

Methods and approaches to advance soil macroecology

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Abstract

Motivation and aim: Soil biodiversity is central to ecosystem function and services. It represents most of terrestrial biodiversity and at least a quarter of all biodiversity on Earth. Yet, research into broad, generalizable spatial and temporal patterns of soil biota has been limited compared to aboveground systems due to complexities of the soil system. We review the literature and identify key considerations necessary to expand soil macroecology beyond the recent surge of global maps of soil taxa, so that we can gain greater insight into the mechanisms and processes shaping soil biodiversity. We focus primarily on three groups of soil taxa (earthworms, mycorrhizal fungi and soil bacteria) that represent a range of body sizes and ecologies, and, therefore, interact with their environment at different spatial scales.

Results: The complexities of soil, including fine-scale heterogeneity, 3-D habitat structure, difficulties with taxonomic delimitation, and the wide-ranging ecologies of its inhabitants, require the classical macroecological toolbox to be expanded to consider novel sampling, molecular identification, functional approaches, environmental variables, and modelling techniques.

Main conclusions: Soil provides a complex system within which to apply macroecological research, yet, it is this property that itself makes soil macroecology a field ripe for innovative methodologies and approaches. To achieve this, soil-specific data, spatio-temporal, biotic, and abiotic considerations are necessary at all stages of research, from sampling design to statistical analyses. Insights into whole ecosystems and new approaches to link genes, functions and diversity across spatial and temporal scales, alongside methodologies already applied in aboveground macroecology, invasion ecology and aquatic ecology, will facilitate the investigation of macroecological processes in soil biota, which is key to understanding the link between biodiversity and ecosystem functioning in terrestrial ecosystems.

KEYWORDS

belowground, biodiversity, distribution, macroecology, soil, spatial scale

1 | INTRODUCTION

Macroecology strives to understand the generality of emergent patterns of aggregate ecological entities (McGill, 2019). The area has moved beyond large-scale biodiversity maps for many aboveground taxa, addressing process-based patterns including latitudinal gradients of diversity (Stehli, Douglas, & Newell, 1969), species–area relationships (Rosenzweig, 1995), species–energy relationships (Gaston, 2000) and broad scale responses of diversity to anthropogenic pressures (Newbold et al., 2015), across spatial and temporal scales. There are, however, still significant knowledge gaps surrounding many questions of macroecology and biogeography, and new techniques to investigate these, in soil ecology (Eisenhauer et al., 2017).

Soil biodiversity regulates nutrient cycling and makes other central contributions to net primary production and carbon sequestration (Bardgett & Wardle, 2010; Wagg, Bender, Widmer, & van der Heijden, 2014) across spatial scales (Delgado-Baquerizo et al., 2020). Given the importance of soil biodiversity, knowledge of spatial and temporal distributions of soil organisms is essential for both management of terrestrial ecosystems and predicting future ecosystem functioning under global environmental change (Crowther et al., 2019; Wagg et al., 2014). Recently, there has been an increased interest in describing the generality of emergent patterns of soil biodiversity (e.g., Shade et al., 2018; Shoemaker, Locey & Lennon, 2017; Thakur et al., 2019), although difficulties in observing many soil organisms directly has limited this. Further, it has been challenging to formulate a common macroecological framework across soil taxa given the sheer range in body sizes and ecologies, from bacteria to macrofauna, which vary in the scale at which they perceive the environment. Methodological and taxonomic challenges have hindered macroecological research into belowground systems concerning species richness, spatial distributions, ecosystem functioning and spatial scaling (Decaëns, 2010;

Schröder, 2008; Shade et al., 2018). The challenges of soil macroecology, therefore, arise not only across spatial and temporal scales, but also across the organizational hierarchy of species, communities and ecosystems.

At a species level, species distribution models (SDMs) are frequently employed to relate the spatial distribution of aboveground species to their environment (Elith & Leathwick, 2009), yet, there are very few examples of SDMs applied to soil-dwelling species other than earthworms (e.g., Marchán et al., 2015; Palm, van Schaik, & Schröder, 2013). For many soil taxa, this is a result of not having sufficient species-level occurrence data from various geographical locations spanning environmental gradients at relevant spatial scales (Schröder, 2008). For other taxa (i.e., Collembola, but see Caruso, Hogg, Carapelli, Frati, & Bargagli, 2009) these data are already available, which begs the question of why the modelling of belowground species distributions has been so limited. There is, therefore, a huge opportunity to expand soil macroecological research through species distributions modelling, as long as we are able to overcome the challenges of the soil system itself.

