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The efficacy of acoustic indices for monitoring abundance and diversity in soil soundscapes

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ABSTRACT

Soil ecoacoustics is a rapidly emerging field heralded as a non-invasive method for monitoring soil fauna. Ecoacoustic analysis commonly uses acoustic indices to analyse soundscapes, linking them to 'traditional' biodiversity value metrics such as species richness and abundance, but it is not clear if this approach is appropriate for soil soundscapes. Furthermore, there are very few controlled experiments assessing how commonly used acoustic indices respond to different sound types, and none belowground. We address this by synthesising soil soundscapes with differing levels of acoustic richness, abundance, and evenness using soil recordings from the UK, France, and Brazil.

Applying 14 acoustic indices on 1-minute soundscapes, we assessed: 1) how changes in acoustic diversity impact acoustic indices and 2) how accurately combinations of indices predict biodiversity metrics. Finally we assessed 3) whether gamma acoustic richness can be predicted accurately using multiple acoustic index scores from repeated surveys, whilst experimentally altering the alpha and beta diversity components.

We find that acoustic abundance strongly affects values of acoustic indices designed to quantify the number of sound events in a soundscape, and that a combination of these indices can accurately predict abundance at 1 minute timescales. Combinations of indices could predict acoustic richness when richness values were low, but were ineffective for evenness. Additionally, acoustic indices were poor predictors of gamma diversity, especially when gamma was driven solely by beta diversity. Overall, we found that acoustic indices were good predictors of acoustic abundance, but should be used with caution for other diversity metrics.

1. Introduction

The use of ecoacoustic techniques belowground is an emerging field ([Sutherland](#page-14-0) et al., 2024). This non-invasive monitoring of soil fauna and ecosystem processes could be widely applied in agricultural and ecological investigations. Whilst soil acoustics has been used to detect individual species, usually pests in agricultural settings, recent soil ecoacoustic studies have addressed whole soundscapes (e.g., [Maeder](#page-13-0)

et al., 2022, [Robinson](#page-13-0) et al., 2023, Metcalf et al., 2024). Ecoacoustics assumes that the combination of geophony (sounds generated by nonliving environmental sources), anthropophony (human-generated sounds), and biophony (biotically-generated sound) creates an acoustic signature that is consistent between sites with similar ecologies. Soundscapes can be ecologically informative in above ground acoustic surveys, usually through either the detection and classification of specific sounds, or the use of acoustic indices summarising variation in the

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sound energy of recordings (Sueur et al., 2014, [Bradfer-Lawrence](#page-14-0) et al., [2024\)](#page-14-0).

Acoustic indices are generally used either as broad descriptors of a soundscape that can be used to classify habitat types and describe temporal trends, or as a proxy for more traditional forms of biodiversity metric, like species richness [\(Bradfer-Lawrence](#page-13-0) et al., 2023). Both approaches have been applied to soil ecoacoustics, with significant differences in acoustic index values between habitat types ([Maeder](#page-13-0) et al., 2022, [Robinson](#page-13-0) et al., 2023, Metcalf et al., 2024) and temporal patterns in activity (Maeder et al., 2022, [Metcalf](#page-13-0) et al., 2024). Studies have also found significant correlations between acoustic index values and traditional measures of soil invertebrate diversity, with positive relationships between species richness and community composition (Acoustic Complexity Index (ACI), [Maeder](#page-13-0) et al., 2022), abundance (Bioacoustic Index (BI), [Robinson](#page-14-0) et al., 2023), and invertebrate abundance and richness (ACI/BI, [Robinson](#page-14-0) et al., 2024a). These findings are consistent with results from above ground studies correlating acoustic indices with traditional biodiversity metrics. In that context, a large number of studies have found positive relationships between indices such as ACI, BI, and Acoustic Entropy (H), and species richness (e.g. [Eldridge](#page-13-0) et al., 2018, Bateman and Uzal, 2022, [Bradfer-Lawrence](#page-13-0) et al., 2020, Budka et al., [2023\)](#page-13-0).

Despite the associations between acoustic indices and diversity above ground, there are three key reasons why acoustic indices may not be suitable for assessing diversity in belowground soundscapes. First, many of the most widely applied indices are philosophically predicated on the Acoustic Niche Hypothesis [\(Krause,](#page-13-0) 1987). This assumes animals compete for 'acoustic space' to avoid signal interference from overlapping communications, and therefore evolve so that their sounds are emitted in a unique niche in time, frequency, and space. The hypothesis postulates that a more saturated soundscape has fewer vacant acoustic niches and thus reflects higher species richness. Indices can therefore reflect high species diversity if calculations are reflective of the saturation or occupancy of a soundscape. Much of the belowground soundscape is derived from incidental sound – reflecting the movement of animals in the soil substrate. Unlike communicative sounds, these incidental sounds are not subject to selection pressures for acoustic space, hence breaking the potential link between soundscape saturation and diversity. Second, in above ground studies indices show inconsistent performance as diversity proxies, with variable and declining effect sizes over time [\(Alcocer](#page-13-0) et al., 2022). Other studies have shown that none of the commonest acoustic indices have a consistent relationship with avian species richness that can be generalised across differing biophysical and biogeographic gradients [\(Sethi](#page-14-0) et al., 2023). Hence, it is unclear whether acoustic indices can be considered a reliable tool for assessing belowground biodiversity, without clarifying the links between soundscape characteristics and index responses. Third, there is a lack of validation from controlled experiments assessing how even the most commonly used acoustic indices respond to particular sonotypes (i.e., unique sound types analogous to a species morphotype). Those studies that do exist tend to be focussed primarily on bird calls (e.g. [Gasc](#page-13-0) et al., [2015,](#page-13-0) Zhao et al., 2019). Understanding how acoustic indices respond to different sonotypes, and in particular differing levels of acoustic diversity and abundance at different temporal scales, is vital to understand the utility of acoustic indices for ecological assessments of the soil.

