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The Use of Ecoacoustics to Monitor Soil Ecology: A Critical Review With Reference to Earthworms

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ABSTRACT

The use of ecoacoustics to monitor soil ecology was identified as a priority in the 2024 horizon scan of global biological conservation issues. Proponents suggest it will have societal impacts by improving soil health assessments, enhance soil biodiversity monitoring and facilitate the conservation, remediation and management of soil ecosystems. Here we review soil ecoacoustics in terms of its definition, theoretical basis, acoustic indices and statistical inferences. To do this we explain mechanical wave behaviour, mechanoreception by fauna, and tactical signal design with reference to earthworms as ecosystem engineers. Ecoacoustics emerged from research on animal long-distance communication systems, and its direct application to soils has been identified as a problem area. A new field within ecoacoustics has been created for soils, sonoscape investigations, to capture spatio-temporal complexity of ecological features (rather than soil ecology). There is a good case for reclassifying soil ecoacoustic 'soundscape' studies as sonoscapes. We identify that further refinement of ecoacoustics is required for applications to soil habitats. The performance of sonoscape investigations is dependent on acoustic indices and statistical inferences, and we question why stationary signal processing is used as the base transform for soils data, and highlight the issue of unbalanced data sets, particularly pertinent to soils as there is limited understanding of what exactly is being detected. We list the key research needs and highlight that integrating soil science and mechanistic modelling of soil processes and wave propagation as an essential component of developing reliable monitoring solutions. Embracing these interdisciplinary avenues will help develop sensing capabilities for soils in robust scientific principles and mitigate the risks of speculative overreach.

1 | Introduction

Research on the use of ecoacoustics to monitor soil ecology has started to expand in the scientific literature but is still limited in extent and maturity. Its potential application has been widely broadcast; for example, the annual horizon scan of worldwide biological conservation issues ranked the use of ecoacoustics for monitoring soil ecology in the top 15 issues for 2024 (Sutherland et al. 2024). Concomitantly, a new systems theory for soil emphasises a radical shift in thinking away from conventional, disconnected soil features, for example, a worm count, towards dynamic properties to understand the relationships between

Summary

- Ecoacoustics is reviewed as a method to monitor soil ecology.
- Studies are sonoscapes reporting the spatio-temporal complexity of soil ecological processes.
- Sensory drive model can be applied to soils to predict sensory systems and signalling properties.
- Interdisciplinary collaborations are needed to improve understanding of what is being detected.

components, complexity and function (Harris et al. 2022). It is therefore timely to review ecoacoustics in the context of capturing both temporal dynamism and ecological complexity (Farina et al. 2024).

Traditionally, acoustics studied pressure waves that propagate in fluids at frequencies that can be heard by the human ear. However, over the decades, the meaning of the term has expanded to include inaudible frequencies, and waves in other media, including poroelastic solids. According to the newest edition of a seminal textbook on sound (Pierce 2019), the terms 'acoustics' and 'sound' refer to any mechanical wave phenomena governed by analogous physical principles. Irrespective of the constitutive laws governing a medium, these mechanical waves involve transport of energy without net transport of mass, associated with local particle vibration. Acoustical transducers capture propagating waves by measuring pressure fluctuations in fluid media (e.g., microphones and hydrophones), or particle/surface vibration (e.g., accelerometers, geophones, laser vibrometers, and piezoelectric ceramics). Without initiating another discussion on the rigour of this terminology, we acknowledge that the more capacious definitions of acoustics and sound are widely accepted by the community.

However, such broad terminology has implications for soil ecology, because an event such as an arthropod drumming its limbs on a burrow surface, will produce a range of mechanical waves, but not all wave types are used by animals as signals (e.g., transmission, reception, and ease of remembering pattern). Seminal research in species sensory systems and signalling properties (Sensory Drive model) maintains that the physical properties of the habitat support the development of particular sensory signals and modes, which drive evolution to match these properties (Endler 1992). The substrate imposes many constraints on signalling, and these environmental conditions influence the evolution of signalling systems. Conventional wisdom had it that mechanical waves were unsuitable for animal signalling (medium too heterogeneous, too inelastic, wave speed too fast) but seminal research demonstrated that scorpions localise burrowing prey (cockroaches) in sand from 50 cm away (Brownell 1977). Here it was shown that scorpions have spatially separated sense organs on their legs, with the tarsal sensory hairs responding to the higher frequency components of the signal, mostly compressional body (P) waves (travelling at 120 m/s) and the slit sensillum responding to the slower Rayleigh waves (travelling at 50 m/s), using the time delay between early and late arriving waves to locate burrowing prey. As environmental constraints impose selective pressures on sensory systems, coupling the knowledge of environmental physics (e.g., mechanical wave types that occur in soils) to tactical signal design (maximising the received signal relative to background noise and minimising signal degradation), should in principle, allow for predictions about the structure of signals used by animals in that environment (Endler 1993). This led to a 25-year research trajectory that was critically assessed to understand the evidence base (habitats and sensory modes) where there is an environmental influence on signalling traits (Cummings and Endler 2018).

The concept that monitoring animal signals could be an indicator of environmental health emerged at around the same time—but independently of the sensory drive model, with a different theoretical background comprising two broad hypotheses that have been later formalised. The Acoustic Niche Hypothesis attributed to Krause (1993), proposes that animals partition their vocalisations to minimise interferences with each other (i.e., biotic rather than environmental constraints). The Acoustic Adaptation Hypothesis, attributed to Morton (1975) from field studies on long-distance bird communications, and Forrest (1994) reviewing long-range pair-forming signals in terrestrial and aquatic habitats, proposes that animals maximise signal transmissions in the environment. This led to a 20-year research trajectory which has culminated in a field called ecoacoustics, which was formalised in 2014 and is described as the "holistic field of study with the aim to offer a broad multidisciplinary approach to assess the environmental quality of sonic signals and monitor their ecological dynamics at multiple scales from individual species to land- and seascapes" (Farina et al. 2024). Soundscape ecology (Pijanowski et al. 2011) is a component of ecoacoustics; and *soundscape* is defined as (ISO 12913): "acoustic environment, as perceived or experienced and/or understood by a person or people, in context". The most recent annual horizon scan of worldwide biological conservation issues ranked the use of ecoacoustics for monitoring soil ecology in the top 15 issues for 2024 (Sutherland et al. 2024).

An assumption that investigations of ecoacoustics could be made in soil habitats was made nearly a decade ago (Sueur and Farina 2015), despite the above-ground terrestrial and marine habitat bias, and emphasis on perception of mechanical waves through the sense of hearing. However, soil is much more complex than a single-phase fluid (e.g., air or water), as it is comprised of having solid, liquid and gaseous states partitioned in a given control volume. Soil qualities are property (i.e., texture class, pore/particle size distributions, and organic fraction) and status (i.e., water content, bulk density, and temperature) dependent, meaning "universal" soil quality assessments are particularly difficult to develop (Nortcliff 2002). Conventional soil quality assessments use a test point or benchmarking approach to generate scorecards of isolated metrics, but this paradigm is being challenged because soils are dynamic, emergent systems and a new systems theory for soils is proposed (Harris et al. 2022). This new theory calls for a paradigm shift in soil science towards systems-based approaches. Practically, the complex composition of the soil matrix acts as the propagation medium through which diverse mechanical wave transmit, amongst seismic noise wavefields and ambient sound which penetrates soil surfaces. Soil dwelling inhabitants are both generators and detectors of mechanical waves in soils. But the details of the mechanisms of generation and detection are relatively unexplored. For example, burrowing activities will excite the soil framework

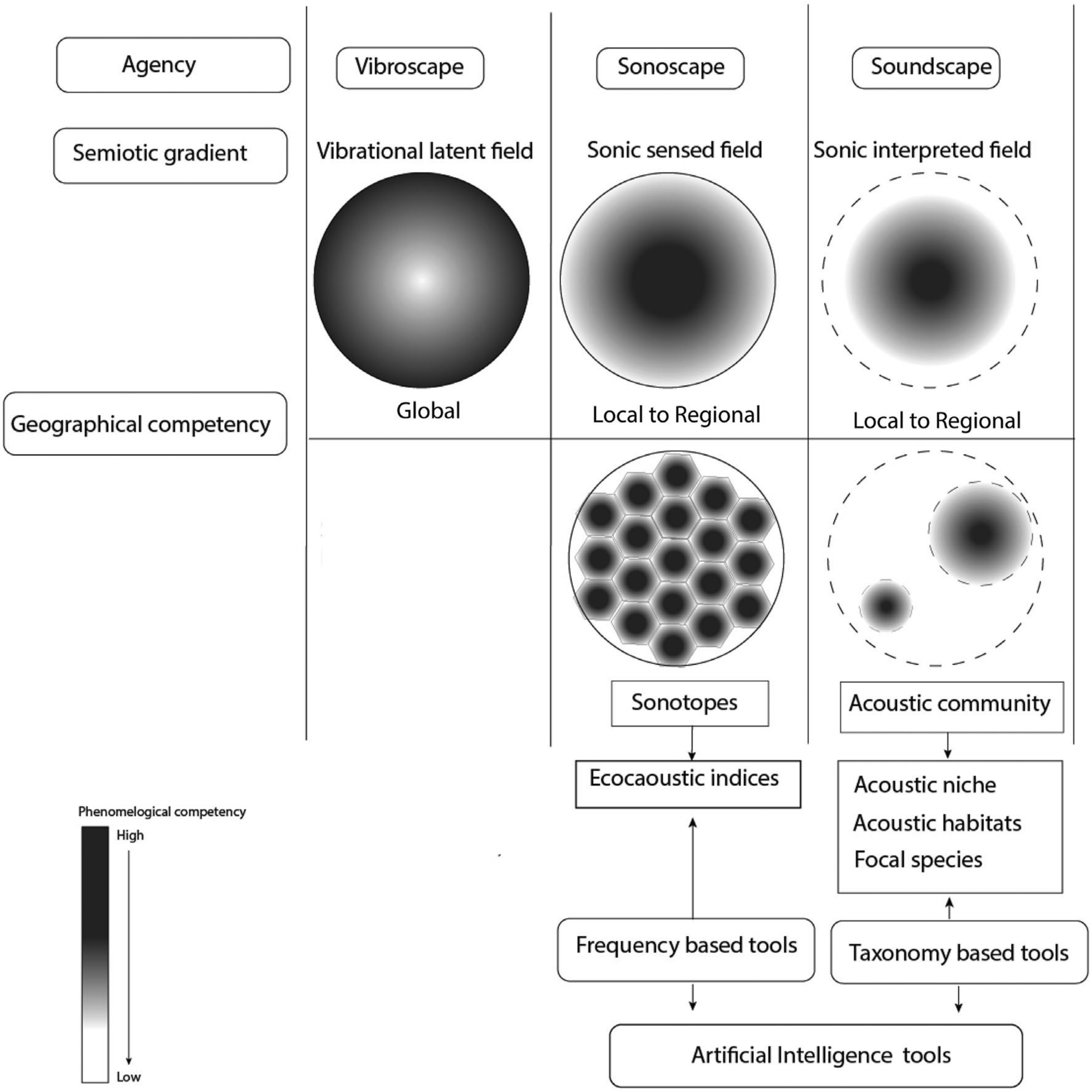

FIGURE 1 | A graphical representation of the ecoacoustic narrative (taken from figure 1, Farina et al. 2024). Soil investigations fit into the 'sonoscape', utilising indices and statistical classification to improve understanding of the spatio-temporal complexity of ecological processes.

but once a burrow is formed it can act as a waveguide for signals both along the sides of the burrow and in the air filling the burrow that could be detected by the occupant. Unlike aboveground terrestrial and aquatic settings, there are no substantial libraries of soniferous inhabitants in soils (Metcalf, Nunes, et al. 2024), and the phenology of soil organisms is largely unknown (Bonato Asato et al. 2023) to inform and check the performance of the acoustic indices such as the Sonic Heterogeneity Index which underpin ecoacoustic investigations (Farina 2025). Soil has been identified as a problematic area in ecoacoustics and a framework for such ecoacoustic investigations is called the sonoscape (Figure 1) (Farina et al. 2024). These sonoscape investigations bypass the ecoacoustic theoretical basis and the taxonomy based tools (which enable testing of acoustic indices performance), and go straight to the use of acoustic indices and statistical classifications to 'inform on the spatio-temporal complexity of ecological processes without the interference of classification labels' (Farina et al. 2024).