Community biodiversity patterns include well-established macroecological relationships, such as the species–area relationship and latitudinal gradients (e.g., Rosenzweig, 1995), distance–decay curves (Nekola & White, 1999), as well as models linking biodiversity patterns to environmental variables such as the species–energy relationship (e.g., Evans, Newson, Storch, Greenwood, & Gaston, 2008). These relationships have formed the basis of macroecological theory and our knowledge of how diversity is arranged in space and time, at a range of spatial, temporal and hierarchical scales. Although community assembly in soil organisms has been investigated (Caruso, Taormina, & Migliorini, 2012; Dirilgen, Juceviča, Melecis, Querner, & Bolger, 2018), generalizable spatial and temporal patterns of soil biodiversity have yet to be determined to the degree that they have above ground (but see Caruso, Schaefer, Monson, & Keith, 2019). For microbes in particular, studies have tended to focus on individual

taxa and metabolic genes, yet, it is the emergent properties of communities that influence ecosystem functioning and services (Ladau and Eloe-Fadrush, 2019), and, therefore, need to be considered if we are to expand the field of soil macroecology.

At the ecosystem level, there have been huge advancements in our ability to model whole ecosystem functioning, particularly within the context of global change (Allan et al., 2015; De Laender et al., 2016). The development of measures of functional diversity (the range and variation of ecological traits present within an area) has facilitated this. Aboveground, these measures have been used to investigate key conservation issues such as biotic homogenization (White, Montgomery, Storchová, Hořák, & Lennon, 2018). Given the importance of soil and soil biodiversity in ecosystem functioning and global cycles (Delgado-Baquerizo et al., 2020), functional traits have much to offer soil macroecology. The measurement of functional traits is becoming increasingly feasible from a technical perspective (e.g., proteomics and isotope tracer-enabled analysis of proteins and metabolites, trait database availability), and they can be directly linked to ecosystem level processes (Hooper et al., 2005). There is a need, therefore, to continue to develop methods to measure functional diversity and broad scale functioning of soil organisms, and understand, for example, how these respond to environmental gradients. Applied properly to soil organisms, macroecological approaches will provide us with another tool to tackle global challenges related to soil functioning and soil protection.

2 | AIMS AND SCOPE OF THIS REVIEW

To move beyond mapping of soil taxa in space and identify broad, generalizable spatial and temporal patterns of soil biodiversity and their underlying mechanisms, we need to consider: the biodiversity data; the spatio-temporal context of the system and mechanisms under investigation; the biotic components shaping these patterns; and the abiotic components shaping these patterns. We discuss each of these sets of considerations and review current methods and future directions for each. Our intention is not to provide a systematic review of macroecological patterns of multiple soil taxa, but instead, to focus on the specific characteristics of the soil system that have limited soil macroecology, and review and propose methods that would help address these limitations. To accomplish this, we use earthworms, mycorrhizal fungi and soil bacteria as focal taxa. These groups have all had their global biodiversity modelled (earthworms, Phillips et al., 2019; fungi, Kivlin, Hawkes, & Treseder, 2011; Pärtel et al., 2017; Tedersoo et al., 2014; soil bacteria, Delgado-Baquerizo et al., 2018), and they reflect the diversity of taxa that inhabit soil through their variation in body size, life-forms and ecology, which leads to differences in the spatial scale at which they perceive and interact with their environment. They, therefore, provide a range of robust examples of the issues that have hindered soil macroecological research to date, and the diversity in approaches required to overcome these difficulties.

3 | DATA CONSIDERATIONS

3.1 | Data availability

Initiatives exist to establish standardized sampling protocols to collect new data on soil biodiversity (Philippot, Ritz, Pandard, Hallin, & Martin-Laurent, 2012), for example, the Earth Microbiome Project (Thompson et al., 2017) and EcoFINDERS (Lemanceau, 2011), as well as bring together existing soil biodiversity data (see Table 1) into accessible databases and frameworks, for example, the Global Soil Biodiversity Initiative (www.globalsoilbiodiversity.org) and Ramirez et al. (2015). Pärtel et al. (2017) use a standardized data set of meta-barcode information (MaarjAM database, Öpik et al., 2010) to model spatial variation in species pool, local and dark diversity (members of the species pool that are absent locally) alongside their respective environmental correlates. These standardized data provide a suitable means for investigating large-scale biodiversity patterns (e.g., species–area relationships, latitudinal gradients etc.), and, in fact, better satisfy the criteria of comparability across sites and studies than many data sets of macro-organism distributions, which show large variation in sampling methodology and effort.