We address these knowledge gaps by synthesising soil soundscapes with differing levels of acoustic richness, evenness, diversity, and abundance using biophony from real-world soil recordings from temperate (UK and France) and tropical (Brazil) locations. We examine:

- 1. How does variation in **a.** acoustic richness, **b.** single-sonotype abundance, **c**. multi-sonotype abundance, and **d.** acoustic evenness affect 14 acoustic indices?
- 2. Are combinations of indices able to predict **a.** acoustic richness, **b**. multi-sonotype abundance, and **c.** acoustic evenness in 1 min recordings?

Understanding the link between richness and indices at 1 min timescales is foundational. Yet biodiversity monitoring is often more concerned with gamma diversity, to compare land-uses and inform conservation policy and legislation. Consequently we also tested:

- 3. How does variation in gamma richness affect 14 acoustic indices when gamma richness is driven by **a.** both alpha and beta diversity components and **b**. mostly beta diversity?
- 4. Can the mean values of multiple acoustic index scores predict gamma richness when it is driven by **a.** both alpha and beta diversity components and **b**. mostly beta diversity?

2. Methods

2.1. Acoustic indices

We tested a total of 14 acoustic indices from the scikit-maad package ([Ulloa](#page-14-0) et al., 2021, v1.4.2) reflecting different aspects of the soundscape. These indices fall into four groups. The first group are simple descriptors intended to capture broad information about the distribution of sound: Temporal Median, Peak Frequency, Spectral Bandwidth, and Spectral Signal-to-Noise Ratio [\(Towsey,](#page-14-0) 2013) (Table 1). We hypothesised that these would not correlate strongly with any of our acoustic diversity metrics. The second group are event detectors, providing information on the number of sound events per file: Mean Temporal Events-per-Second ([Towsey,](#page-14-0) 2013), Spectral Event Counts ([Towsey,](#page-14-0) 2013), and Surface Roughness. We hypothesised these would positively correlate with acoustic abundance − at least at the one minute timescale. Mean Temporal Event Duration [\(Towsey,](#page-14-0) 2013) is similar but unlikely to correlate with abundance on its own, but may be useful when considering multiple indices as predictors of acoustic diversity. Indices in the third group identify clusters of events: Spectral Event Fraction ([Towsey,](#page-14-0) 2013), the Fraction of Spectral Activity above a 6 dB threshold [\(Towsey,](#page-14-0) 2017) and Region of Interest Cover. This may be useful for stridulations where

individual elements are too brief to be reflected in the second group of indices, and so these indices may correlate with acoustic richness or abundance. Finally, we included three acoustic indices that have been widely used in the above ground ecoacoustic literature as soundscape descriptors that may correlate with species richness; the Acoustic Complexity Index (ACI, [Pieretti](#page-14-0) et al., 2011), the Bioacoustic Index (BI, [Boelman](#page-13-0) et al., 2007) and Total Entropy (H, Sueur et al., [2008a](#page-14-0)). We hypothesise these should correlate positively with acoustic richness.

We calculated acoustic indices using the scikit-maad package in Python. All index values were calculated over 1 min files. Each file was resampled to 22,050 Hz − a window size of 512 was used where required, and spectrograms were produced with an overlap of 256. Full index parameters can be found in [Appendix](#page-11-0) 1, including whether indices were calculated over waveform $(n = 5)$, spectrogram $(n = 5)$ or noisereduced spectrogram ($n = 4$). All computed index values were scaled between zero and one using the scales package [\(Wickham](#page-14-0) et al., 2023) in R (R Core [Team,](#page-14-0) 2024, v4.4.1).

2.2. Soundscape synthesis

2.2.1. Selection of sonotypes

To test acoustic indices in a controlled manner, whilst making soil soundscapes as realistic as possible, we synthesised soundscapes from real soil biophony recordings. To maximise the geographic generalisability of our results, we used twenty sonotypes from two regions; ten sonotypes recorded in tropical rainforest close to Manaus, Amazonas,

Brazil and ten sonotypes from a range of temperate habitats in the UK and France (Fig. 1A). Recordings were made with the recordist present using a Sound Devices Mix-Pre 3, Mix-Pre 6, Mix-Pre 10 [\(https://www.](https://www.sounddevices.com/mixpre/) [sounddevices.com/mixpre/](https://www.sounddevices.com/mixpre/)), or an Elekon Allsounder [\(https://www.](https://www.allsounder.com/en/) [allsounder.com/en/\)](https://www.allsounder.com/en/). We used contact microphones − JrF C-series (<https://jezrileyfrench.co.uk/contact-microphones.php>) with Mix-Pre recorders; the Elekon Allsounder includes a proprietary contact microphone. In all but one case, a waveguide was used to aid transfer of vibrations from the soil to the microphone. We recorded in wav format and with gain adjusted to a suitable level by the recordist (see [Table](#page-11-0) A1 for full details of each sonotype).

