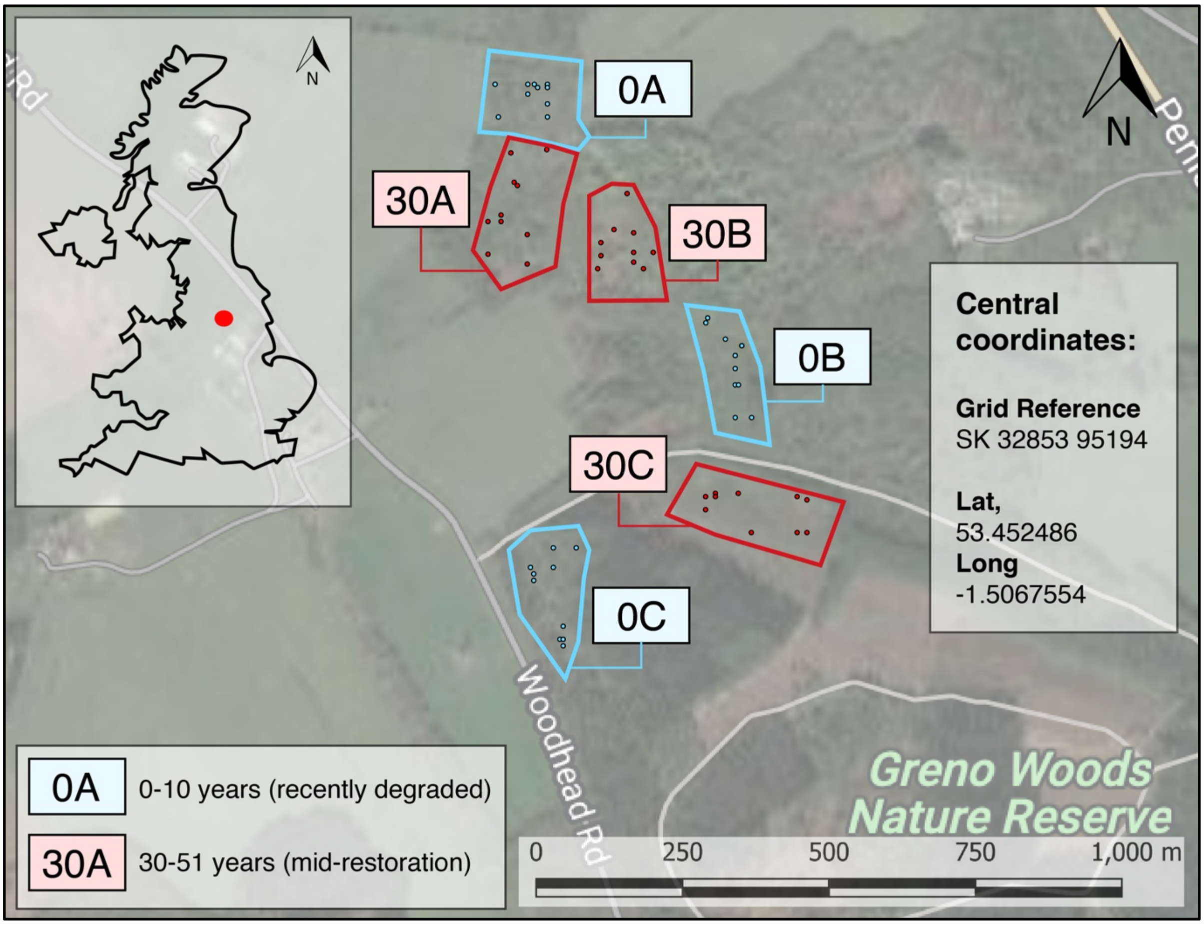

Figure 1. Site location (Greno Woods, South Yorkshire, UK), sampling plots within the blue polygons for degraded and red polygons for restored, and the ten randomly selected sampling locations within each plot. The inset shows the study location (red dot) in the broader UK context.

Soundscape sampling: We used a relatively inexpensive ecoacoustics sampling device for below-ground sampling: a JrF C-Series Pro contact microphone sensor (jezrileyfrench.co.uk) with a 2 m cable and a 1/4” Neutrik jack. The C-series contact microphones provide a broader frequency response than others, meaning more low-end and mid-frequency range responses. This broader frequency response is optimal for recording below-ground soundscapes (Maeder et al. 2019; Gamal et al. 2020). The JrF microphone was attached to a metal probe and linked to a handheld acoustic recording device (Zoom H4n Pro) prior to inserting the probe into the soil. We recorded .wav sound files, at 16 bit depth, and with a sampling rate of 48 kHz, which is a similar rate used in other soil acoustic research (Abrahams 2019), capturing sounds to a maximum of 24 kHz and therefore covering the entire audible range (Maeder et al. 2022). To record above-ground (ambient) sound—for instance, to detect soniferous species such as birds—we installed a Tascam DR-100MKII audio recording device onto a tripod in each plot, using its inbuilt omni-directional microphones to record sounds with the same file format.

We selected below-ground acoustic sampling locations using a geographical information system (GIS). We created polygon boundary shapefiles around each of the six spatially-independent sampling plots and generated ten random sampling points for each plot using the random points algorithm in QGIS (version 3.24.3 'Tisler'). Below-ground sound samples were collected from the predetermined random points within each plot. We repeated the sampling on three occasions across three months (June, July, and August) in the summer of 2022 (Table S1).