The Global Soil Biodiversity Initiative and Ramirez et al. (2015), on the contrary, aim to maximize the potential of existing data by establishing global platforms that combine databases of all types of soil biodiversity data, including molecular, taxonomic, and morphological measurements and traits. Assembling data from multiple sources is complicated due to variability in taxonomic resolutions, unresolved taxonomies (Cameron, Decaëns, Lapied, Porco, & Eisenhauer, 2016) and lack of standardization of sampling techniques that cause technical factors (e.g., sampling protocol, primer and sequencing platform) to be an important source of inter-study variability (Ramirez et al., 2018). Some studies choose to only include data collected using specific methodologies to reduce inter-study variability (e.g., European earthworm diversity maps, Rutgers et al., 2016, 2019), yet, non-standardized data sets can still provide important global insights into the ecological preferences and geographical ranges of species (Ramirez et al., 2015). These data will complement standardized sampling protocols when analysed appropriately, for example using meta-analytical or machine learning approaches (Hendershot, Read, Henning, Sanders, & Classen, 2017; Ramirez et al., 2018). Substantial geographical gaps in sampling, however, need to be addressed (Cameron et al., 2018) if we are to determine generalizable patterns of biodiversity, and model predictions should be refined and updated as empirical data sets become increasingly available.

3.2 | Measuring and defining soil biodiversity

To study many macroecological patterns such as species-abundance distributions, species–area relationships and latitudinal gradients, we first need to identify the species. However, challenges remain with identification of many soil taxa (Soininen, 2012); the huge diversity of soil organisms, combined with their small size

TABLE 1 Examples of existing databases that include soil biodiversity or distribution data

Database website	Database name	Taxa	Geographical coverage	Taxonomic resolution	Year compiled
https://data.bioplatforms.com/organization/about/bpa-base	Biome of Australian Soil Environments	Microbes	Australia and Antarctica	Molecular (OTU)	2016
http://drilobase.org/	Drilobase—the World Earthworm Database	Earthworms	Global	Species	2014–present
http://www.earthmicrobiome.org/	Earth Microbiome Project	Microbes	Global	Molecular (OTU)	2017
https://edaphobase.org/	Edaphobase	Soil fauna	Germany (predominantly)	Species	2014–present
http://maarij.m.botany.ut.ee/	MaarijAM	Arbuscular mycorrhizal fungi	Global	Molecular (small subunit rRNA sequences)	2010
https://catalogue.ceh.ac.uk/documents/53210c27-87fc-46e4-a3d6-e731003dc541	Model estimates of topsoil microbes [Countryside Survey]	Bacteria	Great Britain	Molecular (terminal restriction fragments)	2007
https://hbnatlas.org/	National Biodiversity Network Atlas	Various, including soil biota	Great Britain and Northern Ireland	Variable	2000–present
http://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database	PREDICTS	Various, including soil biota	Global	Predominantly species	2016
https://catalogue.ceh.ac.uk/documents/fccd86b0-f5b6-4716-b4f7-f43ad82daee	Soil Invertebrates Countryside Survey	Soil invertebrates	Great Britain	Class/order	2007

OTU = operational taxonomic unit; rRNA = ribosomal RNA.

(Schaefer, Norton, Scheu, & Maraun, 2010), has led to a distinct lack of taxonomic knowledge of soil biodiversity (Decaëns, Lavelle, & Jiménez, 2008; Phillips et al., 2017). Biogeographical realms at multiple spatial scales, therefore, exist where every new place sampled, especially remote locations, can give huge volumes of undescribed species or sequences that cannot be matched to any known species or genus-level taxon (Decaëns, 2010; Fierer, 2017). Indeed, even urban systems such as Central Park in New York City, can harbour large volumes of undescribed soil biodiversity (Ramirez et al., 2014), and earthworms, a comparatively well-studied group with relatively low diversity, have had a large number of cryptic species revealed through DNA barcoding (King, Tibble, & Symondson, 2008).

Gene-based diversity assessments of environmental DNA (eDNA) are a promising toolset for facilitating large-scale sampling of soil diversity (Bik et al., 2012; Deiner et al., 2017). Species can be identified using short metabarcodes and small samples of soil (e.g., earthworms, Bienert et al., 2012). eDNA has already furthered macroecological research, for example, through the detection of earthworm diversity at the landscape scale, revealing impacts of abiotic factors not detected using traditional survey methods (Pansu et al., 2015). Nevertheless, the degree to which eDNA-based diversity estimates capture the living soil biota (rather than 'relic' DNA) is unclear (Lennon, Muscarella, Placella, & Lehmkuhl, 2018; Ruppert, Kline, & Rahman, 2019). Furthermore, this technique can vary with soil organic matter content and type, complicating the comparison of biodiversity patterns across environments and highlighting the continued, pressing need for the standardization of methodologies (Geisen et al., 2019; Philippot et al., 2012).