The novelty of soil ecoacoustics and subsequent paucity of recordings makes it very difficult to assess what a representative soil soundscape would consist of in any habitat. Consequently the authors (Carlos Abrahams/Oliver Metcalf for UK and France, Érica do Vale/ Oliver Metcalf for Brazil) selected sonotypes that met both of the recording quality requirements (i.e., had high a signal-to-noise ratio and only contained a single sonotype that could be isolated in a 1 s clip). The twenty clips comprised sonotypes from Blattodea ($n = 5$, all Brazil), Hymenoptera (n = 4, Brazil), Hemiptera (n = 1, Brazil), Opisthopora (n $= 1$, UK), Rodentia (n $= 1$, France), Coleoptera (n $= 1$ identified, France and $n = 1$, presumed, UK) and unknown sources ($n = 6$, UK). The choice of using 1 s clips allowed us to include very short sounds without them being swamped by silence either side (e.g., Fig. 1 G and S), but also enough pulses and emissions from organism movement that represented sounds that continue for more than 1 s. (e.g., Fig. 1 E, F and H). Full

Fig. 1. An overview of data synthesis and soundscape simulation. Panels inside the blue box show the 20 unique sonotypes used to generate 1 min soundscapes. Panels inside the green box show 1 min soundscapes with varying diversity attributes. Top row shows soundscapes with acoustic richness values of 1, 10 and 20 (left to right) all with acoustic abundance of 60. The second row shows soundscapes with a single-sonotype abundance of 5, 30, and 55, the third row shows multisonotype abundances of 5, 30 and 55 and acoustic richness of 3. Bottom row shows soundscapes with Pielou's Evenness values of 0.139, 0.501 and 0.96 calculated on acoustic abundances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

details of the sonotypes used are available in [Appendix](#page-11-0) 2.

Due to the lack of publicly available soil acoustic libraries from which to identify sounds, it was impossible to only use sonotypes emitted by known species whilst including a representative sample of soil biophony. In Brazil, sonotypes were clipped from targeted recordings in which the sonifying taxon was identified after, but most of the UK recordings were from passive recordings. Consequently, six of the sonotypes used are from unknown sources, but judged to be biophony by the authors. We therefore refer to 'acoustic' rather than 'species' richness, evenness, diversity, and abundance throughout, as it is currently not possible to know whether multiple sonotypes were generated by the same species.

We edited each of the 1 s sonotype clips to standardise recording quality. We used Adobe Audition ([Adobe,](#page-13-0) 2023 v 24.03.3) to remove as much background noise as possible, before matching amplitude using the 'Match Loudness' setting. Next, we imported all clips into Audacity ([Audacity](#page-13-0) Team, 2023, v3.6.0), applied a 20 Hz High-pass filter and normalised the peak amplitude to -1.0 dB. Finally, we used the Audacity 'White noise generator' tool to create 1 s of white noise with a relative amplitude of 0.01 (unitless), and combined it with our sonotype files using the 'Mix and Render' tool, before downsampling where required, and exporting as a wav file with a 44,100 Hz sampling rate. We retained a 1 s wav file of the white noise to use as 'quiet' periods without sonotype presence in the synthesised soundscapes.

2.2.2. Relating indices to diversity at alpha scales

To answer **Questions 1** and **2**, testing how acoustic diversity impacts acoustic index values at alpha temporal scales (i.e., at the level of individual recordings), we synthesised a series of acoustic datasets following approaches used in above ground studies (Sueur et al., [2008a,](#page-14-0) Gasc et al., [2015,](#page-14-0) Chen et al., 2022). We varied the occurrences of 1 s sonotypes across 1 min soundscapes to simulate differing levels of acoustic richness (**a**), single-sonotype abundance (**b**), multi-sonotype abundance (**c**) and acoustic evenness (**d**). To assess how changes in acoustic diversity impacted index values (**Question 1**), we used the diversity values from each 1 min soundscape as predictors for acoustic index values. To test how well a combination of indices can predict acoustic diversity (**Question 2**), we used the index values as predictors in lasso models.

For acoustic richness (both **Question 1a** and **Question 2a**), each 1 min file contained 60 1 s units, and each unit was assigned a sonotype, so that acoustic abundance (i.e., total number of sound events per file − see below) was constant at 60. We created 100 1 min replicates for each level of acoustic richness: 1, 2, 3, 4, 5, 6, 10, 12, 15, and 20, with sonotypes randomly selected and randomly assigned a position in the 1 min file using the sample function in R. This meant that replicates with richness of one contained a single sonotype replicated 60 times, replicates with richness of two contained two randomly selected sonotypes repeated 30 times and randomly distributed across the 1 min file, and replicates with richness of 20 contained all 20 sonotypes with each repeated three times. The 100 replications of 60 sonotypes with 1 call each necessarily required duplication of some 1 min files. Sound file manipulation in R was conducted with the tuneR ([Ligges](#page-13-0) et al., 2023) and Seewave packages (Sueur et al., [2008b](#page-14-0)).

For acoustic abundance, or the total number of sound events per file, we assessed both the impact of variation in the number of calls in a soundscape containing only a single sonotype, and the number of calls from multiple sonotypes. For single sonotype abundance (**Question 1b**) we created 1 min files with 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55 and 60 replicates of each sonotype, with spaces filled with the 1 s white noise file. We replicated each of these files 60 times, randomly varying the temporal location of the sonotype replicates and white noise within each 1 min file − except those containing 60 sonotype replicates which could not vary temporally. This resulted in 3,605 1 min soundscapes. For multi-sonotype abundance (both **Question 1c** and **Question 2b**), we created 1 min files with a fixed acoustic richness of 3 and acoustic

abundance of 3, 6, 9, 15, 21, 30, 45, 40, and 60, with the three sonotypes randomly selected from the global pool of 20 for each file. Each increment of abundance was replicated 100 times, giving a total of 900 1 min soundscapes.