To determine the appropriate sampling duration for below-ground samples, we first ran a pilot study, testing the potential saturation and decay of acoustic indices using different sampling durations (20 s, 1 min, 3 mins, and 5 mins). The sampling durations were randomised and collected over two visits (n = 14 per sampling duration). Each recording followed a separate probe insertion into the soil to represent the main study approach. To control for initial geophony (e.g., displaced soil particles) and potential disturbance to biophony from the physical disturbance of entering the soil, recordings always followed an initial 30 s resting period. We also controlled for higher frequency anthrophony by setting a low-pass filter to 2 kHz during analysis. This testing process identified a sampling duration of 3 mins as optimal. There was no significant effect of time post-3 mins (i.e. 3 mins vs. 5 mins) on acoustic complexity ($t = 1.7$-2.1; $p = 0.48$-0.64) (Fig. S1).

Following the pilot study, we collected data for the main part of the study. During the three sampling occasions, we set the Tascam DR-100MKIII to record above-ground soundscape samples at each plot. We then recorded the 3 mins below-ground samples ($n = 10$) in each plot, alongside simultaneous control samples of the same duration. The latter involved recording ‘blanks’ by leaving a recorder and contact microphone outside the soil, supported on sound attenuation foam. In total, we collected $n = 180$ below-ground samples (3 mins each) with their matching control recordings, and $n = 18$ above-ground samples. The above-ground recordings were post-processed by being divided into 3 mins sections to simultaneously match the below-ground recordings ($n = 180$ subsamples).

Sound attenuation chamber: We used an additional sampling method to record the soil soundscape in each plot. This involved collecting soil samples with a 3L plastic container and placing them into a sound-attenuation chamber, allowing us to record a ‘snapshot’ of the soundscape under controlled conditions (Fig. 2C). We used the same recording equipment for the *in situ* and sound-attenuation chamber samples. In total, we collected $n = 18$ chamber samples (3 mins each). To determine the optimal sound-attenuation chamber design, we first ran a pilot study using different sound barrier configurations (Fig. S2). The final design comprised a 60 L plastic chamber, with sound-attenuation foam installed on each internal wall, including the base and lid (Fig. 2C).

Invertebrate counts: We recorded the abundance and richness of meso- and macrofauna in the soil by collecting 3 L soil samples from a random point (determined using a digital number randomiser). We subsequently counted the invertebrates on the sound-attenuation chamber lid (Fig. 2D) by systematically searching through the soil, working from left-to-right and carefully displacing soil particles, thereby revealing the invertebrates (Stroud 2019). The invertebrates were photographed and recorded in a spreadsheet on-site. The soil and the invertebrates were placed back in their source location once the counting was completed.