In this paper, we aim to critically review soil ecoacoustics, with particular attention to sonoscope investigations; introducing wave behaviour in Section 2, a discussion of theories relating to animal signalling with reference to earthworm biology and ecology in Section 3, an overview of studies on mechanical waves and ecoacoustics in the literature in Section 4, concluding with key research needs in Section 5, with reference to advancing a systems theory of soil. In addition to the aforementioned soil ecoacoustics for monitoring soil ecology, the threat of 'large scale earthworm decline' was also identified as a priority issue in the 2024 horizon scan (Sutherland et al. 2024), thus, in what follows particular attention has been directed towards earthworms.

2 | Mechanical Waves in Soils

2.1 | Characteristics of Wave Types That Can Occur in Soils

To understand the nature of mechanical wave signals received and generated by subsurface biota, it is useful to explore the different mechanical wave types that can occur in soils. Soils

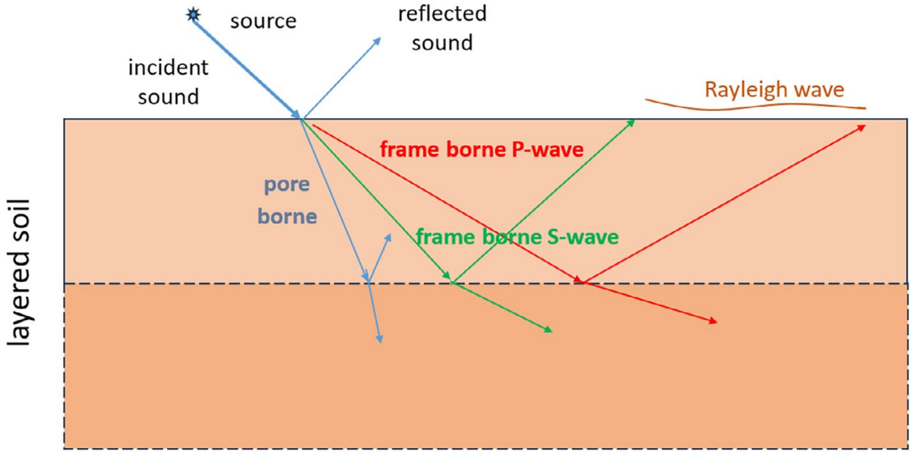

FIGURE 2 | Mechanical waves in soils.

are composed of aggregates of minerals and organic matter forming a porous solid in which the pores contain air, water or both. In common with non-porous solids, soils support mechanical or elastic body waves, that is, primary or compressional and shear or transverse, known as seismic P- and S-waves, respectively (Narins 2001). However, the porosity of soils means that the wave types they support differ somewhat from those in non-porous elastic solids. Relevant theoretical work, carried out initially in the context of oil exploration (Biot 1956a, 1956b), considered waves in fluid-saturated two-phase porous elastic media; the two phases being the fluid filling the pores and the solid frame of aggregated particles. As well as predicting compressional and shear waves, (corresponding to the seismic P- and S-waves), travelling mainly through the solid frames, the theory predicts an additional compressional wave travelling mainly in the pore fluid. The speed of this wave is less than the speed of sound in unbounded fluid and as a result is called a slow wave. Also, the mainly pore-borne wave attenuates much faster than the mainly frame-borne wave as a result of viscous drag and heat exchanges at the pore walls. The mainly pore-borne waves are out of phase with the mainly frame-borne waves. Although thermal exchange contributes to the attenuation of slow waves in air-filled porous materials, it is not important in water-filled media. The mainly frame-borne waves have speeds closer to those that might be expected of those in a non-porous solid with the same elasticity and are detectable by vibration sensors. The granular nature of soil frames leads to contact friction between soil particles which, together with the viscous friction between the pore fluid and the pore walls, increases the attenuation of the P- and S- seismic waves in soils compared with the attenuation of waves in non-porous solids with similar elasticity. The mainly pore-borne waves and mainly frame-borne waves in soils may be regarded as responsible for the mechanical waves received and generated by subsurface biota. However, frame and pore-borne waves are coupled. Predominantly frame-borne waves have a pore-borne component and predominantly pore-borne waves have a frame-borne component. The relative magnitudes of the frame and pore-borne components will depend on the mode of excitation. Direct excitation of soil particles will result in mainly frame-borne waves. Direct excitation of the air (or water) in the pores will produce mainly pore-borne waves. However, either mode of excitation can create both frame-borne and pore-borne waves.

Sound waves arriving at the soil surface are reflected and transmitted (Figure 2). Most of the energy incident from sources above the surface is transmitted into the slow pore-borne wave (Attenborough 1987; Attenborough et al. 1986; Richards et al. 1985). In typical soils, the slow speed of the wave travelling mainly in the pores means that most of the sound energy penetrating from above is refracted towards the normal to the surface and little spreads horizontally (little energy travels parallel to the surface). Excitation of pore-borne waves also causes frame-borne vibrations with less attenuation. This is known as acoustic-to-seismic coupling (Sabatier, Bass, Bolen, and Attenborough 1986; Sabatier, Bass, Bolen, Attenborough, et al. 1986).

If there are connected paths through the water in a partially saturated soil, then it can be regarded as a three-phase medium with the possibility of a third compressional mainly water-borne wave (Brutsaert and Luthin 1964; Shin et al. 2016). Partly frozen soil can be regarded as a three-phase medium, that is, soil frame, ice and water, and can support a second type of shear wave (Leclaire et al. 1994). In otherwise water-saturated media, the presence of air bubbles is known to have an important influence on compressibility and, therefore, attenuation (Degrande et al. 1998).

Suitably protected probe microphones can be inserted into soils to measure the extent to which sound penetrates through air-filled pores (Figure 3, Moore and Attenborough 1992). The results of measurements made at 1 cm depth intervals in a friable soil (Harrop 2000) using a specially protected probe microphone suitable for insertion in soils (Figure 4). The graph shows the level difference between the signal at the buried probe microphone and the identical probe microphone at the surface. Since the buried microphone responds mainly to airborne pressure fluctuations, the measured level difference represents the relative amplitude of the wave travelling mainly in the pores of the soil. Note that the rate of decrease is not uniform (Figure 3). There is a comparatively large decrease over the first 2 cm and an even larger decrease between 2 and 3 cm depth suggesting a compacted soil layer near the surface. Beyond a depth of 9 cm, the component of the pore-borne contribution due to frame-borne waves excited at the surface adds to the component of the pore-borne contribution

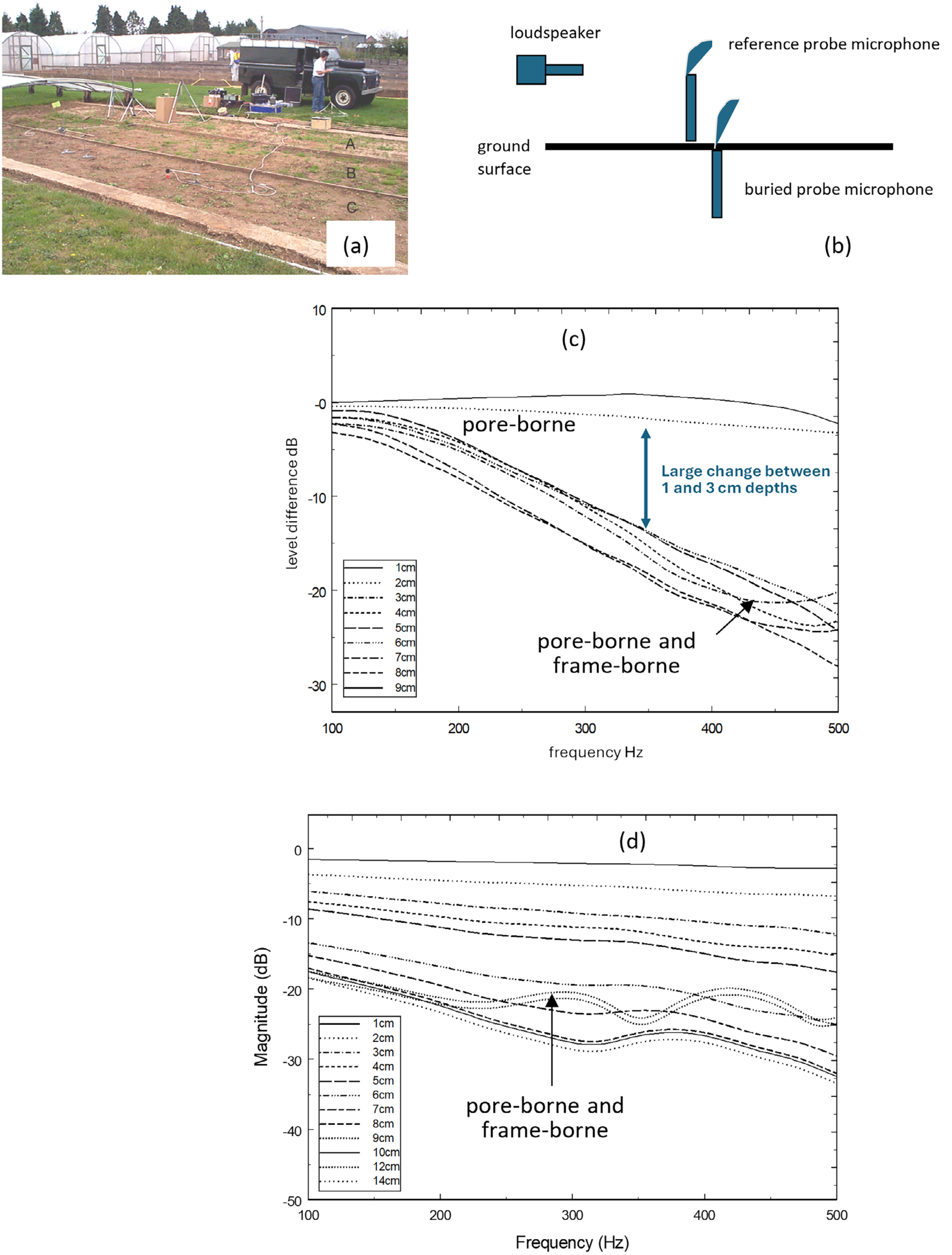

FIGURE 3 | (a) Probe microphone measurements on a compacted friable soil (flow resistivity ~ 450 kPa s/m^2) at Wellesbourne, Warwickshire, UK. (b) A schematic of reference and buried probe microphone locations. (c) Spectra of level differences between surface and buried probes in Wellesbourne soil. (d) Corresponding probe microphone data in a sand quarry (flow res. ~ 20 kPa s/m^2; 105 m/s < V_{pore} < 182 m/s).