For acoustic evenness (both **Question 1d** and **Question 2c**)**,** we first generated all possible 1 min scenarios with between two and five sonotypes present, and with abundance of each sonotype ranging from 0, 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, and 50. Pielou's evenness values ([Pielou,](#page-14-0) 1966) were calculated for each scenario, and 10 scenarios were randomly sampled from each decile of evenness score, giving 100 scenarios. Each scenario was then replicated ten times, with one of the 20 sonotypes randomly assigned to each sonotype present per scenario, giving a total of 1,000 1 min files. Where total abundance of all the sonotypes in a scenario was less than 60, the remaining 1 s periods were filled with white noise. The order of the sonotype sounds and white noise was randomly determined for each 1 min file. In addition we tested the impact of temporal evenness (i.e., the clustering of sonotypes in the soundscape) $-$ for further details see [Appendix](#page-11-0) 3.

For all of the above synthesised datasets, we added 101 1 min soundscapes containing only white noise to represent periods without soil biophony. We generated a 1 min clip of white noise in Audacity using the default settings, then varied the gain from -10 to $+10$ by increments of 0.2, giving 101 files.

To assess the impact of varying diversity in our simulated soundscapes on acoustic index values (**Question 1**), we built generalised additive models (GAMs) in R. Each acoustic index was modelled against each diversity metric (acoustic richness, single-sonotype acoustic abundance, multi-sonotype acoustic abundance, and acoustic evenness) respectively, resulting in 56 GAMs. In each model, the diversity metric values from each 1 min file was used as the explanatory variable, and the corresponding acoustic index values as the response variable. All GAMs were fitted using the mgcv package ([Wood,](#page-14-0) 2017) called through the geom_smooth function in ggplot2 [\(Wickham,](#page-14-0) 2016) with cubic splines subject to shrinkage and allowing for the maximum number of basis functions.

To test how effective combinations of indices were at predicting each biodiversity metric (**Question 2)**, we built four lasso models using the glmnet package [\(Friedman](#page-13-0) et al., 2010) with all 14 acoustic indices used as linear predictors, with each biodiversity metric as the response. For acoustic abundance, we only tested multi-sonotype abundance, as it seemed a more plausible real-world scenario, and that the predictive capacity of the indices for single sonotype abundance would be intuitively apparent from these results. We used lasso models as they allowed us to keep all indices in the model and use the absolute value of the effect size of each acoustic index as a measure of variable importance.

2.2.3. Gamma diversity

Whilst understanding the relationship between acoustic diversity and acoustic indices at alpha scale (i.e., within 1 min file) can be useful in some scenarios, many temporal replicates will usually be necessary to ensure adequate sample representation. Similarly, spatial replication will be required to understand the total diversity of a heterogenous site or region (Buckland and [Johnston,](#page-13-0) 2017). In both cases, we need to determine whether acoustic indices can predict total richness of multiple replicates, which we define here as gamma diversity (**Question 3**). Gamma diversity consists of two components: species richness in each of the individual communities in the survey pool (alpha diversity), and the turnover in species between the surveys (beta diversity). As acoustic index scores have no species identities associated with them, accounting for beta components is problematic and potentially hinders accurate estimation of gamma diversity.

We simulated two scenarios to test whether multiple acoustic indices could predict gamma diversity when gamma is driven by both alpha and beta diversity (**Question 3a**), and when it is driven mainly by beta diversity (**Question 3b**). For each scenario, we predicted the gamma richness from index scores calculated on 1,440 1 min simulated soundscapes, replicated 100 times. We chose to use 1,440 sound files to simulate a ten-day passive acoustic monitoring survey, estimating richness at a single site − the recorder location − and using a sampling regime of recording 1 min every 10 mins. However, it is important to note that the 1,440 samples (hereafter referred to as a 'survey') could also represent spatial replication (e.g. 1,440 spatially distinct samples) or any combination of spatial and temporal combinations used to ensure an adequate balance of replication and representation.

For each survey, we randomly set a gamma richness of between one and 20. To increase realism, we set half the files in each survey to contain only white noise (i.e., acoustic richness $= 0$). For the remaining 720 files, we used simulated 1 min soundscapes containing our soil sonotypes. Using a unique 1 min soundscape for each sample in both scenarios would require generating and analysing 144,000 files. Instead we generated a pool of 2,000 1 min soundscapes (hereafter 'soundscape pool'), resampling this pool to obtain appropriate gamma diversity. Each of the 2,000 clips in the soundscape pool contained between one and three sonotypes randomly sampled from our pool of 20, and a total acoustic abundance of six, with any combination of sonotype repetitions possible within these limitations. These restrictions allowed us to isolate the effect of acoustic richness from abundance for both components of **Question 3**.

For **Question 3a**, where gamma diversity was driven by both alpha and beta diversity, we allowed both alpha and beta to vary by randomly sampling the soundscape, summing the sonotypes contained in each selected file until we reached the predetermined gamma richness for that survey. If the predetermined gamma richness was reached in less than 720 files, we restricted the pool of 2,000 files to those containing only the sonotypes previously sampled, and continued to randomly sample from the restricted pool until we had 720 files. For **Question 3b**, where gamma was mainly driven by beta diversity, we held alpha constant by limiting the soundscape pool to only files with a single sonotype, thus fixing alpha richness at 1.