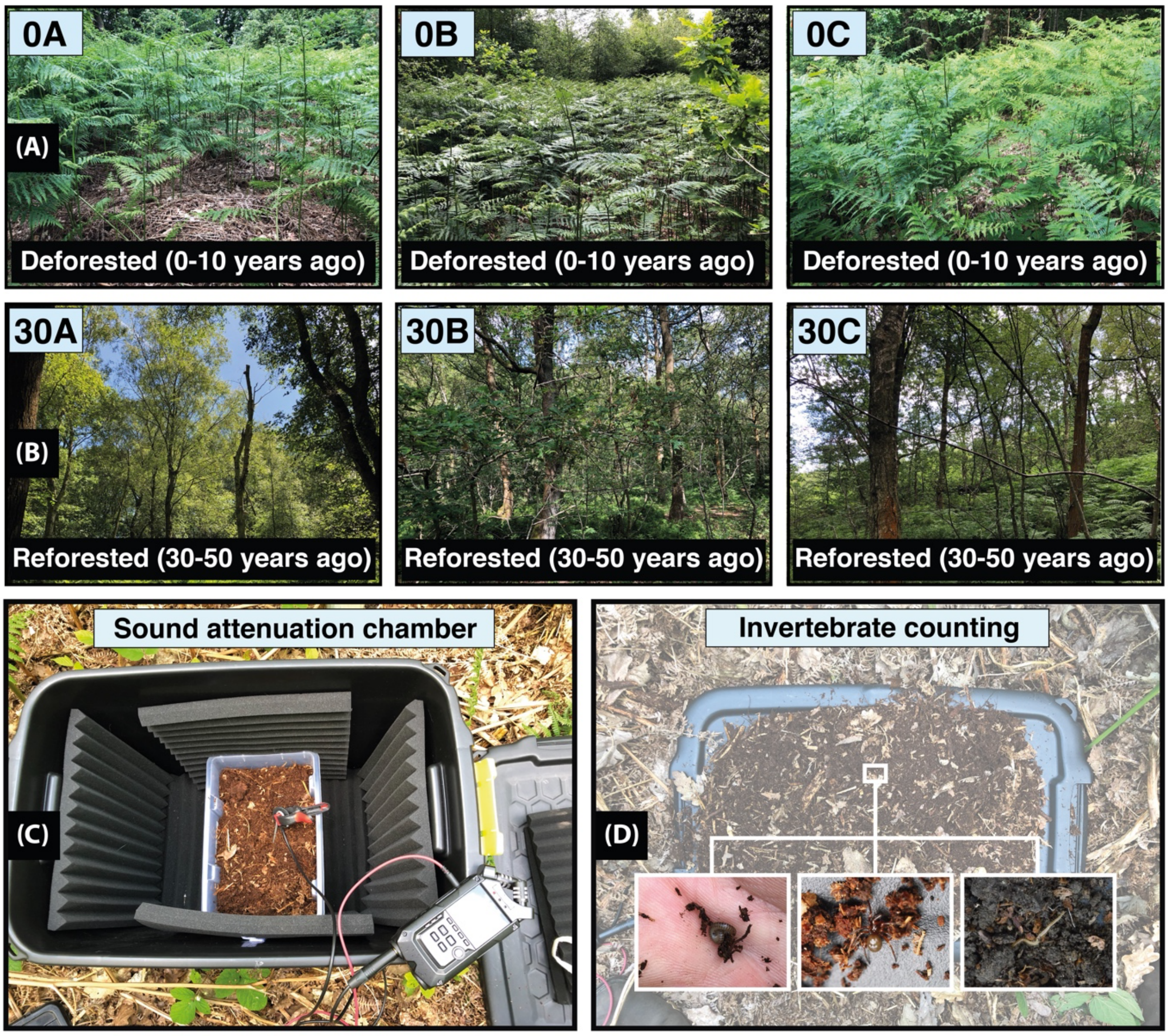

Figure 2. (A) Degraded study plots. (B) Restored study plots. (C) Sound attenuation chamber with the Zoom H4n recorder and JrF C-series contact microphone. (D) The invertebrate counting method.

Data analysis: To process the sound recordings (.wav files), we used the wildlife sound analysis software Kaleidoscope Pro (Version 5.4.7; Wildlife Acoustics, 2022). This software allows for the analysis of full-spectrum recordings to measure multiple acoustic indices, including the ACI (Pieretti et al. 2011), NDSI (Kasten et al. 2012) and BI (Boelman et al. 2007) selected for this study. We chose two diversity indices (ACI and BI) and one index to measure the biophony-to-anthrophony ratio (NDSI), allowing us to test our three hypotheses.

ACI directly measures the variability in sound intensity in both frequency and time domains, comparing the normalised absolute difference of amplitude between adjacent FFT windows in each frequency bin over a period of K seconds. First, it computes the absolute difference between adjacent values of intensity:

$$d_k = I_k - I_{(k+1)}$$

The changes in the recording's temporal step are encompassed by the summation of the *d*'':

$$D = \sum_{k=1}^{n} d_k$$

To obtain the relative intensity and reduce the influence of the distance between the microphone and biophony source, the result *D* is divided by the total sum of the intensity values (Maeder et al. 2022):

$$ACI = \frac{D}{\sum_{k=1}^{n} I_k}$$

The total ACI is the sum of the ACIs across bins for each period K in the recording.

BI is computed as “the area under each curve including all frequency bands associated with the dB value that was greater than the minimum dB value for each curve. The area values are thus a function of both the sound level and the number of frequency bands” (Boelman et al. 2007).

NDSI is computed as follows:

$$NDSI = \frac{(\beta - \alpha)}{(\beta + \alpha)}$$

Where β and α are the total estimated power spectral density for the largest 1 kHz biophony bin and the anthrophony bin, respectively. The NDSI is a ratio in the range [− 1 to + 1], where + 1 indicates a signal containing only high-frequency biophony and no low-frequency anthrophony (Kasten et al. 2012).

Standard settings in Kaleidoscope Pro were used for the calculation of above-ground acoustic indices. However, as sounds above 2 kHz do not propagate well through the soil (Maeder et al. 2022), for the below-ground acoustic indices, we set a maximum frequency of 2 kHz, and a lower threshold of 500 Hz for biophony in NDSI and BI.

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All statistical analysis was conducted in R Version 2022.02.2 'Prairie Trillium' (R Core Team 2022) with supplementary software (e.g., Microsoft Excel for .csv file processing). To test for the effect of restoration on acoustic index values, we applied the two-samples t-test using the rstatix package (Kassambara 2022). We also fit linear mixed effects models (LMM) to the data using R and its lme4 package (Bates et al. 2015), with separate models fitted for different plots and visits. LMMs included random effects (plots and visits), which are essential to account for the spatial and temporal correlation between the plots and visits in our experimental design. Acoustic index outputs were included as response variables, and the degraded vs. restored plots were included as fixed effects (predictor variables). Tests of significance were conducted using Satterthwaite's degrees of freedom t-test, which is a function of the LmerTest package in R (Kuznetsova 2020). Soil invertebrate beta diversity was visualised using nonmetric multidimensional scaling (NMDS) ordination of Bray–Curtis distances using the Vegan package in R (Oksanen et al. 2022). The ordination plots show low-dimensional ordination space in which similar samples are plotted close together, and dissimilar samples are plotted far apart. We used the analysis of similarities (ANOSIM) approach to test for compositional differences between treatment groups. Data visualisations were produced using a combination of R and the Adobe Illustrator creative cloud 2021 version (Adobe 2021).

Results

Soil invertebrate observational surveys

Restored/degraded soil invertebrate abundance and richness

Restored soils had higher invertebrate abundance (t-test: t = -2.2, df = 8, p = 0.02), and there was no significant effect of restoration/degradation status on invertebrate richness (t = 0, df = 8, p = 1).

Beta diversity

Soil invertebrate community composition was significantly different between degraded and restored plots (stress 0.01, R: 0.55, p = 0.05, permutations = 999) (Fig. 6). Earthworms (sub-order: Lumbricina) were the dominant invertebrate in the soil for both treatment groups (n = 13 from n = 64 for degraded vs n = 32 from n = 102 for restored plots) (Fig. 3 and 4), and were more abundant in the restored plots (degraded $\bar{x}$ = 1.4; restored $\bar{x}$ = 3.5; t = -2.9, df = 8, p = 0.01) (Fig. 3 and 4).