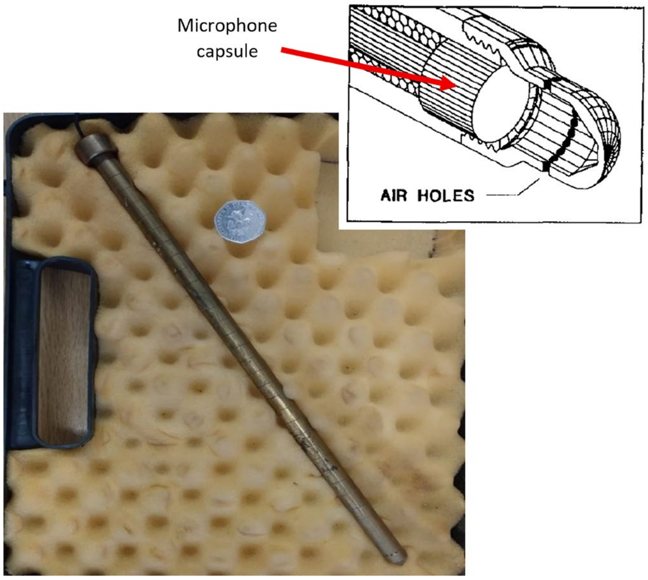

FIGURE 4 | Probe microphone.

due to the air particle motion at the surface which attenuates more rapidly with depth. This increases the microphone signal and arrests the decrease with depth.

Soils can also support surface waves. Sources of vibration at a soil surface can generate frame-borne Rayleigh waves. Frame-borne Rayleigh waves are exploited in animal communications (Narins 2001; Hill et al. 2022). The Rayleigh wave is one of two surface waves that can occur at a poro-elastic surface (Richards et al. 1985). The other is an airborne surface wave which has been observed extensively in laboratory measurements over artificial porous surfaces (Kelders et al. 1998) but only over snow outdoors (Albert 2003). To the authors' knowledge, so far there have not been studies of whether this latter wave type is exploited by biota.

2.2 | Physical and Biological Sources of Mechanical Waves in Soils Informed by Laboratory Studies

Soil is a theatre for various processes which may give rise to mechanical waves measurable at a distance. The idea of using them to characterise these processes was suggested at least several decades ago (see Koerner et al. 1981). In the literature, these signals are often referred to as acoustic emissions (AE), regardless of whether they have a fluid- or solid-borne character. AEs may have biotic or abiotic origins, but insights into their formation have a universal merit. The latter have been investigated using high-frequency (>20 kHz) sensors in an idealised granular multi-phase medium (glass beads with water), focusing on two mechanisms—water transport and granular shearing. AEs can be expected to accompany multiple events when particles or surfaces come into contact, such as friction, collisions, crack initiation, and similar phenomena. Moebius et al. (2012) conducted a series of experiments to record acoustic emissions accompanying fluid displacement through assemblies of glass beads with varying flow rates. Their results confirm the link between the number of AE events and fluid front dynamics and confirm their attribution to Haines jumps (DiCarlo et al. 2003).

Another mechanism with significant links to waves produced by soil fauna, such as earthworm burrowing, is granular shearing. Michlmayr and Or (2014) considered grain collisions and particle-to-particle friction as source mechanisms for mechanical waves. Their measurement confirmed the link between stress fluctuations and AEs and supplemented it with models for restructuring the granular chain in response to deformation. Whilst these studies used glass beads as an idealised granular medium, they captured the source mechanisms responsible for soil AEs. Whilst statistical analysis (with counting emissions being its simplest form) is a reasonable choice for this type of data, it is expected that more information could be extracted from a detailed analysis of individual waveforms.

The relevance of the aforementioned source mechanism to the biotic origins of waves was studied by Lacoste et al. (2018), who conducted experimental campaigns aimed at proving the potential of passive monitoring of soil biophysical processes. The authors recorded acoustic emissions associated with earthworm activity in soil columns and compared them to visual observations of tunnels, demonstrating a strong link. Similarly, plant root growth could also be associated with an increase in AE rates and shown to be unrelated to water movement. Whilst the potential was successfully demonstrated, numerous factors related to the medium (the effect of moisture, texture, temperature, and inhomogeneity), origin (species), and instrumentation (frequency and range limitations) remain to be explored. Measuring mechanical waves (frame-borne) is a promising tool for monitoring soil fauna (Lacoste et al. 2021). It contrasts to computed tomography scanning, as more accessible and easier to deploy in the field. However, the uncertainty related to the information extracted from such measurement is yet to be rigorously quantified.

The significance of the evidence that acoustic emissions might be indicative of earthworm activity encouraged scientists to investigate much smaller-scale phenomena. Biofilm sensitivity to sound/ultrasound is a well-documented phenomenon (Murphy et al. 2016), which has led some authors to speculate that meaningful acoustic emissions may occur in the rhizosphere. Rillig et al. (2019) hypothesised that microbial communities are sensitive to waves generated by biotic (e.g., earthworms) and anthropogenic sounds (e.g., traffic). They also suggested the existence of acoustic emissions from microbes; however, both observations are purely speculative at present, and no rigorous, comprehensive study on sound-based interactions with microbial communities in the rhizosphere is known to the authors. Few papers on the acoustic effects on rhizosphere microbes exist, but their methodologies raise serious questions (arbitrary selection of sound profiles, limited repeats, and no attempt to link to the physics). There is limited evidence on the effect of acoustic stimulation on the microbiome, as reviewed by Robinson et al. (2021). Whilst no studies on rhizosphere microbial communities were reviewed in that work, the authors highlighted the underexplored nature of these sound interactions with bacteria and called for further studies in this area.

2.3 | Habitat Characterisation Measurements to Advance Understanding of Signalling Systems

To advance understanding in ecoacoustics, it has been recommended that field studies should quantitatively characterise the physics of sound propagation in the habitat and focus on signals where transmission distance is important (Freitas et al. 2025). A playback method coupled to modelling has been described for the above-ground component of terrestrial habitats, so-called coefficient of attenuation of the habitat (a_0) which is expressed in dB/kHz/m (Haupert et al. 2023). Signal masking by ambient sound and variation over time has been proposed as an important driver of signalling-sensing systems, and habitat characterisation means it would be possible to assess frequencies with significant detection probabilities and examine their use by biota (Freitas et al. 2025). It is important to note that the 'best signal' biologically is not automatically the one with maximal signal-to-noise ratio; because under environments with significant background noise, it can be expected that a weak signal—creating a 'lull'—is the signal of interest (Endler 1992).

Typical frequencies to which ecosystem engineers (earthworms, ants, or termites) respond include 80–100 Hz (*Diplocardia* earthworms, Catania 2008; Mitra et al. 2009), 800–1500 Hz (*Myrmica* ants—mature pupae, workers and queen to communicate social status of these eusocial insects (Casacci et al. 2013)) and 500 Hz (*Macrotermes* termites, noting that the nest—burrow substrate conditions strongly attenuate an individual's signal, and social amplification is a strategy used by these eusocial insects to overcome substrate attenuation (Hager and Kirchner 2013)). Termites construct clay walls and sense predatory ant footsteps to avoid predation to compete for the same food resources (Oberst et al. 2017), whilst the termite nest also draws water and regulates airflow which probably generates noise (Ruiz et al. 2023). Bioturbation by earthworms is comprised of burrowing, ingesting, cast smearing and general layer mixing (Ruiz et al. 2023), which influences the noise features and sensory environment of the soil habitat (Keen et al. 2022). Ants invade or construct nests in the soil, and *Maculinea* social parasites of *Myrmica* have evolved sophisticated acoustic mimicry of the queen ant to achieve a high social status and live within the subterranean brood chamber exploiting ant resources for up to 23 months (Barbero, Bonelli, et al. 2009; Barbero, Thomas, et al. 2009). Comparing this superficial but ecologically reasoned 80–1500 Hz range to sonoscape evaluations (unsubstantiated claim that the critical range for describing sonic activity in soil is 450–1200 Hz (Farina and Mullet 2025)) and noise measurements, the range is higher than most seismic noise surveys (noting > 1 Hz is categorised as high frequency) but lower than standard acoustic noise surveys (categorised as low to mid-frequency), whilst surveying seismic and acoustic noise across this range shows different frequency-dependent attenuation and peak frequencies of 25 and 60 Hz, respectively (Albert and Decato 2017).

There are a range of studies which could be adapted and used to characterise soil habitats to help interpret the detection of soil biota in relation to air-borne noise. Permeability is a typical characteristic of porous materials, which can be described as the ability of porous media to allow the passage of fluid. Permeability is used widely to describe the transport of water in soils. However, air permeability is also an important issue here as an indicator of the extent to which airborne (ambient) sound can penetrate a soil surface. It has units of m^2. There are many, not very accurate measurements of the air permeability of soils in the laboratory and in situ (Lu et al. 2023). When discussing the acoustical properties of porous media, it is more usual to refer to flow resistivity, which is related to the inverse of permeability. A low flow resistivity medium has a high permeability, and a high flow resistivity medium has a low permeability. Flow resistivity corresponds to the ratio of the applied pressure drop per unit thickness to the resulting volume flow rate and has units of $kPa\,s/m^2$. There is an international standard for the laboratory measurement of flow resistivity (ISO9053-1 2018), and there are measured values for soils (Martens et al. 1985). However, it is possible to estimate 'effective' values of flow resistivity of soils from acoustical measurements by using models for the acoustical properties of rigid framed porous media (Embleton et al. 1983; Moore and Attenborough 1992; Sabatier et al. 1993; Attenborough et al. 2011). Table 1 lists example values. The root system of vegetation has an important influence on the flow resistivity of soils. Examples of the differences in flow resistivities due to the presence of roots are given in Table 1.

TABLE 1 | Measured values of flow resistivity in order of ascending values (Attenborough and Van Renterghem 2021).

Ground type	Flow resistivity ($kPa\,s/m^2$)	Porosity—total or (air-filled/water-filled)
Snow (new)	4.73	0.86
Pine forest litter (0.06–0.07 m thick)	9 ± 5	0.389/0.286
Snow (old)	16.4	0.574
Wet peat (μL)	24 ± 5	0.55/0.29
Beech forest litter layer (0.04–0.08 m thick)	22 ± 13	0.825
Litter layer on mixed deciduous forest floor	30 ± 31	—
Grass root-filled layer (0.02–0.05 m thick)	189 ± 91	—
Loamy sand (0.06 m thick with roots)	237 ± 77	0.505
Friable soil at Wellesbourne	450	—
Mineral layer substrate in deciduous forest	540 ± 92	0.365/0.15
Loamy sand beneath lawn (no roots)	677 ± 93	0.288/0.137
Compacted silt (no roots)	1477	0.12
Wet sandy loam (no roots)	1501	0.11

A Biot-based theoretical framework has been used in situ to deduce a vertical profile of soil strength up to 50 cm depth, assuming horizontal layering, along with wave speeds, flow resistivities and porosities in each layer, from non-invasive measurements using a loudspeaker source emitting swept pure tones between 400 Hz and 4 kHz, vertically separated microphones and a laser Doppler vibrometer. The latter was used to measure the soil particle motion at its surface both without crops (Shin et al. 2013) and in the presence of crops (Shin et al. 2017). In an arable field consisting of a loamy sand with typically around 80% sand, 10% silt and 10% clay planted to winter wheat (*Triticum aestivum* L.) upper layer P-wave speeds of between 50 and 75 m/s and upper layer S-wave speeds of between 22 and 44 m/s were deduced.

A non-invasive in situ method using directional ultrasonic transducers at different angles with respect to soil surfaces has been proposed for determining soil porosity (Bradley et al. 2024). The ultrasonic frequency used (25 kHz) has much shorter wavelengths than those used by Shin et al. which means the incident sound is scattered significantly by surface roughness and any vegetation present, and allowances have to be made for this. On the other hand, the use of directional ultrasonic transducers allows the assumption of plane wave incidence. Also, the method could be used to give estimates of surface roughness and vegetation density as well as porosity.