In particular, many molecular studies use targeted sequencing of specific marker genes or gene regions, which serve as 'barcodes'. Sequence differences within the 'variable regions' of the marker genes are used to identify operational taxonomic units (OTUs), which may serve to delineate taxa below the genus level (e.g., earthworms, Pansu et al., 2015; fungi, Pellissier et al., 2014; Tedersoo et al., 2014). However, there is no universal threshold for an eukaryotic OTU, and this may well be clade-specific, and dependent on the barcode length and region of choice (Mysara et al., 2017). Despite recent technological advances in sequencing and bioinformatic pipelines to process high-throughput amplicon sequences, considerable challenges remain when using gene-based methodologies (Nesme et al., 2016). Errors or biases can arise from different DNA extraction methods (Inceoglu, Hoogwout, Hill & van Elsas, 2010), primer specificity, sequencing chemistries (i.e., short read length, Tedersoo et al., 2015; Tremblay et al., 2015), and bioinformatic processing, as well as difficulties with OTU delimitation and chimeras (Orgiazzi, Dunbar, Panagos, de Groot, & Lemanceau, 2015), and lack of matching current database entries (e.g., fungi; Tedersoo et al., 2014, bacteria; Ramirez et al., 2014; Thompson et al., 2017). These can confound diversity estimates in cross-study comparisons (Fierer, 2017; Thompson et al., 2017). Recent developments in clustering algorithms, that is, a reference-free approach to resolve sequence variants at a single nucleotide resolution (Callahan, McMurdie, & Holmes, 2017; e.g., Deblur, Amir et al., 2017), could offer stable identifiers across

different studies (Thompson et al., 2017), facilitating data reusability and integration of multiple data sets (Amir et al., 2017), thus, maximizing the potential of gene-based surveys in soil macroecology (Geisen et al., 2019). Alternatively, DNA-targeted enrichment (bait capture) allows more efficient recovery of sequence information, not relying on sequence affinity as strongly as PCR (Dowle, Pochon, Banks, Shearer, & Wood, 2016). DNA enrichment can be applied to a range of different sample sources, in individual or pooled samples and can be used for recovering exogenous DNA present in environmental samples (Shokralla et al., 2016).

Many studies now focus on alternative dimensions of biodiversity to taxonomic diversity. Functional diversity, which measures the diversity and range of traits within a community, can be closely linked to ecosystem functioning (Heemsbergen et al., 2004; Hooper et al., 2005). Shifting from taxonomic to functional information can provide a way to unify the study of soil macroecology: the units are no longer species, or taxa, but functions and the diversity of functions expressed, which are relevant across taxonomic groups. Macroecological patterns that emerge from traits include trait-area and -time relationships (e.g., White, Montgomery, Pakeman, & Lennon, 2018), and functional diversity gradients (e.g., Meynard et al., 2011), which further our knowledge on the spatial, temporal and environmental structuring of ecological traits and ecosystem functioning (Violle, Reich, Pacala, Enquist, & Kattge, 2014), and provide new insights into community assembly theory (Smith, Sandel, Kraft, & Carey, 2013). Due to the key ecosystem functions that soil biodiversity provides (Heemsbergen et al., 2004), we advocate a concerted shift towards functional approaches within soil macroecology through the following methodological and data options.

Trait databases facilitate the investigation of trait composition of soil communities. Morphological, physiological and phenological traits are present in the literature for many soil invertebrates due to their relative ease of measurement (e.g., carabid beetles, Barbaro & van Halder, 2009; earthworms, Hedde et al., 2012; Collembola, Bonfanti et al., 2018; Martins da Silva et al., 2016; ants, Bishop et al., 2016). For soil bacteria and fungi, on the contrary, characterization of morphological, physiological and phenological traits can be more challenging since isolation of individual species for trait measurements is not feasible in most cases (Krause et al., 2014; Zanne, Powell et al., 2020). Two recently published, large global databases, FungalRoot (Soudzilovskaia et al., 2020) and the Fungal Functional Database (FUNfun, Zanne, Abarenkov et al., 2020), however, will facilitate better understanding of trait composition of fungal communities, their interactions with plants, and their effects on worldwide ecosystem functioning (Powell & Rillig, 2018). However, as with many taxa, fungal trait databases are often incomplete (Zanne, Abarenkov et al., 2020). There has also been a concerted effort to quantify microbial functions in soil due to their importance for key ecosystem functions (Aguilar-Trigueros et al., 2015; Zanne, Abarenkov et al., 2020) through standardized 'omics' and enzymatic approaches (Dawson et al., 2019), as well as the measurement of climate tolerances to investigate life history trait trade-offs at large spatial scales (Maynard et al., 2019).