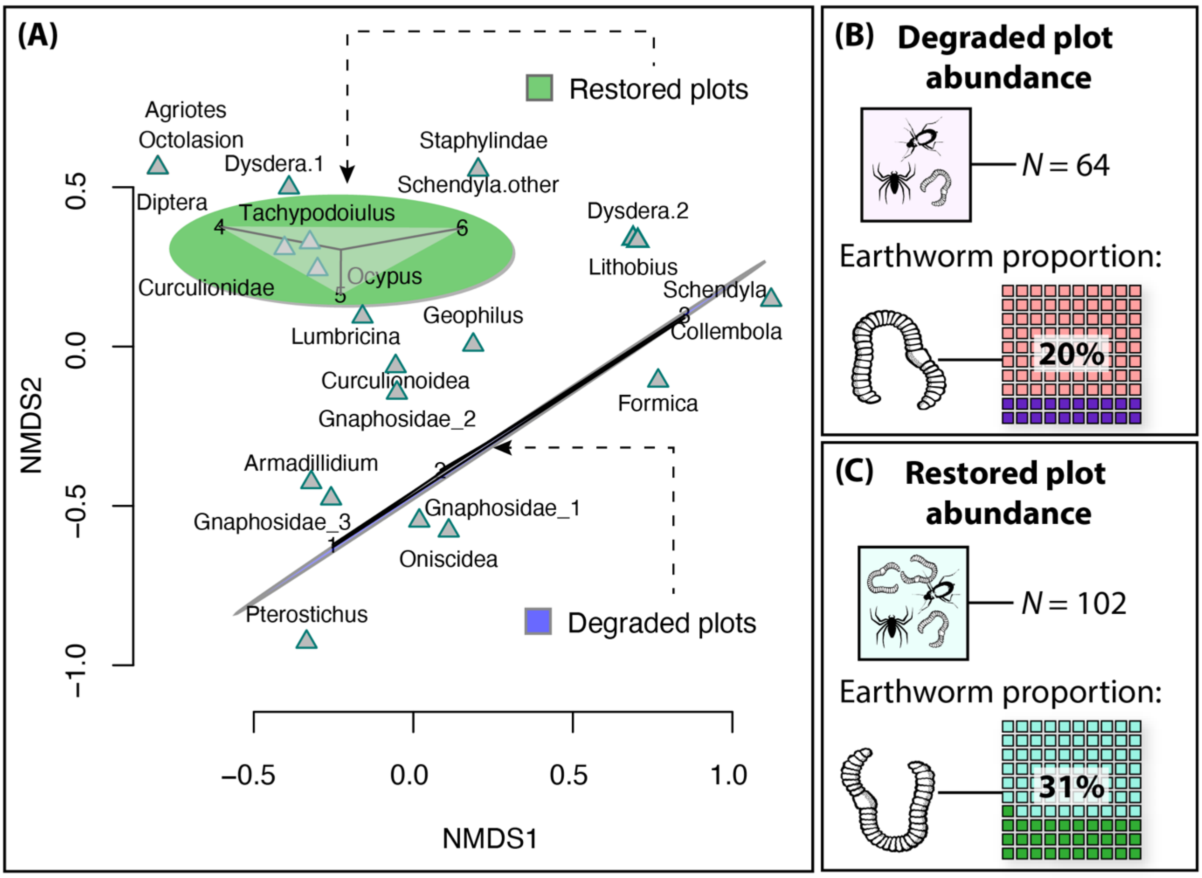

Figure 3. (A) Nonmetric multidimensional scaling (NMDS) ordination plots for visualising soil invertebrate beta diversity (community composition) for all plots (Stress: 0.01; Bray dissimilarity). Ellipses represent the standard error of the (weighted) average of scores. Clusters suggest clear differences between communities of the different treatment groups, as indicated by the colour purple ellipse for degraded plots (the linear ellipse) and green ellipse for restored plots. (B) Abundance of invertebrates counted in degraded plots and the proportion of earthworms. (C) Abundance of invertebrates counted in restored plots and the proportion of earthworms.