A more invasive in situ ultrasonic method for characterising soils is a waveguide-based approach developed by Long et al. (2004). This requires the insertion of a metal bar into the soil. A model of wave propagation in a metal bar embedded in an elastic solid is used to link the characteristics of a wave induced by an actuator and reflected from the end of the bar to establish properties of the soil. The method has been tested in situ at multiple locations but the results at ultrasonic frequencies require extrapolation to lower frequencies using elastic wave theory.

The extent to which saturation or partial saturation with water affects the speed and attenuation of the mainly frame-borne waves has been demonstrated using buried transducers in a specially instrumented field site to show that the frame-borne compressional wave speed varied according to the amount of rainfall on the surface (Lu and Sabatier 2009). Although this study was carried out outdoors, it was restricted to a single frequency of 6.5 kHz and was site specific.

The influence of saturation on shear waves has been investigated in laboratory measurements of propagation between piezoelectric vibration transducers in prepared soil samples where the water content was controlled (Whalley et al. 2011, 2012). Oelze et al. (2002) have conducted a laboratory investigation on sieved and repacked soil samples with varying proportions of sand, clay, and organic content under controlled conditions of moisture and compaction. They investigated how the attenuation in soils depends on soil composition, compaction and moisture content between 2 and 6 kHz. They report attenuations ranging from 0.12 to 0.96 dB/cm/kHz and wave speeds between 86 and 260 m/s.

2.4 | Uses of Pore Borne Waves by Biota: The Owl and the Vole Example

For sources and receivers above the ground, snow and forest floors produce a significant 'soft' ground effect, that is, destructive interference between direct and ground-reflected sound paths (Attenborough and Van Renterghem 2021). So, sound levels are reduced over a wide range of frequencies.

Soil surfaces can be covered by snow and by plant litter, which influences the types of waves and their uses by biota. For example, the Great Grey Owl is able to hear sounds made by its vole prey moving beneath the snow surface (Clark et al. 2022). These vole sounds and sounds from a loudspeaker buried in snow have been tracked using an acoustic camera consisting of a phased array of microphones that could be focused on small areas of the snow surface. Since the microphones used in an acoustic camera respond only to sound pressure fluctuations, they must have been detecting the pore-borne sound emerging from the snow surface. Sound in air-filled pores can propagate easily in snow because of its low flow resistivity (see Table 2). Indeed, the flow resistivity of snow is sufficiently low that the slow wave speed is comparatively high and there can be components of pore-borne sound travelling parallel to its surface, that is, for a listener above the surface there is refraction of sound from a source below the surface. This means that the flying owl only pinpoints the exact location of its prey when directly above it. Since leaf litter on forest floors has similarly low flow resistivity, biota that dwell in them and predators seeking prey in them should be able to use pore-borne sound in a similar way.

Vertebrates and invertebrates that can detect and generate pore-borne sound may use pore-borne waves for communicating or locating. None the less, typical soils have much greater flow resistivity than snow or forest floors (see Table 1), and this is the reason that frame-borne waves, are generally more useful both for the observation and detection of biota in soils (Cocroft et al. 2014).

2.5 | Comparison of Pore and Frame-Borne Wave Uses by Biota: Fossorial Mammal Example

For subterrestrial inhabiting fauna, air-filled burrows surrounded by substrate create both auditory and vibratory signal detection opportunities. Signal detection through frame vibrations rather than the air space of burrows is proposed to confer the greatest fitness benefits (decisions that have major implications for survival and reproduction) due to their conduction over considerable distances without significant attenuation (Rado et al. 1987). The fossorial mammal *Georychus capensis* was identified as a good candidate for applications of microphones (pressure gradients) and geophones (direct pressures) to characterise their burrow habitat, as the burrows are closed and sealed (and openings rapidly plugged with soil) and typically span 130 cm in length with a mean diameter of 10 cm (Narins et al. 1997). Both auditory and vibratory signals are produced by drumming their hind legs on the burrow floor to communicate with conspecifics for mate attraction (Narins et al. 1997). Here, frame-borne signals propagated an order of magnitude better than auditory signals and could be detected above background noise in an adjacent burrow (unlike the air-borne component) with Rayleigh waves thought to be the least attenuated component of the frame-borne signal and proposed to be responsible for the biological response (Narins et al. 1992).

3 | Biological Sensory Systems and Signalling Properties

The various types of mechanical energy constitute signals that animals can receive sensory information about their

TABLE 2 | An overview of the published work used to investigate soil fauna, showing the range of field hardware, analysis methods and habitat types.

Paper	Species	Sensors	Frequency (Hz)	Analysis method	Habitat type	Country	Ecoacoustic?
Mankin et al. (2000)	*Diaprepes abbreviatus* larvae, Phyllophagas spp. and Cyclocephala spp	Accelerometers, electret microphones, and piezoelectric disks	0–25,000 Hz	Custom spectral and temporal analyses, including spectral profile comparisons	Citrus groves	USA	N/A
Mankin et al. (2001)	*Diaprepes abbreviatus*, *Phyllophaga*	Accelerometers	300–2000 Hz	Manual/listener analysis and computer spectral profile analysis between 0.3 and 2 kHz	Citrus groves	USA	N/A
Brandhorst-Hubbard et al. (2001)	Multi	Electret microphones	—	Spectral profile analysis combined with counts of sounds per min (pulse rate)	Farmland (hayfields)	USA	N/A
Zhang et al. (2003)	*Phyllophaga crinita* and *Cyclocephala lurida*	Electret microphones	600–2000 Hz	Spectral profile analysis combined with counts of sounds per min (pulse rate)	Turf fields and golf course fairways	USA	N/A
Mankin and Benshemesh (2006)	Ant and termite species	Geophones and accelerometers	10–500 Hz (geophone), 0–12,000 Hz (accelerometer)	Insect Sound-Pulse Analysis with DAVIS software	Desert	Australia	N/A
Mankin et al. (2007)	Multi	Electret microphones	100–3000 Hz	Spectral profile/pulse analysis followed by geostatistical modelling and Spatial Analysis by Distance Indices (SADIE) analyses of acoustic indicator probabilities	Forage fields	USA	N/A
Inyang et al. (2019)	*Vitacea polistiformis*	Piezoelectric sensors	1000–22,000 Hz	Insect Sound-Pulse Analysis to identify characteristic signals, followed by spectra comparisons with DAVIS software	Vineyards	USA	
Maeder et al. (2019)	Multi	Piezoelectric ceramic disks	50–25,000 Hz	Acoustic Complexity Index (ACI)*	Farmland, forest	Switzerland	Yes

(Continues)

TABLE 2 | (Continued)

Paper	Species	Sensors	Frequency (Hz)	Analysis method	Habitat type	Country	Ecoacoustic?
Keen et al. (2022)	Earthworm species	AudioMoth loggers with micro-electro-mechanical systems microphones	50–5000 Hz	Acoustic emission (peak) analysis, spectral analysis and comparison of six acoustic indices: Acoustic Complexity Index (ACI)*, Acoustic entropy (H), Acoustic Evenness (AEven), Acoustic Diversity Index (ADI) and Normalised Difference Soundscape Index (NDSI)	Arctic tundra	Sweden	
Maeder et al. (2022)	Multi	Contact microphones	5–2500 Hz	Acoustic Complexity Index (ACI)*, Acoustic Evenness Index (AEI), Acoustic Richness (AR) and Median Amplitude Envelope	Forest	Switzerland	Yes
Robinson et al. (2023)	Multi	Piezo contact microphones	500–2000 Hz	Acoustic Complexity Index (ACI)*, Normalised Difference Soundscape Index (NDSI), Bioacoustic Index (BI)	Temperate woodland (restoration)	UK	Yes
Robinson, Taylor, et al. (2024)	Multi	Piezo contact microphones	500–2000 Hz	Acoustic Complexity Index (ACI*), Normalised Difference Soundscape Index (NDSI), Bioacoustic Index (BI)	Grassy woodland (restoration)	Australia	Yes
Metcalf, Baccaro, et al. (2024)	Multi	Piezo contact microphones	500–5000 Hz	Acoustic Complexity Index (ACI)*, Bioacoustic Index (BI), Spectral Events (EVNspCount), Normalised-Difference Sound Index (NDSI), Regions of Interest (ROIcover), Frequency Entropy (Hf)	Tropical rainforest	Brazil	Yes

(Continues)

TABLE 2 | (Continued)

Paper	Species	Sensors	Frequency (Hz)	Analysis method	Habitat type	Country	Ecoacoustic?
Vang Sørensen et al. (2024)	*Formica rufa*	Contact microphones	0–48,000 Hz	Average Power Density (APD), Peak Power Density (PPD), Acoustic Complexity Index (ACI)*, and Bioacoustic Index (BI)	Boreal forest	Sweden	Yes
Farina and Mullet (2025)	Multi	Piezo contact microphones	0–6000 Hz	Sonic Heterogeneity Indices (SHI)	Agricultural land	Italy	Yes

*The ACI has been renamed the Sonic Heterogeneity Index.

environment (Schwartzkopff 1974). Biological mechanoreceptors offer opportunities to sense mechanical energy in the environment which confer lifetime fitness benefits. For example, mechanoreceptor sense organs shaped like a stalk can vary in thickness and flexibility (hair or spine), length (same or mixed), abundance (individual or densely packed pads), arrangement (random or line), offering different sensing capabilities spanning pressure, vibration, displacement, velocity, etc.

Mechanical wave sensory systems particularly relevant to soils include (i) rhythmic touch (direct contact, requiring the receiver to just identify the signal and sender), (ii) nearfield medium motions which excite mechanoreceptors (pore-borne, rhythmic mass flow in the surrounding air or water medium which requires signal structure and receiver sensitivity coupling) and (iii) boundary motions which excite mechanoreceptors (frame-borne, the medium is set into motion and the perception of signals is at an interface, e.g., burrow soil/air interface which requires signal structure and receiver sensitivity coupling) (Markl 1983). The evaluation of mechanical wave phenomena offers sensing opportunities which were listed by Schwartzkopff (1974) including: determining position in space, effects of forces on different parts of the body, forces of inertia, movement of surrounding objects, currents of air or water, substrate vibrations and sound oscillations in the surrounding medium. The performance of mechanoreceptors is coupled to processing—behaviour links, and whilst attention is typically directed towards 'tuning in', for example, communications, 'tuning out' also confers fitness benefits. For example, self-generated noise from burrowing movements could mask important signals about the environment. Therefore processing, for example, neuronal mechanisms which facilitate pattern learning, would enable the filtering out of self-generated noise would also confer fitness benefits. The term 'hearing' comes from vertebrate mechanoreceptor research, where special attention is paid to mechanical stimuli transmitted over long distances over the medium of air or water, received through specially adapted sense organs, and the fine spectral structure to decode the content of the signal. For soils research, it should be noted that rhythmic touch research requires a different investigative approach; it is the pore or frame borne waves that are amenable to instrument detection (pressure gradients, particle/surface motion detectors).

Mechanoreceptor sensory systems in soil habitats may seem intractable for investigation, but soil macrofauna are simply not buried in soil; they inhabit burrows, galleries, chambers, etc. The architecture of such habitats means that the body plan of organisms directly influences their physical interaction with the air-filled burrow space and burrow surface (e.g., arthropod limbs or limbless tube-shaped body of worms), which means that these habitat features are evolutionarily coupled to sensory systems, signals and behaviours. Both the burrow void and the surface offer opportunities to receive sensory information about the environment, and whilst attention is typically focussed on the voids, it is important to note that: 'all types of mechanical waves can set a surface into motion in one, two or all three spatial directions, relating to the body axes on that surface', which means that surface waves could excite mechanoreceptors (Markl 1983). Signals are typically attenuated and distorted during transmission (Section 2), and so it has been predicted and shown that the time pattern of vibration pulses and general differences in bandwidth are predominantly behaviourally significant, rather than the fine spectral structure of the signal (Markl 1983). Under these environmental constraints, physical properties of the habitat support the development of particular sensory signals and modes, and suites of traits should co-evolve in predictable directions.