We repeated the same statistical analysis for gamma diversity as we did with alpha diversity. First, we assessed the impact of gamma diversity on mean index values from each survey (**Question 3**), using GAMs for both scenarios **a** and **b**. GAMs were fitted with cubic splines with shrinkage and allowing for the maximum number of basis functions. We used gamma diversity as the explanatory variable and mean values of each index as the response variable. To test the predictability of gamma richness based on index mean values in both scenarios (**Question 4**), we built lasso models with all 14 acoustic indices as linear predictors of gamma diversity.

3. Results

3.1. The effect of acoustic diversity on acoustic indices

The response of acoustic indices to increasing acoustic richness (**Question 1a**) was highly variable and differences among sonotypes had a much larger effect on index values than total acoustic richness. However, a visual assessment reveals two broad groupings (Fig. 2). Temporal Median, Peak Frequency, Spectral Bandwidth, Temporal Events and Total Entropy seem to show almost no relationship with acoustic richness. The other indices appear to show positive relationships with acoustic richness at low values, before saturating as richness increases, often at values as low as three sonotypes. Of this latter group, Surface roughness, Region of Interest Cover, and ACI continue to show a slight increase in mean value as acoustic richness increases up to 20.

The relationships between single sonotype abundance and acoustic index value (**Question 1b**) was highly variable, both by index and by sonotype [\(Fig.](#page-6-0) 3A). Indices quantifying the number of sound events (Temporal Events, Spectral Events, Surface Roughness, but not Event Duration) and indices detecting clusters of events (Spectral Event Fraction, Spectral Activity and Region of Interest Cover) had strong positive relationships with acoustic abundance. Some of the simplest indices (e.g,. Peak Frequency, Spectral Bandwidth) and some of the most commonly used indices (e.g., ACI, BI) were almost entirely insensitive to acoustic abundance.

All indices with strong relationships with acoustic abundance showed high variability across sonotypes. Some index values saturated at higher abundances of certain sonotypes, with other indices even decreasing at higher values, with the peak values typically occurring around 30––50 % of the available time slots in the spectrogram ([Fig.](#page-6-0) 3A). Which sonotypes saturated or peaked varied among indices. To investigate the cause of this, we visually inspected spectrograms with detected events and acoustic activity highlighted in the scikit-maad package. This suggested that at higher abundances, index parameters were causing events from certain sonotypes to either be combined into a single event, or to go undetected as background noise. The exception to this was Surface Roughness, which maintained a near linear positive relationship for all sonotypes, although the magnitude of the relationship still varied greatly among sonotypes. Index relationships with multi-sonotype abundance (**Question 1c**) showed very similar relationships as for single sonotypes, with the variation caused by different sonotype communities being apparent through the spread in observation points ([Fig.](#page-6-0) 3B).

Acoustic evenness had little effect on acoustic index scores (**Question 1d**, [Fig.](#page-6-0) 4). Most indices showed a weak positive relationship (Spectral Bandwidth, Spectral Signal-to-noise Ratio, Spectral Events, Surface Roughness, Spectral Event Fraction, Spectral Activity, Regionof-Interest Cover, ACI, and BI) whilst the rest showed no clear

Fig. 2. The effect of alpha acoustic richness on acoustic index values. The point colours indicate acoustic indices with similar qualities (see [Table](#page-2-0) 1 for details).

Fig. 3. The effect of sonotype abundance on acoustic index values. Panel A shows the effect on single sonotype abundance, with a line plotted for each sonotype. Line colour and legend labels refer to the sonotype spectrogram panels in [Fig.](#page-3-0) 1. Panel B shows the index response to multi-sonotype abundance, with sonotype richness set at 3. Note the spread of points reflects the patterns of individual sonotypes in Panel A. The point colours indicate acoustic indices with similar qualities (see [Table](#page-2-0) 1 for details).

Fig. 4. The effect of acoustic evenness on acoustic index values. The point colours indicate acoustic indices with similar qualities (see [Table](#page-2-0) 1 for details).

relationship.

3.2. Predicting soil acoustic diversity with acoustic indices

The multi-index prediction of acoustic richness (**Question 2a**) was fairly accurate at lower values of richness [\(Fig.](#page-7-0) 5a), with predictions at richness values between 3 and 6 being overestimated by 2.2 sonotypes. At higher values the model considerably underestimated acoustic richness, so that the predictions for richness of 20 were averaging just 13.38 sonotypes. However, there was high variation in predictive accuracy; the standard deviation for acoustic richness values between 3 and 6 was \pm 1.95 and 2.5 sonotypes.

Multi-index prediction of multi-sonotype abundance (**Question 2b**) was far more accurate than for sonotype richness ([Fig.](#page-7-0) 5c), suggesting

that acoustic indices can accurately predict sonotype abundance at alpha scales. Average predictions were close to the observed abundance for all values. However, standard deviation in prediction error increased considerably as observed abundance increased, particularly for values over 30. As expected, acoustic indices that quantify the number of sound events in a spectrogram had the largest effect sizes in the lasso model ([Fig.](#page-7-0) 5d).

For acoustic evenness (**Question 2c**), multi-index predictions with the lasso model showed a similar trend to acoustic richness. Evenness was overestimated at low values and underestimated at high values, but overall had higher error and larger variance in predictions. This suggests that acoustic indices are not effective predictors of acoustic evenness ([Fig.](#page-7-0) 5e).