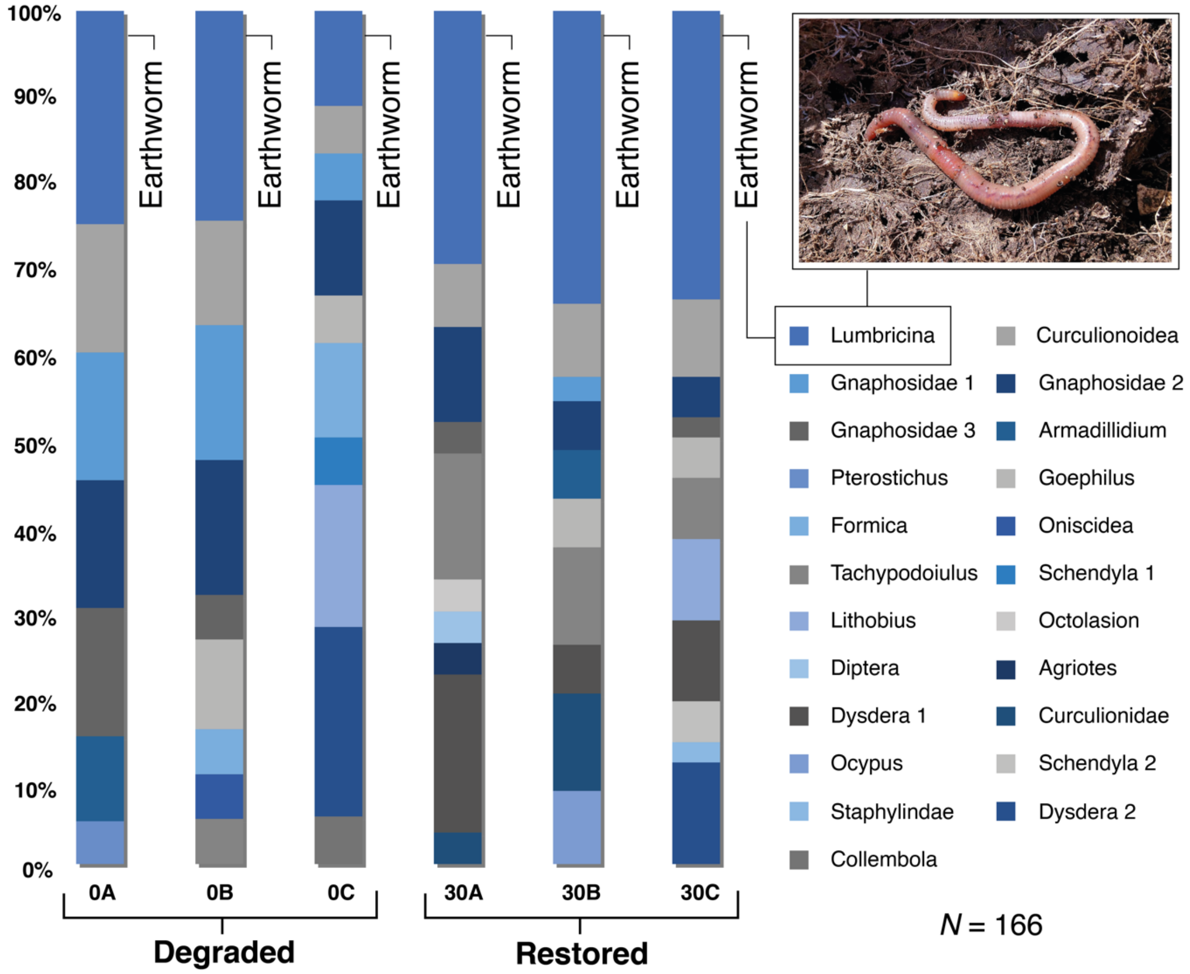

Figure 4. Stacked bar chart showing the relative abundance of soil invertebrates between plots (individual bars) and treatment groups (degraded vs restored). The top blue segment denotes earthworms (inset: earthworm), indicating a higher relative and absolute abundance of earthworms (*n* = 13 for degraded vs *n* = 32 for restored plots) in the samples from the restored forest plots.

Correlation of ecoacoustics variables and invertebrate abundance and richness

The ACI correlated with invertebrate abundance, with higher scores in the restored plots (Estimate = 0.2, R^2 = 0.36, SE = 0.07, *p* = 0.01). A significant effect also occurred when changing ACI for BI (Estimate = 0.9, R^2 = 0.31, SE = 0.03, *p* = 0.02). This suggests that restoration status and acoustic complexity and diversity metrics can predict invertebrate abundance. However, there was no significant effect of restoration/degradation or invertebrate richness on acoustic complexity based on the ACI (Estimate = -0.16, SE = 0.25, *p* = 0.5). This was also the case for acoustic diversity measured using the BI (Estimate = -1.63, SE = 1.18, *p* = 0.18). This corroborates the t-test for differences in means between invertebrate richness in the degraded vs restored plots (t = 0, df = 8, *p* = 1).

Soil ecoacoustics in sound attenuation chamber

There was significantly greater ACI (Estimate = 1.6, R^2 = 0.56, SE = 0.3, *p* = <0.01) (Fig. 5A) and BI (Estimate = 7.95, R^2 = 0.58, SE = 1.8, *p* = <0.01) in restored compared with degraded soils, indicating bioacoustic complexity and diversity was higher in the restored plot soils in the sound attenuation chambers. However, there was no effect of restoration/degradation status on NDSI, indicating similar high-frequency to low-frequency ratios in the sound attenuation chamber for restored and degraded soils (Estimate = 0.04, SE = 0.13, p = 0.7) (t = -0.33, df = 8, p = 0.37) (Fig. 5A3).