The language to describe such sensory systems and signalling properties is overly simplistic in the soil ecoacoustic literature to date (Table 2), including human perception of mechanical waves applied to soils (Belaud et al. 2025) and classifying recordings in terms of assumed sources of mechanical waves (human, biological, and geophysical) (Robinson, Annells, et al. 2024).

3.1 | Ecoacoustics

3.1.1 | Acoustic Niche and Acoustic Adaptation Hypothesis and Related Concepts

The Acoustic Niche Hypothesis is an informal presentation reporting field observations that vocalising species signals do not overlap (Krause 1993). The formal prediction is that there is acoustic partitioning of the acoustic space (temporal, spectral and/or spatial separations of sound production) to reduce interferences from other species (Sueur and Farina 2015). The Acoustic Niche Hypothesis underpins applications to estimate the biological health due to the predicted selection pressures for acoustic space: fewer vacant acoustic niches reflect higher species richness. The evidence supportive of the acoustic niche hypothesis, for example, frog, bird and insect choruses, relates to specific situations of sound communication in the presence of groups of sound communicators (Cummings and Endler 2018). These biological attributes are not associated with soil habitats. The mention of the Acoustic Niche Hypothesis theoretical background in soil habitat field research is absent, except for one study referencing the application of an acoustic index (Metcalf, Baccaro, et al. 2024).

The Acoustic Adaptation Hypothesis is frequently linked to a field study characterising avian long-distance communications (in situations when the birds are too far away for visual contact) (Morton 1975) and a review paper detailing long-range pair forming signals (Forrest 1994). The 'acoustic adaptation hypothesis' was defined in an avian field study to distinguish between other hypotheses (e.g., genetic adaptation, social adaptation, and deceptive/honest convergence) (Rothstein and Fleischer 1987). The unique feature of the acoustic adaptation hypothesis is that 'if a particular type of sound is transmitted most effectively in a specific habitat, the repeated occurrence of specific acoustic characteristics will be found, if the species occupies that habitat elsewhere', however, the authors did not find any evidence supporting the acoustic adaptation hypothesis for the flight whistle of the Brown-headed Cowbird (Rothstein and Fleischer 1987). The acoustic adaptation hypothesis described within soundscape ecology means species evolving the structure and function of their calls or songs to maximise transmission fidelity (Pijanowski et al. 2011). Under ecoacoustics (which encompasses soundscape ecology) the acoustic adaptation hypothesis means the acoustic properties of habitats shaping animal sounds to maximise their propagation (Sueur and Farina 2015). Thus it seems that the Acoustic Adaptation Hypothesis has a capricious definition and it is difficult to critically assess because few studies quantitatively characterise the physics of sound propagation in the habitat (Freitas et al. 2025). The mention of the Acoustic Adaptation Hypothesis is missing in soil habitat field research.

Together, the Acoustic Niche Hypothesis and Acoustic Adaptation Hypothesis are linked to the Acoustic Habitat Ambient Theory, an informal presentation proposing that habitats have emergent, unique acoustic signatures and respond to audio changes, and splitting audio recordings into three components: human-induced, biological (biophony) and geological sounds (Krause 1987). This was later formalised in soundscape ecology, as anthrophony (human-induced), biophony (organisms) and geophony (geo-physical) sounds, and together these give a landscape a unique acoustical pattern (Pijanowski et al. 2011). This view has been influential in soils research, with the terminology used in both review articles (Belaud et al. 2025; Robinson, Annells, et al. 2024) and soil ecoacoustic field studies (Table 2).

The omission of ecoacoustic theory in soils research to date has two implications. Firstly, the physics of wave propagation in the habitat is unknown, leading to assumptions of measuring 'biophony', when it cannot be excluded that there are other sources. Secondly, there is an inherent bias towards communications, with implications for taxa such as earthworms and incidental events such as burrowing and feeding, which are not insignificant to soil habitats (e.g., compaction, porosity, decomposition, and root herbivory). One research team has highlighted the discrepancy with the acoustic niche hypothesis, as soil recordings include incidental noises like movement, which do not have the selection pressures for acoustic space (Metcalf, Nunes, et al. 2024).

3.1.2 | Sonoscape for Soil Investigations

The model sonoscape investigation is the next development in ecoacoustics, specifically highlighted for applications to soils (Figure 1). This focusses on sensing and utilising indices and statistics to capture 'unique spatio-temporal complexity of ecological features of the sonosphere' (Farina and Mullet 2025). This may prove to be so vague it does not facilitate significant advances in knowledge; none the less, this development acknowledges theoretical discrepancies and methodological shortcomings such as classifying outputs as 'biophonies' (which can be verified in most ecoacoustic investigations, e.g., calls or songs by bird species) where soils are largely unknown; unknowns so 'ecological features' is more apt. The development of the sonoscape legitimises a pathway for the development of soils research within the field of ecoacoustics.

All soil ecoacoustic research to date, whilst described as a soundscape approach, would better fit the sonoscape investigation. For example, the reported instrument detection level starts around mesofauna (e.g., groups of ants) and mature macrofauna (Mankin et al. 2011; Mankin 2022) (Figure 5), so it can be reasoned these studies are biased towards the ecosystem engineers (earthworms, ants and termites) and conspicuous subterranean arthropods with drumming and stridulating vibration excitation

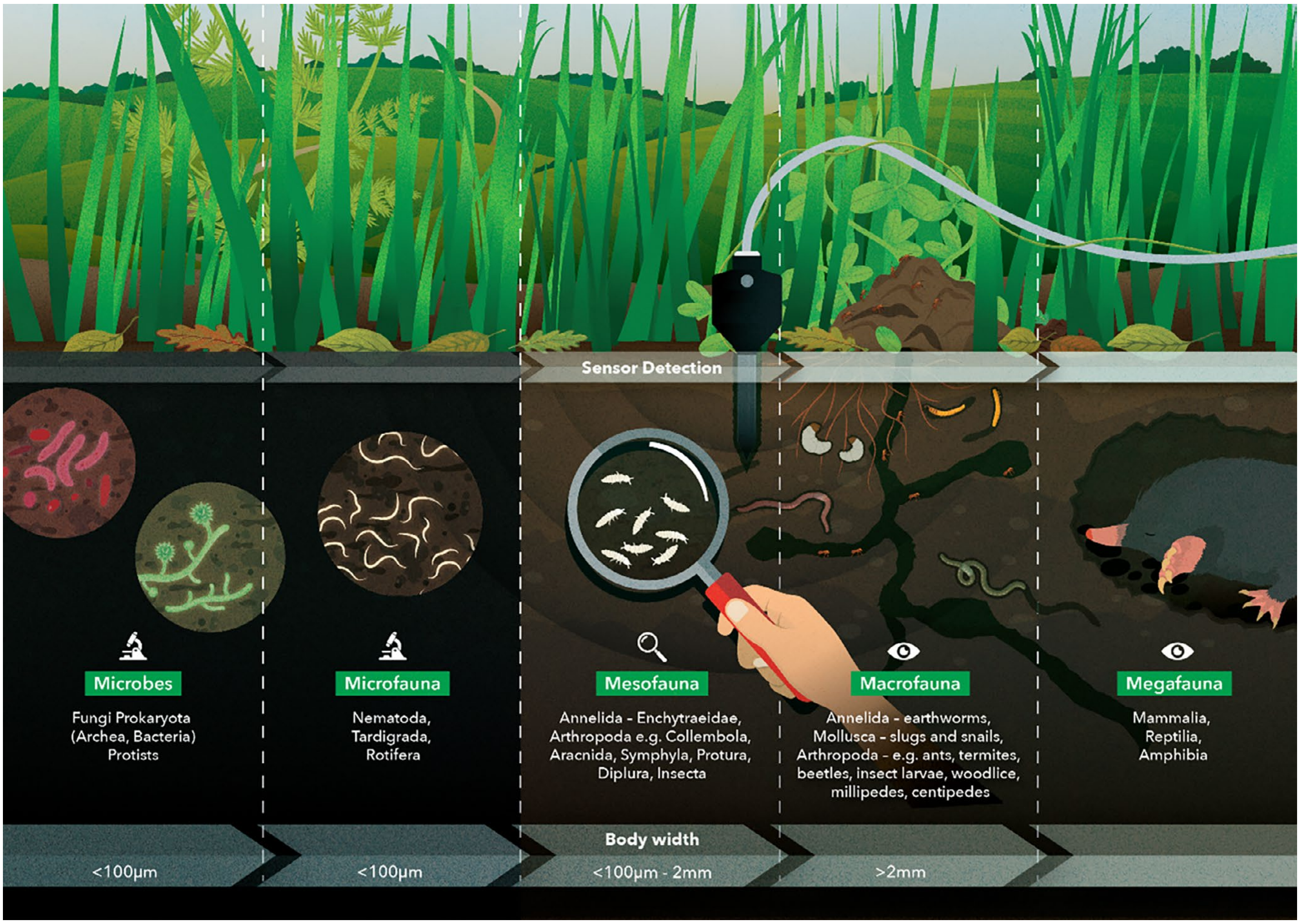

FIGURE 5 | Sensor detection is biased towards larger mesofauna and macrofauna.

behaviours. There is no equivalent bird call/song library for soil organisms to check acoustic index performance. Enumerating soil fauna is sometimes used to compare to acoustic indices; causality is uncertain because small fauna (including juvenile macrofauna) are unlikely to make detectable signals/cues, best timings are uncertain as the phenology of soil organisms is unknown (Bonato Asato et al. 2023) and whether an organism is there (not signalling), not detected (e.g., soil compaction) or not there, is also uncertain. There are above-ground and below-ground sources of signals which are not readily separated, both practically and ecologically. For example, wind acting on dune grass created mechanical waves which transmitted through a sandy substrate forming a "seismic" beacon across tens of metres, enabling fossorial mammals to hone in on microhabitats, before they detected the decimetre range signals generated by their insect prey (Narins et al. 1997). In this way, 'spatio-temporal complexity of ecological features' is a reasoned description given the preliminary status of soil ecoacoustic investigations.

Arthropod biophonies are conspicuous in soil recordings (Farina and Mullet 2025) and theoretical explorations using biodiversity simulations and the performance of acoustic indices indicate good prediction of acoustic abundance, but not other diversity metrics (Metcalf, Nunes, et al. 2024). The latter approach has critical limitations including a small library for testing (14 arthropod and rodent signals), confounding factors and temporal dynamics which reduce generalisations for real recordings as has been found in attempts to validate metrics for bird populations (Gasc et al. 2015). Linking biodiversity to soil functioning is not straightforward, whilst exhaustively determining the acoustic emissions of all living organisms in soils is an impossible task given it is the most biodiverse habitat on the planet (Anthony et al. 2023). Therefore, whether soil investigations can achieve soundscape standards (and associated impacts) is uncertain. No soil ecoacoustic studies have used soil quality measurement development procedures: identifying an objective, involving stakeholders/users, addressing a specific soil threat and providing a clear interpretation scheme of measured indicator values, to inform contextual soils management (Bünemann et al. 2018).