'Omic'-based functional analyses (e.g., proteomics, metabolomics) have been used to determine broad scale patterns in fungi (Tederloo et al., 2014) and bacteria (Delgado-Baquerizo et al., 2018; Fierer & Jackson, 2006). These methods enable the categorization of soil microbes by their ecological strategies (e.g., Fierer, 2017), therefore, bypassing the taxonomic deficit problem and focusing on functional diversity. Functional 'omics' approaches can be used in experimental community ecology studies to provide information on potential ecosystem functioning (Maron, Ranjard, Mougél, & Lemanceau, 2007), such as the diversity of protein-coding gene categories, for example, antibiotic resistance genes and osmoregulatory genes (Bahram et al., 2018; Fierer et al., 2012), and soil enzyme substrate specificity (Caldwell, 2005) in nutrient cycling, as well as community structure and dynamics within the soil (Arsène-Pløetze, Bertin, & Carapito, 2015). Unlike gene-based approaches, protein-based 'omic' approaches (metaproteomics) capture the active component of soil biomass (Blagodatskaya & Kuzyakov, 2013), and thus, avoid overestimating diversity from dormant or dead biomass (Carini et al., 2016; but see Papp et al., 2018).

Despite limitations (i.e., transcriptomics may reveal potential, rather than fulfilled functions, Prosser, 2015), elucidating the underlying molecular mechanisms supporting functions could help to unlock the functional networks that interact to sustain soil properties (e.g., Bonfante & Genre, 2010). Semi-controlled experiments can build novel bridges with complex natural systems. For example, we recommend mesocosm experiments coupled with 'omics' approaches designed to identify longitudinal biological responses of soil biota to microbiomes (e.g., soil and rhizosphere) and plants, although destructive sampling is a limitation. Further still, defining a global transcriptome-based delineation of functional entities, and obtaining a landscape of their similarities and differences based on differential expression of genes across different combinations of hierarchical levels and abiotic factors, for example, could help to derive the sets of genes involved in specific ecological processes that could be targeted in the field using metagenomics as a ground-truthing approach. Integrating multiple 'omic' approaches, therefore, into community studies will lead to a rapid transformation in our empirical understanding of soil functioning and interactions (Swenson & Jones, 2017), and complementary approaches to DNA sequencing remain a priority for soil biodiversity research (Eisenhauer et al., 2017) as they will reveal new information on the mechanisms underlying ecosystem processes.

4 | SPATIO-TEMPORAL CONSIDERATIONS

4.1 | Scale and structure

Intra- and interspecific aggregations (Ettema & Wardle, 2002), which result from the microscale heterogeneity of the soil system and limited dispersal of organisms, structure soil communities across spatial scales (Bach, Williams, Hargreaves, Yang, & Hofmockel, 2018; Decaëns, 2010; Noguez et al., 2005; Thakur et al., 2019). In a Brazilian

agricultural system, for example, geographical distance explained nearly 18 times more variance in soil fungal community composition than environmental factors such as soil and climate characteristics (Gumiere, Durrer, Bohannan, & Andreote, 2016). Biogeography of soil bacteria has been investigated at a range of scales from continental and global scales (e.g., Bahram et al., 2018; Barberán, Bates, Casamayor, & Fierer, 2012; Fierer & Jackson, 2006) to the landscape scale (Bru et al., 2011; Pasternak et al., 2013), and even at the centimetre scale (O'Brien et al., 2016). By taking multiple soil cores separated by only a few centimetres at sampling plots spaced 6 m apart, O'Brien et al. (2016) showed that there was extreme patchiness in community structure at the centimetre scale, but more general patterns in diversity, linked to fertilization, were observed at the plot-level. This scale-dependent heterogeneity arises from the operating scale of mechanisms underlying community assembly. This needs to be accounted for in sampling design for investigations of spatial patterns of soil diversity with multiscale sampling protocols (e.g., Rasmussen et al., 2018). Additionally, macroecological analyses of soil diversity need to use techniques that model space, such as autoregressive models (Beale, Lennon, Yearsley, Brewer & Elston, 2010), to address the strong spatial structuring in soil ecosystems, as demonstrated by spatial analyses of earthworm abundance, biomass and diversity (Joschko et al., 2006), and ectomycorrhizal fungi (Pickles et al., 2010). Similarly, techniques such as principal coordinates of neighbourhood matrices (PCNM) are useful in differentiating between spatial and environmental structuring of communities at different spatial scales (e.g., Columbian earthworm communities, Jiménez, Decaëns, Lavelle, & Rossi, 2014).