Fig. 5. Predictions of acoustic diversity using all indices as predictors. Panels a, c, and e show lasso model predictions against actual diversity values. Red dots show mean predictions, in panels a and d for each diversity value, and in panel e for every decile of simulated evenness. Error bars show standard deviation. The dotted line shows where perfect predictions would lie. Panels b,c, and f show the absolute value of the effect size (equivalent to variable importance) for each acoustic index in the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Acoustic index response to gamma richness

Acoustic indices were largely unresponsive to changes in gamma acoustic richness without a fixed alpha diversity component (**Question 3a**). Spectral Signal-to-Noise Ratio and Surface Roughness showed a strong positive relationship at low richness values before saturating, whilst ACI and BI showed weaker but linear positive relationships ([Fig.](#page-8-0) 6A). When the alpha component of gamma diversity was fixed

(**Question 3b**), all positive relationships disappeared, so that gamma diversity did not have a strong impact on any index values ([Fig.](#page-8-0) 6B).

3.4. Predicting gamma richness with acoustic indices

The lasso models predicted gamma richness well when increases in richness were derived from both alpha and beta diversity (**Question 4a**) − i.e., when mean sonotype richness per minute increased [\(Fig.](#page-8-0) 7A).

Fig. 6. The effect of gamma acoustic richness on mean acoustic index values. The point colours indicate acoustic indices with similar qualities. Panel A shows gamma acoustic richness values derived from increasing both alpha and beta diversity − i.e., when mean sonotype richness per minute was allowed to vary. Panel B shows gamma acoustic richness values derived from increasing beta diversity only − i.e., when mean richness per minute was fixed, but there were different sonotypes present between minutes.

Fig. 7. Lasso model predictions of gamma acoustic richness using the mean index values calculated for each site as predictors. Panel A shows richness derived from varying alpha and beta diversity whilst Panel B shows richness derived from varying only beta diversity. The dotted lines in both panels show the 1:1 line where perfect predictions would lie.

Predicted values closely matched observed values at all values of richness, with low error and variance. However, when gamma diversity was driven by sonotype turnover rather than alpha acoustic richness (**Question 4b**) − i.e., when the mean richness per minute remains the same but there are different sonotypes present between minutes – the relationship between acoustic index values and acoustic richness disappeared (Fig. 7B).

4. Discussion

4.1. The efficacy of acoustic indices for monitoring soil diversity

4.1.1. Single indices

Our results show that acoustic indices are good predictors of the abundance of soil sonotypes at alpha scales, with many showing strong and near-linear relationships with single and multi-sonotype abundance. The indices with the strongest responses to sonotype abundance were, as expected, those intended to count events. However, in most cases, index values saturated or peaked below the maximum abundance value for at least some of the sonotypes tested. Visual inspection of spectrograms suggested this was mostly due to the event detection parameters in the index calculations. As events became more abundant, gaps between individual events decreased, so that multiple events merged into single events. Surface Roughness was the exception and did not saturate across all sonotypes and abundance values tested here. This was likely because the index calculation does not include an event detection process based on predetermined amplitude thresholds and instead reflects fine-scale temporal variations in amplitude across the whole recording.

Saturation of index values at higher levels of sonotype abundance could potentially be resolved by fine-tuning index parameters against a test data set. However, this is time-consuming and, as most event detection processes use relatively unsophisticated methods, it is unlikely to fully resolve this issue without creating additional problems of overcounting in other scenarios. This complication may be particularly prevalent in soil recordings containing a variety of stridulations that occur at different speeds.

Even where index responses to abundance take similar shapes, the magnitude of the effect differed across sonotypes for all indices ([Fig.](#page-6-0) 3A). This sensitivity is perhaps not surprising given previous studies have shown that indices are impacted by sonotype characteristics of birds (Gasc et al., [2015,](#page-13-0) Zhao et al., 2019), although variation in bird calls and song is much greater than the variation among sonotypes used in our simulations. As it is likely that a far greater range of soil biophony exists globally than we were able to test here, we urge caution in the use of single acoustic indices to assess alpha abundance. Sensitivity to sonotype form could be accounted for with either *a priori* knowledge of the sonotypes likely to be encountered and knowledge of the corresponding index response (for instance derived from mesocosm experiments) or, as with most above ground use-cases for acoustic indices, case-by-case validation using manual counts of sonotype abundance. Fortunately, this sensitivity did not strongly reduce indices' predictive capacity, which showed low error at all but the highest values.

Acoustic indices could effectively predict sonotype richness at relatively low levels (*<*10 sonotypes per minute), although at the risk of a degree of overestimation. There is very limited evidence for rates of acoustic richness in real soil recordings, but this seems to be a plausible level of richness over 1 min recordings in most scenarios based on the authors' own data and the few published studies ([Maeder](#page-13-0) et al., 2022, Robinson et al., 2023, [Robinson](#page-13-0) et al., 2024a). Greater predictive accuracy at lower richness values could initially appear contradictory, given that variation in the effect of richness on individual indices appears to decrease at higher values [\(Fig.](#page-6-0) 3). However, this reduction is likely because there are fewer possible permutations of the sonotype community at these values, rather than stabilisation of variation in index values, and this would likely not occur if a larger pool of sonotypes were available.

In addition, we found that acoustic indices are unaffected by variations in acoustic evenness and, even in combination, acoustic indices only poorly predict this metric. That is perhaps unsurprising, given the calculation of Pielou's evenness includes both richness and abundance of sonotypes, and the rather basic descriptions of soundscapes provided by acoustic indices.

4.1.2. Multi-index prediction

Our results suggest that saturating individual index responses need not be an issue for multi-index prediction accuracy. These predictions showed only limited evidence for saturation, despite increased error rates above a sonotype abundance of 40, the central tendency remained accurate across all values. Presumably the combination of different indices saturating or peaking at different abundance values provided sufficient predictive power. This finding highlights both the importance of selecting acoustic indices appropriate for the task [\(Bradfer-Lawrence](#page-13-0) et al., [2023](#page-13-0)), and the benefits of using multiple indices, even when they are calculating similar acoustic features.