3.2 | Sensory Drive Model

The sensory drive model links signals, receptors and signalling behaviour to environmental physics, biophysics and the neurobiology of behaviour. The principle is that biophysical factors drive sensory processes in predictable directions. An evaluation of 25 years of the sensory drive model across all habitats (noting this was predominantly a comparison between aquatic environments and terrestrial habitats) found supportive evidence in a variety of taxa and environments (Cummings and Endler 2018). Supportive studies were principally visual signals in aquatic environments, and this was associated with the aquatic environment being more environmentally constraining on the sensory system in comparison to terrestrial habitats (Cummings and Endler 2018). Key environmental constraints of wavelengths of light in water include absorption and scattering as a function of depth.

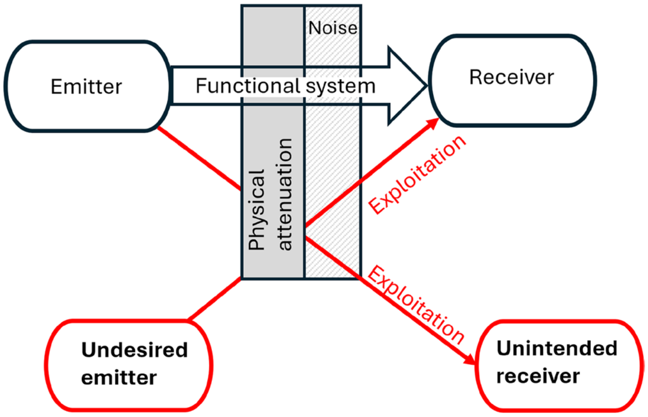

FIGURE 6 | The components of a signal and cue system for mechanical waves in soil habitats, modified from Endler (1992). A functional system is where the emission is transmitted to the receiver through the abiotic environment effects and ambient noise, noting an individual can be both emitter and receiver (e.g., seismic echolocation for spatial orientation in soils (Dong et al. 2023; Kimchi et al. 2005)). There are risks to lifetime fitness from emissions: (i) exploitation by unintended receivers (predators, parasites, and in terms of cues, for example, termites eavesdropping on ant footsteps to avoid predation to exploit the same food source (Oberst et al. 2017)) and (ii) undesirable emitters (e.g., social parasites of ants via mimicking the vibroacoustic signals of the queen (Barbero, Bonelli, et al. 2009; Barbero, Thomas, et al. 2009)). Noting that this can be multimodal, for example, social parasites concomitantly exploit chemical sensing (Barbero, Bonelli, et al. 2009; Barbero, Thomas, et al. 2009).

The sensory drive model describes a functional information exchange system, with two routes for exploitation from undesired emitters or unintended receivers (Figure 5). Considering the extraordinary bioturbation and burrowing fauna in soil habitats, it is possible to predict that both the transmission of signals (purposeful, i.e., communication) and potential cues (incidental, e.g., burrowing, movement in burrows) produced by biota comprise the information exchange system.

Sensory adaptations balance the best signal against predator detection, linking sensing, receiving and behaviour together (Figure 6). Using standard principles of biophysics, biochemistry, neurobiology and behaviour, factors that affect signals can be deduced, which permit predictions about sensory systems and signalling properties to be made (Table 3). In soils, whilst some physical features are fixed (driving the adaptation of sensory and signalling traits), some are amenable to biological influence (e.g., environmental modification) to either provide information or mask information transfer (Table 4). The sensory drive model predicts that the dominant sensory mode is the one with the greatest efficiency of transmission in the local environment. The signals/cues need to be above the detection threshold and the receiver must be able to distinguish the signal/cue from the background noise (Mortimer 2017). For mechanical waves in soils, the greatest efficiency in transmission is for frame-borne waves in soils, and so it would be anticipated to be the dominant mode. For burrow-dwelling vertebrates, it is frame-borne signals that are detected above background noise and reliably produce a behavioural response (Narins 2001). In terms of the type of information, it can be predicted that valuable information is that which increases expected lifetime fitness, enabling the advantages and disadvantages of frame and pore-borne modes to be predicted for earthworms (Table 5). This indicates

TABLE 3 | Reproduced from table 1, Endler (1992), list of factors that shape signal structure, noting it does not read across.

Signal generation and emission	Transmission through the medium	Signal reception and processing	Decisions based on the perceived signal
Biophysical limits to form and intensity	Background noise, Interfering signals	Biophysical and biochemical limits to reception	Other signals
Energetic limits	Attenuation	Sensory adaptive state and attentiveness	Choice time wasted
Biochemical limits	Blocking	Needs to be attentive	Reasons for choice
Energy storage	Absorption	Need for alerting signals	Need for choice
Timing and location:	Reflection and refraction	Short reception time	Quality of different
Predation			signal components:
Short season	Distance	Other signals	Purity
Best place and time			Value to receiver Value to emitter
Environmental effects on emission	Spectral properties	Noise	Predator risk
Information content vs. clarity	Temperature	Jamming	Parasite risk
	Self-interference	Signal reception rate	Physiological state
Information density or rate	Information density	Information processing rate	Quality of signal
Genetic variation	Timing and location	Pattern recognition needs	Signal channel use

TABLE 4 | Summary of the fixed physical features and factors that can be influenced by biota (e.g., signal frequency and water content), noting that more than one wave type can be generated at the same time.

Common soil waveforms	Geometry and particle oscillation direction	Propagation dimensions	Speed dependence	Likely dispersion/frequency dependence?	Other dependencies	Information type	Biological emitter behaviour
Frame-borne: longitudinal (e.g., p-wave)	Body, parallel	3D	Stiffness, density	Yes, frequency dependence	Surface litter layer, particle size, porosity, water content	Cue/signal	Burrowing and locomotion, communication (e.g., drumming) plant rooting
Frame-borne: Rayleigh	Solid-air boundary, elliptical	2D	Stiffness, density	Yes, depth dependence	Surface litter layer, porosity, particle size, water content, depth	Cue/signal	Burrowing and locomotion, communication (e.g., drumming), plant rooting
Pore-borne	Longitudinal pressure wave, minimal particle movement	3D	Speed depends on frequency	Strong frequency dependent attenuation (increasing with frequency)	Porosity, particle size, water content	Cue/signal	Burrowing and locomotion, communication (e.g., drumming), plant rooting, water movement

Note: Modified from table 1 of Mortimer (2017) and table 6.1 from Caldwell (2014) with information from Section 2.

that pore-borne signal detection has a considerable disadvantage of being close-range, linked to the predation risk compared to frame-borne signal detection.

3.3 | Niche Construction/Ecosystem Engineering

Soil habitats represent a remarkable interface between physics and biology for sensory systems and signal properties. Invertebrates have opportunities to engineer their habitat (burrow shape, wall features, connectivity). For soils, a key modification to the sensory drive model has been made (Figure 7) to highlight this habitat feature (rather than taking a position on whether niche formation is an evolutionary process). Overlooking soil structure and physics has compromised the validity of both soil physical and microbiological research and impeded scientific progress in soil science on a number of occasions (Baveye 2021).

3.3.1 | Earthworm Bioturbation Activities

Earthworms are considered to be ecosystem engineers, and so it can be reasoned that their influence on the physical properties of the soil habitat is such that this biases the direction of particular sensory signals and modes for other organisms. Earthworms extensively burrow and bioturbate the soil in temperate regions in reasonably predictable ways. There are three functional groups of Lumbricidae earthworms: model anecic earthworms like *L. terrestris* which are classified as burrowers; model endogeic earthworms like *A. chlorotica* which are classified as shallow-bioturbators; and epigeic earthworms like *L. rubellus* which are classified as litter-dwellers, with bioturbation characteristics quantified and categorised for 50 common earthworm species (Capowiez et al. 2024). Noting that two of these functional groups include species that forage for plant litter on the soil surface (e.g., *L. terrestris* and *L. rubellus*). A caveat here is that the anecic earthworms construct usually a single deep burrow (albeit with branches), and they often reuse these burrows. The endogeic earthworms burrow at shallow depths, but they are often creating new burrows. As such, anecic earthworms usually have lower biomechanical pressure thresholds than their endogeic earthworm counter parts (Ruiz and Or 2018). Further to this point, this means that endogeic earthworms can continue to operate under drier soil regimes, thus potentially enhancing detection of their activity as waves will possibly transmit through more solid material (i.e., frame-borne waves, Ruiz and Or 2018).

Burrowing and bioturbating species are exposed to considerable risks from the exploitation of these movement cues by undesirable receivers (Figure 5). Masking their identity and activity from predators could confer lifetime fitness benefits and so strategies to increase noise, such as opening surface burrows to increase transmission from above-ground noise sources at strategic timepoints could be used. It has been reported that the presence of earthworms increases the background sounds recorded using a buried microphone in the soil (Keen et al. 2022). Surface-opening burrow structure could perhaps be optimised by epigeic or anecic earthworms to inform surface foraging decisions; for example, facilitate the detection of above-ground predators. The

TABLE 5 | Some advantages and disadvantages of different mechanical wave sensory modes in soil systems for soil biota.

Mechanical-wave modes	Advantages	Disadvantages
Only frame-borne (including boundary wave sensing)	Fast but processable	Mixed with noise
	Long-range transmission	Transmission distance poses risks from exploitation
	Impedance matched	
	Several channels (frequency, amplitude)	
	Moderate-high information transfer	
	Not expensive to emit by emitter (e.g., incidental, using burrow features, and tapping/rubbing behaviours)	
Only pore-borne (auditory sensing)	Close-range (private communication channel)	Slow-information timeliness
	Several channels (frequency, amplitude)	Mixed with noise
	Emission typically produces frame-borne waves (multimodal sensing possible)	Emission can produce frame-borne waves (exploitation risks)
		Impedance mismatches
		Close range (predator risk)
	Moderate information transfer	Probably expensive to emit by emitter, for example, maintain open burrow, construct burrow features to amplify signals
Both modes (multimode)	As above, plus: High information transfer	Attentiveness required
	Likely transduced by the same sensory receptors	Sophisticated neural integration required

Note: Modified from table 2 of Endler (1993) with information from Mortimer (2017) and Caldwell (2014).

features of the bioturbated-burrowed physical habitat may result in biophysical constraints, for example, restricted effective mechanical wave signals and may particularly influence the selective pressures on the temporary inhabitants, for example, subterranean larval stages of some terrestrial arthropods.

There are several generic features of a soil inhabited by earthworms, intensive burrowing closer to the soil surface, and a few long vertical burrows down the soil profile (Figure 8). The compaction of the burrow wall is in the range of > 2–13 mm extending into the surrounding soil, and this 'drilosphere' can be directly linked to body size, ecological group and burrowing category (Pham et al. 2024). Excitation of the walls of the burrow could create a burrow-borne sound as well as in the walls travelling outwards as mainly frame-borne disturbances through the surrounding soil, and dependent on the level of compaction in the walls, surface waves could be created. This has been monitored in a lab setting for endogeic activities (see Section 2.2, Lacoste et al. 2018). The widespread compaction caused by earthworms (Pham et al. 2024) would be anticipated to reduce signal transmission. Many earthworm species produce temporary burrows which they backfill with casts (Capowiez et al. 2024) for which the consequences would be to reduce transmissions through both pore and frame-borne pathways.

3.4 | Earthworm Responses to Mechanical Waves

Historically, research was directed towards understanding auditory sensing by organisms. A systematic search of the literature found one uncited study, with the author reporting a structure they had interpreted as resembling an 'auditory' cell in the epidermis of *Pontoscolex corethrurus* (Eisen 1896), an endogeic earthworm found in the tropics. The cells were described to occur in the setal zone (hair-like bristles used for movement) in the shape of a truncated cone, and within the large vacuole, sometimes a spherical feature was present, which was named an 'otosome' because it resembled an otolith (found in the inner ear of fish) with the author speculating it is an auditory sense cell.