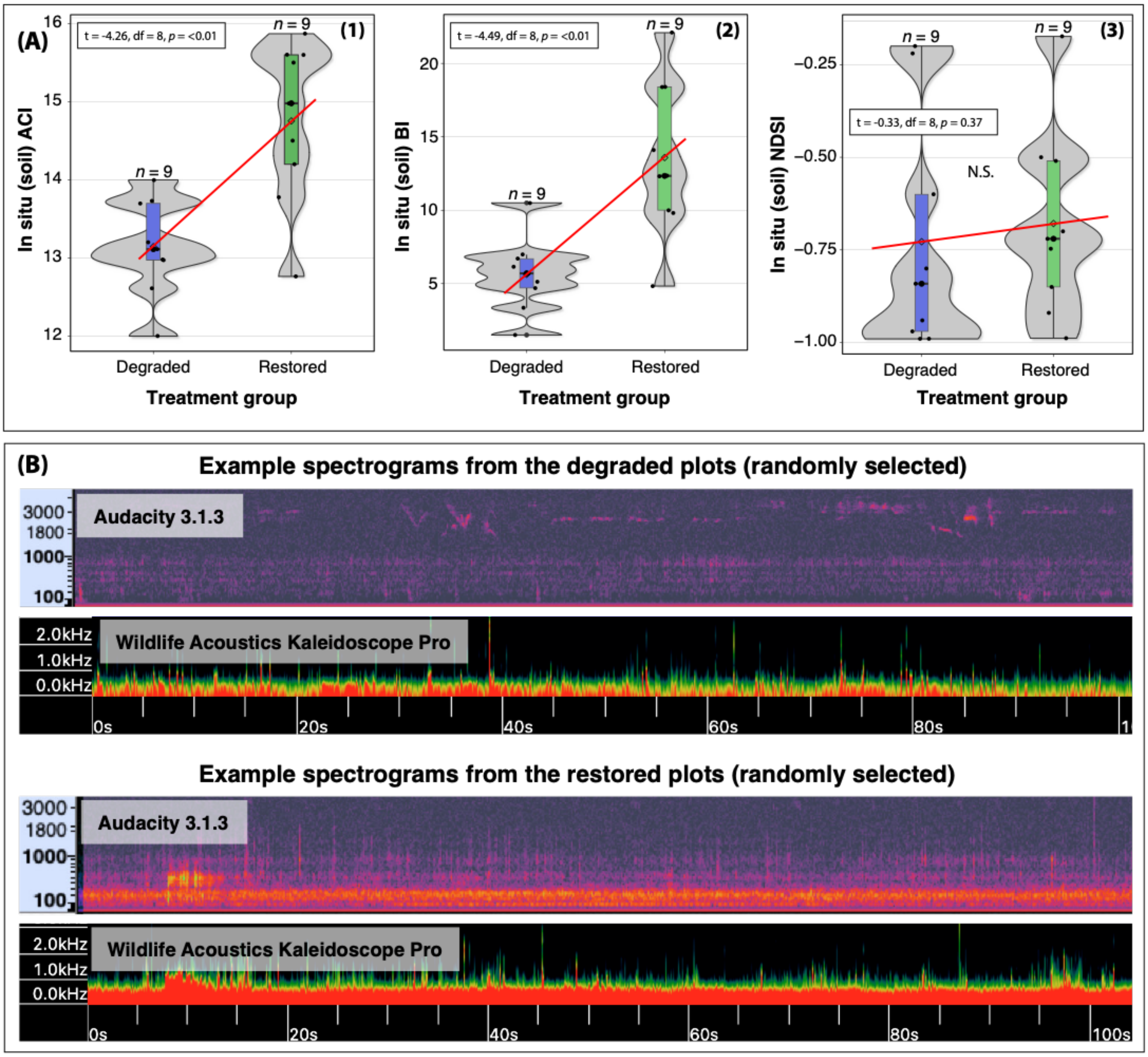

Figure 5. (A) Boxplots of acoustic index outputs for sound attenuation chamber (i.e., soil) samples and separated based on treatment groups (degraded vs restored). From left to right: (1) ACI, (2) BI, and (3) NDSI. Each plot has a red guideline to show trends in the mean values. (B) Examples of soil acoustic spectrogram for both treatment groups, showing the same window in two different analysis programmes (Wildlife Acoustics Kaleidoscope Pro and Audacity v3.1.3). N.S. = not significant.

***In situ* soil ecoacoustics**

There was no effect of the restoration/degradation status on ACI (Estimate = 0.12, SE = 0.14, *p* = 0.3) or BI (Estimate = 0.25, SE = 0.5, *p* = 0.6; Fig. 6). There was a greater NDSI in restored *in situ* soils than degraded soils (Estimate = 0.09, R^2 = 0.15, SE = 0.03, *p* = 0.02) (t = -2.18, df = 89, *p* = 0.01) (Fig. 6, final plot), indicating greater high-frequency to low-frequency ratio in the restored soils.

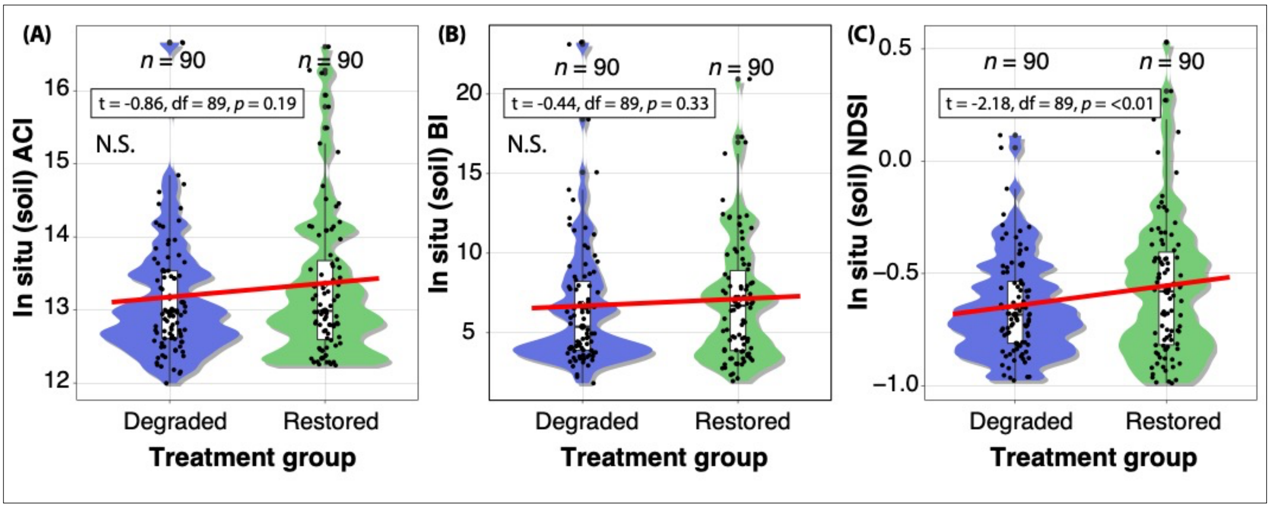

Figure 6. Boxplots of acoustic index outputs for *in situ* (i.e., soil) samples, separated by treatment group (degraded vs restored). From left to right: (A) ACI, (B) BI, and (C) NDSI. Each plot has a red guideline to show trends in the mean values. N.S. = not significant.