Somewhat surprisingly, the lasso model for acoustic richness showed the greatest effect sizes for indices that showed little relationship between richness and index score at the individual level, with Total Entropy having the largest effect size ([Fig.](#page-6-0) 3B). This is most likely because so many of the other indices showed a similar relationship that the small amount of additional information provided by these weak relationships is disproportionately useful. It is worth noting here that all of the effect sizes for the lasso models are relative, and are specific to the use case and dataset. It should not be assumed that the top ranked indices would be effective predictors of biophonic diversity in isolation. Additionally, it is possible that using other statistical approaches, such as generalised linear models with backward model selection or Random Forest may produce better predictive performance than the lasso models which retain collinear predictors.

4.1.3. Predicting gamma diversity

We found that a combination of indices can predict gamma richness, but only when both alpha and beta diversity drive gamma together, and not when beta diversity alone drives gamma richness. As long as mean alpha diversity correlates with gamma diversity, our results showed that gamma diversity can be predicted by the average values of indices. However, it is important to note that alpha and beta contributions to gamma diversity in natural communities depend on several factors ranging from environmental heterogeneity, sampling strategy, functional groups of target organisms and spatio-temporal scales used in the study [\(Barton](#page-13-0) et al 2013, Maaß et al 2014). For instance, in situations where turnover of species and/or sonotypes is high, there is a higher chance that average values of indices will not correlate to gamma diversity, and therefore the utility of indices will be limited. This is applicable for both temporal and spatial gamma, where higher temporal and spatial beta diversity would make the relationship between mean alpha and gamma diversity weak. As in most cases, collecting sufficient field data to understand the relative contributions of alpha and beta diversity would render the use of acoustic indices redundant, it is likely that there are only limited circumstances when indices should be used to predict gamma richness, and using an average of alpha richness may generally be more appropriate.

4.2. Linking acoustic diversity to taxonomic diversity

Whilst predicting soil sonotype abundance may be of direct utility, this study did not assess whether sonotype abundance correlates directly with faunal abundance. However, previous studies have shown correlations between soil invertebrate abundance and acoustic index values (Maeder et al., 2022, [Robinson](#page-14-0) et al., 2023, 2024a), and it is difficult to think of alternative plausible mechanisms for such relationships if increases in faunal abundance do not result in increased acoustic activity. Assuming sonotype abundance relates to species abundance, richness, and/or macrofaunal activity rate – or perhaps more likely a combination of these − then it seems plausible that acoustic indices could be used to predict at least some facets of soil function ([Bardgett](#page-13-0) and Van Der Putten, 2014, Görres and [Kammann,](#page-13-0) 2020). Of these, bioturbation and nutrient cycling seem the most likely to be reflected by faunal abundance [\(Gabet](#page-13-0) et al., 2003). Further research would also be useful to test whether time-series of sonotype abundance could track the degradation or recovery of soil under land use change, forest regeneration ([Robinson](#page-14-0) et al., 2024a, [Robinson](#page-14-0) et al., 2024b) or the impact of environmental stressors such as deforestation ([Franco](#page-13-0) et al., 2019), or recovery from wildfire (de [Andrade](#page-13-0) et al., 2014, Metcalf et al., 2024). Extending acoustic richness to taxonomic richness may be even more challenging − although it seems likely that, in comparison to birds, for which it is most common to compare ([Alcocer](#page-13-0) et al., 2022), sonotypes from individual taxa will be less variable, especially when considering incidental sounds as well as communication. Initial soil acoustic studies [\(Maeder](#page-13-0) et al., 2022, [Robinson](#page-13-0) et al., 2024a) have found positive relationships between soil macrofaunal richness and ACI and BI, suggesting acoustic richness and taxonomic richness are correlated.

4.3. Future research in using acoustic indices to monitor soil biodiversity

This study assessed the response of acoustic indices to various aspects of diversity, using simulated soil soundscapes that allowed us to directly relate index scores to changing biophony. However, while we attempted to maintain ecologically plausible variation in the simulations, there is a need to further investigate how acoustic indices respond in more complex sonic environments before being confident of performance under real-world conditions. This includes varying the distance of sonifying organisms from the microphone, varying amplitudes of sonification at source, and varying the amplitude of background noise − all of which will impact the recording's signal-to-noise ratio. Previous studies have shown that ACI, BI, and H values are impacted by signal-to-

noise ratio (Gasc et al., [2015,](#page-13-0) Chen et al., 2022), although it is worth noting that the simple indices we tested that are most likely to be directly affected by varying signal-to-noise ratio, such as Spectral Signalto-Noise Ratio and Peak Frequency, were poor predictors of diversity metrics. Other indices, in particular those aimed at event detection which include amplitude thresholds in the calculation, could be substantially impacted by varying background noise levels. Fortunately, four of these, Spectral Event Counts, Spectral Event Fraction, Fraction of Spectral Activity and Region-of-Interest Cover are intended for use on spectrograms post-noise reduction [\(Appendix](#page-11-0) 1, [Table](#page-2-0) 1). This preprocessing should greatly limit the effect of variation in background noise level. In this study, Spectral Event Counts and Spectral Event Fraction were two of the top five most important predictors for alpha richness, and Fraction of Spectral Activity and Spectral Event fraction are the first and fourth most important predictors of alpha abundance. This strongly supports the use of noise reduction prior to calculating acoustic indices. Future studies should further investigate the various methods of noise reduction (Xie et al., [2021\)](#page-14-0) and how effectively this can limit the impact of variable background noise on index values in complex sonic environments.