Conventional wisdom has it that earthworms do not perceive air-borne sound, but this can be traced to just one influential source. Darwin conducted experiments ranging from whistles, bassoons, pianos and shouting at (most likely *L. terrestris) earthworms* when the earthworm was presumably foraging or feeding at the soil surface and indifferent to these nearby activities. This contrasted with placing the experimental pot directly on the piano and keys struck, with earthworms rapidly retreating to their burrows and interpreted as 'highly sensitive to vibrations transmitted through solid objects' (Darwin 1898). However, considering the physics of Darwin's experimental environment when the pot was not on the piano, we can predict that whilst the source was air-borne sound, it was intense and 'near to' the pots containing the earthworms meaning acoustic-seismic coupling (i.e., the generation of frame-borne waves) would almost certainly have occurred. It was likely to be above the detection threshold ("played as loudly as possible") suggesting information transfer had likely occurred but did not elicit a visible response. Darwin noted that earthworms were responsive to the 'slightest puff of air' indicating mechanoreceptor sensitivity to

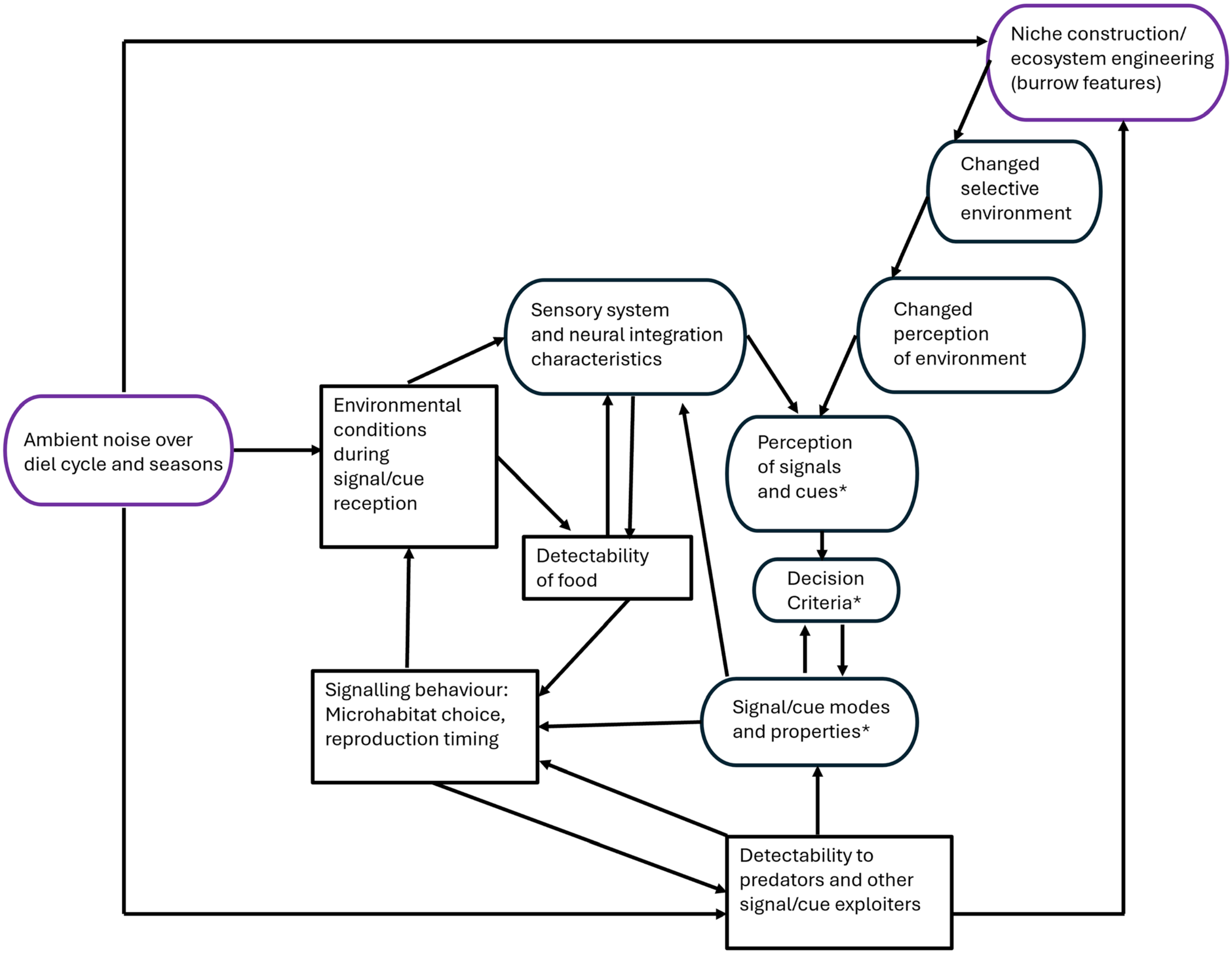

FIGURE 7 | The sensory drive model modified from Endler (1992) for soil habitats (with reference to earthworms as ecosystem engineers), incorporating feedback loops from niche construction and the presence of ambient noise. The features circled in purple are those which can be influenced by human behaviours, for example, by ploughing the soil, niches are deconstructed and burrow features eradicated, whilst human activities can generate noise which may mask signal/cues by organisms. Opportunities for exploitation (see Figure 4) are indicated by an asterisk (*).

air-borne, that is, pore-borne waves across their bodies. That is, these experiments provide contradictory information, but demonstrate that earthworms have mechanosensors.

Studies reporting responses to vibration excitation are biased towards exploitation scenarios (Figure 4), where earthworms respond to undesired emitters at the soil surface which elicit a surfacing behavioural response and their subsequent predation. To collect fishing bait in some regions, a method called 'grunting' is used where a wooden stake in the ground is scraped using a flat metal object. The surfacing response of earthworms to grunting has been investigated in *Diplocardia* species (Catania 2008; Mitra et al. 2009). Mitra et al. (2009) recorded the vibrations generated by 'grunting' using arrays of geophones, finding the signal to be characterised by frequencies below 500 Hz (dominant frequency at 97.3 Hz) and the amplitude to decay quickly over several metres; the number of *Diplocardia* earthworms surfacing also decreased with distance to the source of vibration. Catania (2008) performed a similar experiment and found equivalent results with a peak energy content at 80 Hz and the number of emerging *Diplocardia* earthworms decreasing to zero within 8–9 m. These characteristics depend on several factors, including the materials in contact and associated surface roughness, the speed and the force applied, as well as mechanical properties of the soil used in the experiment, and so it is interesting that these independent studies generated very similar signal characteristics which elicit a response. A second experiment by Catania (2008) strongly supported the surfacing of *Diplocardia* earthworms to be a behaviour to escape mole predators. Three dimensional arenas containing soil and earthworms were used to compare responses to simulated rainfall and the introduction of a mole, with few earthworms surfacing in response to rainfall and distinctly greater numbers of earthworms surfacing in response to mole digging. Further research by Mitra et al. (2009) found no significant surfacing response of earthworm communities dominated by Lumbricadae to 'grunting', suggesting species specificity to vibration characteristics. For Lumbricadae, a surfacing response to stomping birds is reported (Darwin 1882; Kaufmann 1986; Tinbergen 1953) and this behaviour is considered to be learned, but no soil measurements have been made towards understanding this phenomenon. For example, it may not require explicit surfacing (unlike bait collection), as a movement response near

FIGURE 8 | A latex cast of an agricultural field indicating how the sensory environment is influenced by burrowing and bioturbation activities, with intense burrowing at the surface and deep vertical burrows made by anecic earthworms.

to the surface could enable prey localisation or halt movement which creates a 'lull' enabling prey localisation.

3.5 | Earthworm Sensory Systems

Earthworms (Annelida) were once considered to be 'mindless reflex machines' but are increasingly recognised as having cognition in terms of memory and learning. Earthworms can be classically trained, for example, to anticipate a negative stimulus (light) after brief vibration (Watanabe et al. 2005). Whilst researchers anticipated vibration specific receptors on earthworm bodies, instead whole-body surface tactile sensitivity, widely distributed sensory buds across the body surface and/or free nerve endings found in the segmented body wall are linked to vibration sensitivity (Mitra 2009). An examination of the sensory buds on *Eisenia foetida* earthworms found that sensory buds were randomly arranged on the head region, were arranged in line with setae (arrows) along the body, were typically packed with cylindrical and flexible stalks (Figure 9). The authors reported that these structures resembled the sense organs in the lateral lines of fish and amphibians.

To function as a spatially separated sensor array, it would require evidence of neural integration for these multiple sensory inputs.

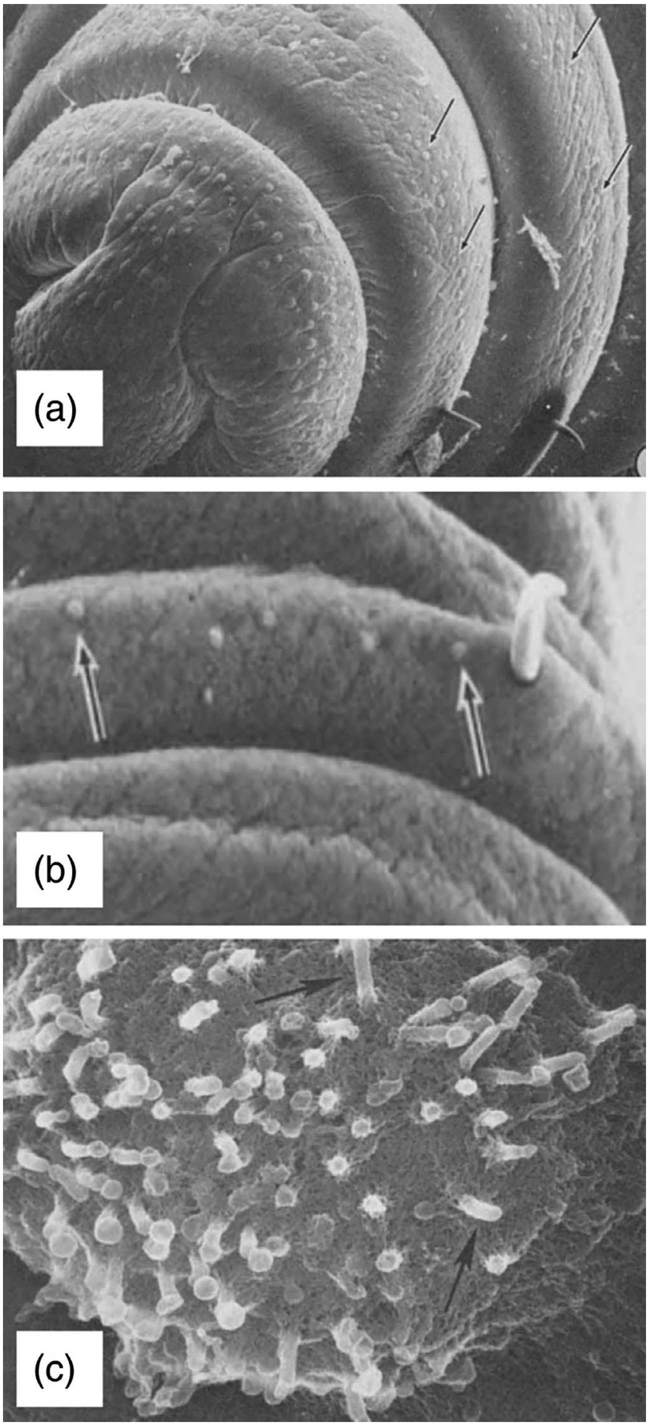

FIGURE 9 | Sensory buds on *E. foetida* earthworm (a) Random arrangement of the sensory buds on the protomium and the line arrangement of sensory buds (arrows) on the anterior part of the segments of an adult earthworm. (b) The arrangement of the sensory buds in line with the setae. (c) Sensory stalks protrude from the sensory bud as dense bundles.