The scale at which similar processes act varies between taxonomic groups due to variation in body size and life history, and is an important consideration when studying spatial patterns of soil communities (Montagna et al., 2018). When studying landscape scale processes, Jackson and Fahrig (2012) highlight the concept of the 'scale of effect' (the scale at which an ecological response is best predicted by the habitat structure) and recommend sampling areas far enough apart to ensure sample points are independent (i.e., taxa in one sample point do not directly interact with those in others). Thakur et al. (2019) present a conceptual framework splitting soil into spatial compartments at which different nested groups of soil organisms can be studied to test biodiversity theories: soil, where all size groups of organisms can be sampled; hotspots (rhizosphere and drilosphere), where meso- and microfauna can be sampled; and microsites (root tips and aggregates), where microfauna can be sampled. This compartmentalization allows integration of body size into the investigation of classical ecological theory. Beyond simply considering 'scales of effect' and spatial compartmentalization, we suggest researchers further draw upon work on investigating scaling issues in complex landscapes to build on the conceptual framework of Thakur et al. (2019) and inform sampling designs. For example, the problem of 'coarse-graining' occurs when fine scale information is aggregated to larger scales to reduce model complexity (Newman, Kennedy, Falk, & McKenzie, 2019). By tracking how this leads to loss of information explicitly and investigating

scaling relationships, corrections for statistical biases may be possible (Newman et al., 2019; Wu, 2004).

The species–area relationship is a classical macroecological relationship that is well established in aboveground biota. Judas (1988) applied the species–area relationship to published data on European lumbricid earthworm diversity, revealing a lower scaling exponent than those established in aboveground systems. One approach to investigate species–area relationships for ectomycorrhizal fungi is to use tree 'islands' of host plants, which, due to their obligate symbiosis, create an island species–area relationship (Peay, Bruns, Kennedy, Bergemann, & Garbelotto, 2007). This approach, however, may not be transferable to other microbial organisms. Taxa–area relationships have also been applied to soil bacteria and fungi using samples taken from the corners of four nested quadrats (Sayer et al., 2013). This method, however, is likely to underestimate diversity at each quadrat size as it is only partially sampled and will be more representative of a taxa–areal extent relationship. It does, however, still provide a useful study design to investigate key macroecological patterns of spatial scaling and turnover of community composition of multiple soil taxonomic groups.

As well as accumulation in space, temporal accumulation of species is an important part of macroecology, and community turnover and can be investigated using the species–time relationship. In aboveground literature, the species–time relationship has been studied far less frequently than the species–area relationship (White et al., 2006), and belowground, this lack of studies is even more pronounced (Ladau & Elie-Fadrosh, 2019). The temporal component of soil biodiversity, however, is critical to consider. As well as hotspots of diversity, Kuzyakov and Blagodatskaya (2015) highlight 'hot moments' of soil microbial diversity, which can occur either occasionally or regularly as a component of periodic processes within a system, often dependent on the temporally dynamic input of C into soil. Additionally, species interactions operate at multiple temporal scales and vary within and between taxa. For example, the connectivity of soil networks on abandoned arable land varies temporally during restoration (Morriën et al., 2017). Hence, for temporal questions, sampling is required at temporal scales relevant for the organisms of interest and the ecosystem properties with which they interact (Bardgett, Bowman, Kaufmann, & Schmidt, 2005; De Deyn & Van der Putten, 2005; Ettema & Wardle, 2002). However, the appropriate scale remains an outstanding question in temporal biodiversity change of most soil organism groups (Eisenhauer et al., 2017; Shade et al., 2018). We, therefore, recommend sampling at multiple time-scales depending on the question at hand to determine the temporal scales at which soil biodiversity varies, from macroevolutionary investigations (e.g., Schaefer & Caruso, 2019) to short-term dynamics (Kuzyakov & Blagodatskaya, 2015).

4.2 | Dimensionality

To date macroecological patterns have been primarily conceptualized in a 2-D context (e.g., species–area relationships, distance–decay

relationships in geographical space, latitudinal gradients). However, where depth and/or height have a strong influence on the biodiversity estimates and community dissimilarity (e.g., marine systems, tropical forests and soils), there is much to be gained by explicitly extending these macroecological concepts to a third dimension. Given that soil community composition varies strongly with soil depth (e.g., fungi and bacteria, Eilers, Debenport, Anderson, & Fierer, 2012; Fierer, Schimel, & Holden, 2003; ants, Wong & Guénard, 2017; microfauna, Pausch et al., 2018), and key ecosystem processes are reliant on sub-soil fauna at different depths (Rumpel & Kögel-Knabner, 2011; Ward et al., 2016), the integration of depth as a third dimension into macroecological theory is a key area to which soil ecologists can contribute. Expanding soil macroecology into this third dimension will be particularly important for obtaining comparable estimates of true soil diversity, for example through extension of species accumulation curves to depth profiles. Furthermore, it will enhance our understanding of species–environment relationships, and provide insights into interaction dynamics in 3-D space. In order to do so, state-of-the-art sampling designs and modelling approaches will be required.