The presence of non-biophonic sound, absent in these simulations, may challenge the fidelity of index responses to changes in biodiversity. We know from a range of above ground studies that acoustic index responses can be masked by geophony (e.g., Ross et al., 2021, [Turlington](#page-14-0) et al., [2024\)](#page-14-0). However, it may be possible to identify periods in soil recordings dominaed by geophony or anthropophony. A range of tools to identify wind [\(Terranova](#page-14-0) et al., 2024), rain [\(Brown](#page-13-0) et al., 2019, Sánchez-Giraldo et al., 2020), and anthropophony ([Quinn](#page-14-0) et al., 2022) already exist for above ground soundscapes. Additional research is needed to determine what forms of above ground biophony, geophony and anthropophony exist in soil acoustic recordings. This will clarify which existing methods can effectively detect and/or remove non-biophonic sound from recordings, or whether new methods are required specifically for soil ecoacoustics.

There is also a need to develop accessible libraries of soil sounds and soundscapes, in order to better understand the sort of sounds which are commonly encountered in the soil and link them with the organisms creating them. This may be best conducted through recording ex-situ mesocosms containing known faunal communities. Such ex-situ research may help to better understand identifying characteristics of species' sonifications, and environmental and behavioural factors affecting the cue rates of individual organisms (Teuben and [Verhoef,](#page-14-0) [1992,](#page-14-0) Keen et al., 2022). It can also help in filtering out sounds that are not informative of soil ecological condition, such as above ground biophony and geophony. In turn this will improve understanding of varying community detectability levels in the field (Görres and [Chesmore,](#page-13-0) 2019; [Harvey](#page-13-0) et al., 2011).

4.4. Summary

Acoustic indices are potentially important analytical tools for soil ecoacoustic data − especially given current limits to our knowledge of characteristic sounds from different taxa. This study provides the first steps in showing which acoustic diversity metrics and indices work the best, and which are unreliable. Further research is required to investigate the relationship between acoustic diversity metrics and biodiversity metrics, as well as confirming that acoustic indices are responsive to

acoustic diversity metrics in real world conditions and mesocosm experiments. Should further studies be able to demonstrate this, acoustic indices could complement existing manual approaches to assessing soil diversity by allowing non-invasive monitoring of belowground biodiversity over long time periods.

5. AI statement

No AI generative writing tools have been used in the production of this paper.

CRediT authorship contribution statement

O.C. Metcalf: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft, Writing – review & editing. **C.A. Nunes:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **C. Abrahams:** Conceptualization, Data curation, Writing – review & editing. **F. B. Baccaro:** Conceptualization, Data curation, Writing – review & editing. **T. Bradfer-Lawrence:** Conceptualization, Formal analysis, Methodology, Writing – review & editing. **A.C. Lees:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review $\&$ editing. **E.M. Vale:** Data curation. **J. Barlow:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review $&$ editing.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Carlos Abrahams reports a relationship with Baker Consultants that includes: employment. Carlos Abrahams is a Director of Baker Consultants, who provide consultancy services for ecoacoustic monitoring including soil acoustics. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices

Table A1

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Acoustic Indices.

1. Waveform produced by reading a wave file into Python using wave.open and resampling to 22050 kHz using sound.resample().

2. Spectrogram computed using

sound.spectrogram(s_resamp, fs, nperseg = 512, noverlap = $512 / 2$).

3. Noise-reduced spectrogram computed using:

Sxx_noNoise = sound.median_equalizer(Sxx, display = False, extent = ext) Sxx_dB_noNoise = util.power2dB(Sxx_noNoise).

Appendix 2. Sonotype details

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(*continued on next page*)

(*continued*)

Appendix 3. Temporal evenness

To test the effect of the temporal distribution of sonotypes across 1 min soundscapes, we created soundscapes with sonotypes clustered to varying extents. We created 100 1 min soundscapes per sonotype ($n = 2000$), so that acoustic richness in each 1 min soundscape was always 1. Each 1 min soundscape contained 20 repetitions of the sonotype, so that acoustic abundance always equalled 20. Clusters consisted of 1, 2, 4, 5, or 10 repetitions of a 1 s sonotype in a row and after each event, a single second of white noise was inserted to separate consecutive events. We randomly allocated the temporal distribution of clusters across the soundfile and the remaining time was filled with white noise. Therefore a cluster length of 1 resulted in 20 1 s sonotypes randomly distributed across the minute, with at least 1 s of white noise proceeding each of them, whilst a cluster length of 5 resulted in four clusters of ten 1 s sonotypes in a row with at least 1 s of white noise between them. Each combination of sonotype and cluster duration was repeated 20 times to ensure the precise temporal placement of clusters was varied for each combination. To ensure uniqueness, each simulated sequence was compared to previously generated sequences, and only non-redundant sequences were retained. Analysis thereafter was the same for other diversity metrics, except that we only tested the effect of acoustic evenness on acoustic indices, and did not examine indices predictive capacity as that seemed to have limited real-world application.

Results

Almost all of the indices showed limited or no response to increasing clump size in the 1 min soundscapes. The exception was Event Duration, which linearly increased with increasing cluster size for one sonotype, likely due to event detection viewing the entire cluster as a single event for that sonotype but maintaining differentiation between each sound event for the other sonotypes.

Overall, this suggests that the acoustic indices we tested are reasonably robust to the temporal dispersion of sound events in a soundscape.

Data availability

The audio files used in generating the syethsised soundscapes are available on Zenodo. DOI 10.5281/zenodo.14277136.

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