In studies of earthworms, signal processing is distributed over the segmental ganglia (rather than the brain ganglia, because its removal does not influence task capabilities) (Watanabe et al. 2005). Each segmental ganglion processes stimuli, and memory formation is distributed over these segmental ganglia (Watanabe et al. 2005). The implications are that the earthworm can learn vibratory patterns, and that localised vibrations, for example, stimulating a few segments could generate different behavioural responses to whole-body stimulation (Mitra 2009).

4 | Critical Analysis of Soil Ecoacoustic Research

The ecoacoustic method is dependent on acoustic indices and statistical inferences as a means of extracting information about the ecological features of the soil habitat.

4.1 | Signal Processing Methods

In examining the applications of signal processing methods used to investigate soils (Table 2), there is a relatively narrow implementation of available methods. Signal processing has a long history having its origins applied to audio signals dating back to the 1940s and 1950s (Shannon 1948), and the underlying mathematical theory of decomposing signals into a frequency domain dating back to the early 19th century (Fourier 1822). It has thus seen many multifaceted developments, such as the development of wavelet analysis in the 1980s and the general domain of time–frequency analysis, in particular with applications to non-stationary seismic signals (Wang 2023). Despite this breadth of methodology available, ecoacoustic analysis is predominantly built on Fourier analysis. Fourier analysis has a wealth of theoretical and practical foundations and yields much insight. However, little attention has been paid to the implications and situations where alternative approaches may provide additional information. More specifically, existing literature (Bradfer-Lawrence et al. 2025) focuses on applying existing ready-to-go indices (derived from Fourier transforms) to soil recordings rather than developing an appropriate index based on the structure of the signal one wishes to detect and quantify.

Fourier transform can identify frequencies but not their occurrence in time, and so its application is best suited for stationary signals (Kiskin et al. 2020). Seismic signals are fundamentally non-stationary as the amplitude and frequency of a sinusoidal representation can change dynamically as a function of travel time (Wang 2023). Time–frequency analysis offers a preferable alternative as it enables an analysis of the local properties of a signal. A diverse range of methods is available to derive the time–frequency decomposition depending on the features one wishes to detect. For example, one of the early applications of wavelet analysis was motivated by the need to analyse signals with both short, high-frequency transients with a small number of cycles, and low-frequency transients (Goupillaud et al. 1984; Percival and Walden 2000).

To date, the acoustic indices being applied to soil systems have often been derived from algorithms developed for the analysis of bird communications, which contrasts with the spectral and temporal features of soil recordings which reveal low-frequency harmonics and low signal-to-noise ratios, best described as weak signals embedded in noise and categorised as non-stationary signals. This problem can be resolved by, for example, wavelet transformations that offer multiple time–frequency resolutions, appropriate for non-stationary data. It follows that indices developed for soils should be derived from time–frequency decompositions that capture specific and meaningful features of the detectable signals. Fundamentally, it is not yet clear *what* should be characterised within soil recordings either in the frequency domain (e.g., characterising the steady state, detecting anomalies) or the time domain (e.g., short transients, circadian rhythms, and long-term monitoring) and requires further research.

4.2 | Unbalanced Data

Unbalanced data was recently demonstrated by Vang Sørensen et al. (2024), demonstrating that whilst acoustic indices separated ant signals/cues from background noise with useful applications for phenology, values increase with increasing numbers of the same species (indicating unbalanced data), with implications for interpreting acoustic indices in terms of a proxy for soil biodiversity. This creates uncertainty relating to previous interpretations relating the soil ecoacoustic studies, including diel and seasonal patterns, to soil fauna composition (Maeder et al. 2019, 2022; Robinson et al. 2023; Robinson, Taylor, et al. 2024). This situation poses a subtle risk for the trajectory of soil science, which is common to all unbalanced datasets in classification learning algorithms that are inherently biased towards the majority class, resulting in a higher misclassification rate for minority classes (López et al. 2013). The problem is best described using medical research: healthy states may represent 95% datapoints, whilst the rest of the data belongs to 30 disease states, so it would be possible to produce an algorithm with an accuracy of 95%, but the other classes have a misclassification rate of 100% of cases, resulting in serious consequences for diagnosing a diseased state as healthy. There are a range of solutions to the challenges created by unbalanced data sets (López et al. 2013). It is critically important to focus on detecting and measuring the most significant data properties (López et al. 2013) to avoid compromising data validity in a way that impedes scientific progress.

4.3 | Trajectory

There is a broad perception that deploying sensors does not require skill, experience or training, as algorithms will work their magic and keep the costs of research and monitoring ecosystems low (Giuliani et al. 2024). This contrasts to our review spanning interdisciplinary topics, and behavioural ecology and soils literature which emphasise engagement with the natural environment is a vital behaviour needed to make advances (Bonato Asato et al. 2023; Bünemann et al. 2018; Endler 2025).

Where and when you put the sensor or sensor array presents somewhat infinite spatial and temporal deployment possibilities. The trajectory of soil ecoacoustics is therefore dependent upon the key tenets of soil health theory. This can be informed using the conventional benchmarking (static, isolated) paradigm, or a paradigm shift towards the systems theory of soil (dynamic, interconnected). To date, generating outputs describing the spatio-temporal complexity of ecological processes (Farina and Mullet 2025); at fine temporal scales (e.g., dynamic diel and seasonal patterns, noting aforementioned challenges of unbalanced data); and emergent system applications, for example, restoration studies (Robinson et al. 2023; Robinson, Taylor, et al. 2024) suggests a trend towards the soil systems paradigm.

This may enable the discovery of important signalling pathways, including those at risk from human activities. For example, the vibration excitation at the soil surface from wind turbines is linked to a reduction of earthworm abundances in agricultural fields in close proximity to this source (Velilla et al. 2021) and vibration excitation reduced the reproductive biology and fitness of soil-dwelling beetles (Phillips et al. 2020).

The outputs are on the very fringes of human senses so it remains to be demonstrated whether humans can expertly and efficiently label soil recordings to produce training data for machine learning applications. If unsupervised machine learning is used to resolve this problem, due to indications of its superior performance to pattern recognition in this domain (Kiskin et al. 2020) selecting experimental conditions is of paramount importance. With such a fast-evolving technology coupled with limited understanding of what exactly is being detected, care is needed to avoid the collation of datasets with inherent biases that have great potential to propagate and amplify misconceptions (Glickman and Sharot 2025; Hall et al. 2022). Integrating soil science and mechanistic modelling of soil processes and wave propagation is an essential component of developing reliable monitoring solutions, to understand what is being detected.

5 | Conclusions and Future Directions

In conclusion, the use of soil ecoacoustics to monitor soil ecology presents many challenges. The principal concerns are the shortcomings in the theoretical frameworks and that what is being detected is largely unknown in soils. However, sonoscape investigations provide a practical framework to develop field research, whilst the principal drive model offers a rich set of hypotheses to test.

Existing studies in this field highlight a disciplinary boundary between ecologists and acousticians/soil scientists. Ecologists primarily focus on detecting population-scale effects, often relying on statistical methods and acoustic indices. In contrast, acousticians and soil scientists have yet to undertake studies that characterise the acoustic behaviour of individual earthworms or groups, particularly in terms of the precise mechanisms governing wave excitation in soil. Reciprocal benefits are very likely to emerge from greater interaction between these communities. Ecologists could leverage the expertise of acousticians and soil scientists in excitation, propagation, and scattering phenomena to decide on appropriate sensors and methods of deployment, refine signal processing algorithms and enhance detectability limits. Conversely, recognising the limited ecological significance of single-organism studies may prompt acousticians to develop more holistic models and physics-informed signal analysis approaches.

Expanding our fundamental understanding of soil ecoacoustics enables broader potential applications for guiding more sustainable land management strategies. As a hypothetical example, if ecoacoustics can be deployed to monitor earthworm activity windows (i.e., detecting burrow formation through mechanical penetration processes and granular interactions), practitioners can adapt their tillage scheduling in real time to mitigate harm they may otherwise cause to the active fauna. Acoustic/elastic wave propagation techniques can also be used to estimate mechanical stiffness of soil aggregate structures, informing soil structural resilience to compaction. This could help inform suitable vehicle loads that will cause minimal disruption to the soil structure, whilst continuing to perform effective field activities (e.g., tillage, fertilisation, and pesticide application). Beyond these biophysical and structural metrics, inferences that could be made regarding biodiversity can aid with civil development. For instance, if road, motorway, or rail line construction is being planned, a quick snapshot from eco-acoustic measurements can rapidly estimate potential proxies for biodiversity and inform how best to adapt the construction to circumvent ecosystem disruption. The prospects show promise, but rigorous advancements have to be made to ensure confidence in these techniques. To advance the field, researchers must embrace interdisciplinarity and foster collaboration between ecology and acoustics. Several key areas of inquiry that could facilitate meaningful progress, in no particular order, are:

- Characterisation of sources: A rigorous investigation of invertebrate targets as acoustic emitters to elucidate the mechanisms by which they generate waves in soil, ideally supplemented by mathematical and numerical models. Fundamental questions should be addressed, such as determining whether different species or movement types excite distinct waveforms—do soil organisms generate pore-borne waves?
- Establishing biologically relevant frequency ranges: identifying signal frequency ranges linked to biological activity, along with their detection ranges, across diverse soil types and detection techniques.
- Advancing sensor technology: developing sensors informed by a deeper understanding of wave characteristics, optimal detection ranges, and ambient noise levels to improve measurement accuracy.
- Controlled experimental studies: generating experimental evidence under controlled conditions to isolate biotic acoustic signals and refine methods for disentangling complex cues and signals, providing essential input for detection and characterisation models.
- Enhancing AI explainability: moving beyond black-box approaches in AI-driven soil recordings by integrating physics-based insights to improve interpretability and reliability.
- Interrogating the ecological significance of soil fauna sounds: making use of the global long term experiment network to determine whether soil fauna-generated mechanical waves are more than mere disturbances to the soil structure.
- Rigorous experimental campaigns to develop phenological research (organism, interaction, mismatches and implications).
- Development of independent validation data and methods. Through increased collaboration, the disciplines of ecologists, acousticians and soil scientists will move closer together providing greater mechanistic meaning to observed data. However, such hypotheses need to be verified through independent validation. Although development of signal libraries has distinct worth, it does not have longevity due to the inevitable evolution of sensor technology. Rather we suggest the development of robust and transferable methodology to develop validation sets.

Embracing these interdisciplinary avenues will help develop our sensing capabilities for soils in robust scientific principles and mitigate the risks of speculative overreach. The challenge cannot be underestimated; it is difficult to shift perspectives in soil science particularly when interdisciplinary research is needed to make progress (Baveye et al. 2024). Strengthening experimental and theoretical foundations will ultimately enable a more accurate and meaningful understanding of soil-borne acoustic phenomena. It is crucial to expand the evidence base regarding the origins, propagation, and significance of soil-borne biotic sounds. Notably, despite the identification of this sensing mechanism decades ago, fundamental experimental studies remain scarce. The dominance of review papers, including this one, has contributed to an overinflation of the significance of isolated research findings.

Author Contributions

Jacqueline L. Stroud: conceptualization, writing – original draft, writing – review and editing, project administration, supervision. **Michał K. Kalkowski:** writing – original draft, writing – review and editing, conceptualization. **Kirsty L. Hassall:** writing – original draft, writing – review and editing. **Miriam Treadway:** writing – original draft. **Jessica Fannon:** writing – original draft. **Aidan Keith:** writing – original draft, writing – review and editing. **Siul Ruiz:** writing – original draft, writing – review and editing. **Keith Attenborough:** conceptualization, writing – original draft, writing – review and editing.

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Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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