To address these questions it is essential that both soil biota and abiotic properties be sampled across depth profiles. For macrofauna,

sampling must involve multiple methods (e.g., pitfall trapping, direct sampling, Berlese extraction, subterranean baiting) as each is known to capture different species (Figure 1). For example, in a review of sampling methods Wong and Guénard (2017) identified seven studies in which more than 10% (range 12.3 to 44.4%) of all ant species recorded were unique to subterranean samples, and would have been missed with conventional sampling methods. For smaller macro-organisms, such as collembolans and arthropods, core samples provide samples from across the depth profile, but these must be carefully sorted to maintain information on sample depths as combining multiple soil depths into a single sample can homogenize microscale variation (Grundmann et al., 2001). For microbial organisms, microsampling of smaller soil quantities across the depth profile is advised (e.g., Dechesne et al., 2003), or 2-D images of soil thin sections at multiple depths can be used to count bacterial cell distributions and construct 3-D distributions (Raynaud & Nunan, 2014). Sampling of root-associated species, such as mycorrhizal fungi, may be facilitated by incorporating information on the depth distribution of roots (e.g., Sosa-Hernández, Roy, Hempel, & Rillig, 2018). Depth distributions of many taxa can vary seasonally, for example, some earthworm species aestivate in lower soil layers during the summer (Gerard, 1967). Therefore, where feasible, sampling should be

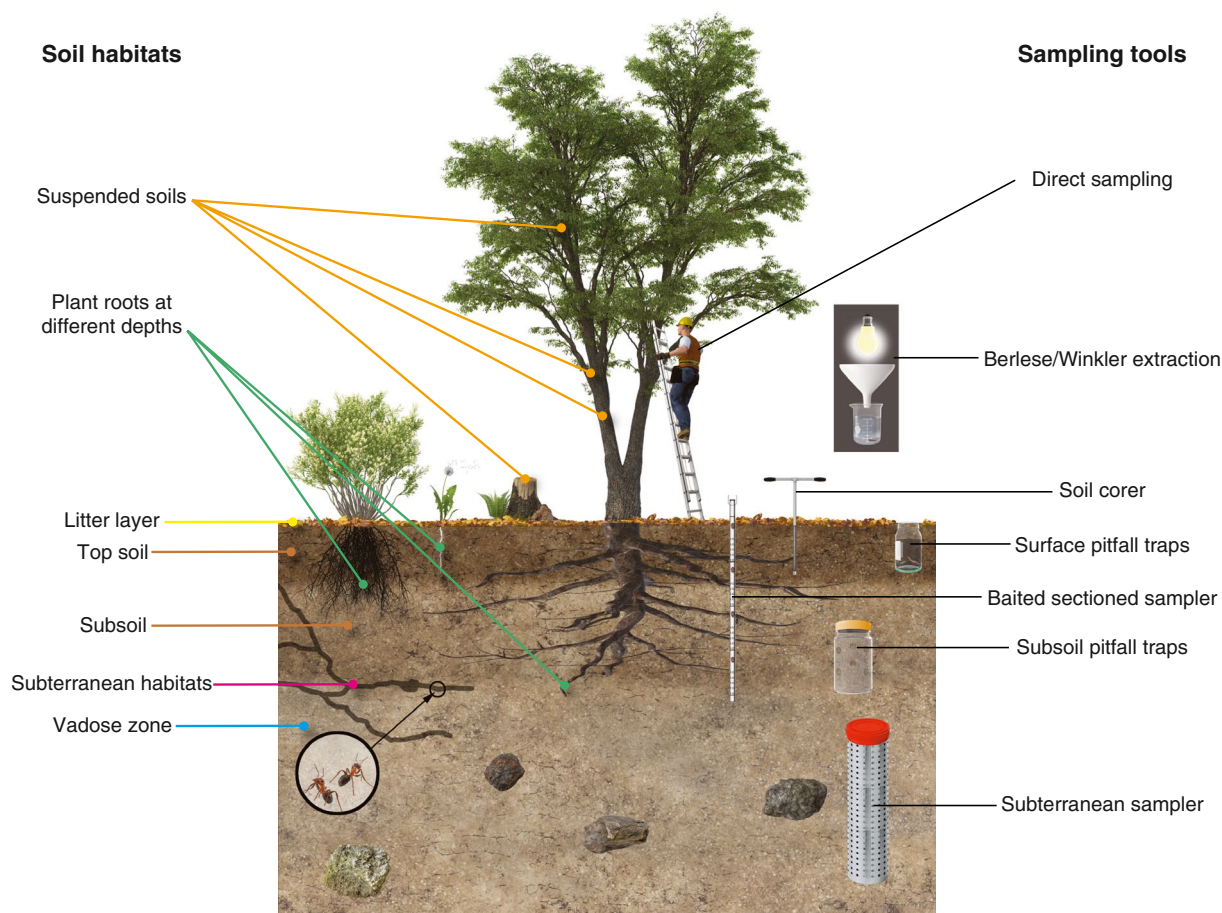


FIGURE 1 Considering different soil habitats and corresponding sampling methods adds dimensionality to macroecological approaches [Colour figure can be viewed at wileyonlinelibrary.com]

conducted seasonally to capture the full breadth of species depth distributions (e.g., Martay & Pearce-Higgins, 2018).