Above-ground acoustic diversity and complexity

There was no effect of restoration/degradation status on ambient ACI (Estimate = -0.5, SE = 0.6, *p* = 0.4) and BI (Estimate = 0.7, SE = 2.0, *p* = 0.7) (Fig. 7). When accounting for the visit and plot random effects, there was no effect of restoration/degradation status on ambient NDSI (Estimate = 0.14, SE = 0.2, *p* = 0.6).

However, we do report a higher NDSI in the restored plots when we did a simple linear regression (Estimate = 0.18, R^2 = 0.46, df = 168, p = 0.04).

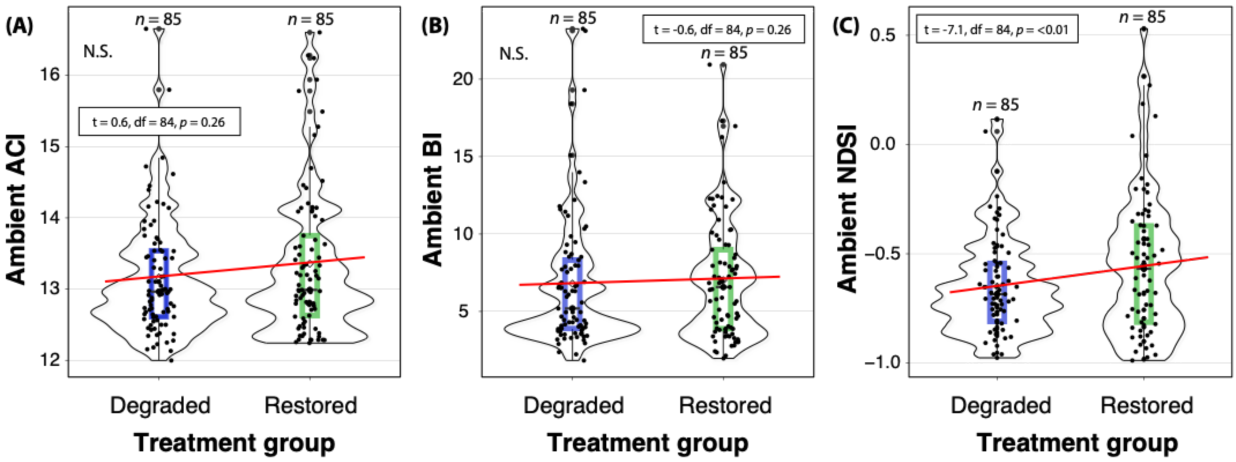

Figure 7. Boxplots of acoustic index outputs for ambient (i.e., above-ground) samples, separated by treatment group (degraded vs restored). From left to right: (A) ACI, (B) BI, and (C) NDSI. Each plot has a red guideline to show trends in the mean values. N.S. = not significant.

Discussion

We show that restored forest soils – in sound attenuation chambers at least – exhibit higher acoustic complexity and diversity than degraded soils, supporting our first hypothesis. Interestingly, there was no significant relationship between ambient (i.e., above-ground) acoustic diversity and degraded/restored status, probably in part due to the broad scale of sound transmission through the forest, compared to the highly localised soil soundscape (discussed below). We report greater high-frequency to low-frequency ratios in restored compared with degraded forest soils measured *in situ,* supporting our second hypothesis. Moreover, we validate our findings by reporting that invertebrate abundance – though not richness – was higher in restored than degraded forest soils. Accordingly, our study provides a case study on how soil ecoacoustics has clear potential to assess biodiversity in – and the restoration status of – forest soils.

Restored vs. degraded soil ecoacoustics

Responses of soil biota to microhabitat conditions have been investigated extensively (Martins et al. 2012; Heiniger et al. 2015), and a recent study explored the temporal and spatial dynamics of soil biophony using ecoacoustics (Maeder et al. 2022). However, to our knowledge, our study is the first to investigate soil acoustic dynamics in a restoration context. It is the first study to relate the acoustic complexity, amplitude and frequency-band characteristics of the soil soundscape (via the ACI, BI and NDSI) to the abundance and richness of directly measured forest soil invertebrates. We reveal significant differences in the acoustic complexity and diversity between degraded and restored forest plots when measured in a sound attenuation chamber. These differences were associated with soil invertebrate abundance but not richness (unlike the findings of Maeder et al. 2022). This relationship between acoustic signals and soil communities, and the variation between degraded and restored plots, suggests that the restoration status of forest soils can be captured by monitoring soil soundscapes. Our models show that we could predict acoustic complexity and diversity based on the degraded and/or restored status of the forest plots, and these relationships were still significant when accounting for plot and visit-associated variability. The Acoustic Complexity Index (ACI) was the only one of the three indices we used that assesses the temporal dynamics of the sound recordings. It has become clear during this study that soil recordings are characterised by broadband stop-start intermittent noises produced by soil fauna, and these dynamics are better represented in the time domain than by analysing patterns across frequency bins (as done with BI and NDSI). Therefore, ACI is the best index to analyse this characteristic.

However, our results contrasted somewhat between samples from the sound attenuation chamber and taken *in situ*. The reason for this could be that the chamber may enhance the quality of the acoustic signal and reduce external noise. Despite the resting period, the act of moving soil into the chamber could also stimulate the movement (and hence sound production) of soil fauna, although acoustic complexity and diversity were still significantly higher in the restored soils. These findings suggest that the sound attenuation chamber sampling approach may be more suitable for detecting soil fauna acoustic signals in this forest restoration context. However, the *in situ* approach has the benefit of being less intrusive (i.e., no soil excavation is required). Therefore, it will be important to further optimise the *in situ* sampling strategy to improve the application of ecoacoustics to restoration.

The lack of association between soil invertebrate *richness* and acoustic index outputs contradicts the relationships found in a recent soil acoustics study (Maeder et al. 2022). This could simply be due to inter-ecosystem variability and the variety of acoustic signals made by soil fauna, which is still poorly understood. Alternatively, it could result from the relatively rapid *in situ* invertebrate-counting method employed in this study, which only provided a ‘snapshot’ of the resident soil fauna. Mean invertebrate richness was the same for both degraded and restored forest plots, although the invertebrate abundance was significantly higher in the restored plots. This aligns with other studies that show higher soil invertebrate abundance in habitats with lower disturbance (Smith et al. 2008; Nkem et al. 2020). The higher abundance of earthworms in the restored soils also corroborates other studies (Wodika et al. 2014; Singh et al. 2020). This could partially explain the higher acoustic complexity detected in restored soils. For instance, earthworms form burrows through the soil as they seek carbon-rich areas, which serve as preferential networking pathways for plant root growth, water flow and gas transport (Lacoste et al. 2018), all of which contribute to the soil soundscape (Gagliano et al. 2017; Del Stabile et al. 2022; Keen et al. 2022). In the future, it would be prudent to take a more robust approach to invertebrate counting, such as using the Berlese method (Sabu and Shiju 2010). This involves specially-adapted funnels to separate soil invertebrates from litter and particles and counting *ex situ* (Maeder et al. 2022). Metagenomics analysis is another option, either alone or in combination with traditional methods. This allows the genomes of soil organisms to be sequenced, differentiated and labelled without requiring morphological analysis (Schmidt et al. 2022). However, the need to control false-positive occurrences resulting from legacy DNA is vital (Laroche et al. 2017).

We report a significant association between NDSI values and the degradation/restoration status of forest plots, where restored plots exhibited a greater high-frequency to low-frequency ratio, aligning with our hypothesis. The NDSI seeks to describe the 'health' of an ecosystem by inferring the level of anthropogenic disturbance received (Eldridge et al. 2016). We hypothesised that our recording devices were more likely to detect higher-frequency biophony in restored plots and lower-frequency anthropogenic disturbance in degraded plots. This was based on the assumption that the increased signals from biological activity in restored plots would outweigh low-frequency noise, with potential effects also from the attenuation properties of the system (Tashakor and Chamani 2021; Sangermano 2022) i.e., the energy loss of sound propagation in a given medium. It could also be that greater earthworm activity changes soil characteristics (making them more air permeable) to allow better propagation of higher-frequency sounds, thereby increasing NDSI scores (Keen et al. 2022). Understanding the factors that affect this biophony-to-anthrophony ratio in a restoration context warrants further research. Examples of next steps could be conducting controlled experiments that manipulate sound sources and adding/removing vegetation and other physical features and media that provide noise attenuation. Applying new physics-based models to evaluate how the frequency and distance-dependent attenuation of sound impact the acoustic detection of soniferous species (Haupert et al. 2022) could also improve outcomes in a restoration monitoring context. Interestingly, there was no significant difference in the NDSI values between degraded and restored soil in the sound chambers, which was probably because the sound attenuation foam in the chamber acts to standardise ambient acoustic conditions.

Above-ground ecoacoustics

Contrary to our expectations, we did not find a significant relationship between above-ground acoustic diversity and complexity and the degradation/restoration status of the forest plots. We hypothesised that we would observe higher acoustic diversity in the restored forest plots as faunal species richness, abundance, biomass and functional diversity are known to increase with restoration age (Derhé et al. 2016). Moreover, studies have shown that bird species diversity (the most soniferous group contributing to the soundscape) increases as restored forests mature, and bird communities in recovering areas become more similar to those of undisturbed areas with post-restoration age (Owen et al. 2021). The lack of a restoration effect on above-ground acoustic diversity and complexity could be due to our degraded and restored plots being relatively small compared to the soundscape of birdsong. Consequently, birdsong acoustic signals could potentially overlap across our plots, which is a limitation of our study. Future studies should pair sampling in time across plots, particularly when degraded and restored plots are within relatively close proximity to each other. Alternatively, mean acoustic diversity might increase as patch size increases, and more complex vegetation is associated with higher diversity (Grant et al. 2016). Therefore, it is possible that the minimum habitat patch size in our study was not sufficient to influence acoustic source variability in the treatment groups.

Our study provides preliminary evidence for using soil ecoacoustics – a minimally-intrusive and cost-effective assessment method – as a soil biota monitoring tool that can evaluate restoration projects. With future work, soil ecoacoustics could develop into an effective tool that measures the abundance, complexity and composition of soil biota that is also sensitive to restoration interventions. Given the rapid pace of biodiversity loss and the rise in anthropogenic noise, the ability to detect the acoustic signals from soniferous species and monitor the level of disturbance from anthrophonies has never been more important. Further exploration of above-ground ecoacoustics in different forest restoration settings, e.g., sites receiving different restoration interventions of varying patch sizes and in different biomes, would be valuable. Building on our findings—that soil acoustic complexity and diversity and noise disturbance differ between degraded and restored forest plots—has the potential to inform and enhance future restoration policy and practice.

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