A final opportunity for macroecological approaches related to dimensionality arises from the existence of soil communities *ex situ*, that is, in soil microhabitats above the soil proper. For example, true soil-dwelling invertebrates including springtails and mites occur in suspended soil at various heights (up to 35 m) in canopies of subtropical and temperate rainforests (Lindo & Winchester, 2006; Rodgers & Kitching, 1998). In Canadian Western redcedar trees, 18 of the 53 springtail (Collembola) species recorded from suspended soils did not occur in the forest floor (Lindo & Winchester, 2006). In Indonesian oil palm plantations, suspended soil in frond axils of palm oil trunks supported much higher densities and biomasses of soil microfauna and mesofauna than belowground soil, with suspended soils contributing an estimated 28% of the overall soil fauna metabolism in plantations (Potapov et al., 2020). These contributions of suspended soils to overall diversity and community turnover suggest that there is much to be gained by extending soil sampling aboveground in forest ecosystems (Figure 1).

Information from vertical sampling may be integrated into the investigation of important macroecological patterns through the explicit incorporation of depth/height as a parameter in standard macroecological approaches, for example, does community similarity decay more rapidly with depth than horizontal distance? However, more complex models will be required to investigate species–environment relationships in 3-D domains. For such applications, it may be useful to turn to the marine literature where development of SDM techniques for 3-D systems is already underway (e.g., Duffy & Chown, 2017; Pérez-Costas et al., 2019). Similarly, investigations into the scaling of interaction strengths within species networks can differ between 2- and 3-D systems in terrestrial and marine realms, where advanced nonlinear statistical approaches, 3-D statistical point pattern models and 3-D agent-based modelling have been successfully applied (see Barrios-O'Neill et al., 2016; Pawar, Dell, Lin, Wiczyński, & Savage, 2019; Raynaud & Nunan, 2014).

5 | BIOTIC CONSIDERATIONS

5.1 | Dispersal

The dispersal capacity of many soil biota, and thus, the environment in which soil communities develop and interact, is often at a much finer resolution than the scale at which environmental variables are commonly measured (Grundmann & Debouzie, 2000; Hendershot et al., 2017), and varies tremendously between and within different soil taxa (e.g., microbes, dispersing as spores, can generally disperse at larger scales than most soil animals). However, dispersal syndromes vary at multiple phylogenetic scales (e.g., fungi versus bacteria and phylotypes within bacteria in Archer et al., 2019). Therefore, sudden environmental changes that favour specific dispersal modes, may then favour certain taxa and so drive community structure through an intensified propagule pressure of those taxa,

thus, dictating macroecological patterns. This process, as well as others, may operate at multiple scales. For example, some biogeographical 'rules' that apply to the distribution of vertebrates at the continental scale, for example, range size–frequency distributions, can be detected in prokaryotes within an 8 m × 8 m quadrat (Noguez et al., 2005), conflicting with the traditional idea that soil microbes are not limited by dispersal (Finlay, 2002). Overall, it is now well established that dispersal limitation is central to explaining the distribution of all soil organisms, and that dispersal may differ at different phylogenetic levels (Archer et al., 2019; Davison et al., 2015). It is, therefore, crucial to include dispersal capacity in models of belowground species and to take into account the fact that dispersal capacity varies greatly with size, ecology and life stage of the organism (Ettema & Wardle, 2002; Soininen, McDonald, & Hillebrand, 2007).

Dispersal kernels are a frequently used tool in invasion ecology that can be used to incorporate dispersal into SDMs (Meentemeyer, Anacker, Mark, & Rizzo, 2008). These describe the probability distribution of the distance travelled by an individual from a parent source and can be used to estimate the probability of colonization (Franklin, 2010). Novel tools for implementing cellular automata models into SDMs that map accessibility from source cells are another promising recent development (Nobis & Normand, 2014). Although implementing such models can be challenging as the dispersal characteristics of many soil organisms remain largely unknown (Schröder, 2008), molecular techniques provide tools to measure whole community dispersal of microbial systems (Peay, Garbelotto, & Bruns, 2010; Peay, Schubert, Nguyen, & Bruns, 2012). For example, within a biogeographical framework of plant host 'islands', Peay et al. (2012) use next-generation sequencing of propagules to demonstrate a dispersal limitation of 1 km across a whole ectomycorrhizal fungal community. For earthworms, on the contrary, visual tagging methods (Butt & Lowe, 2007) and X-ray scanning have been used to measure dispersal in addition to molecular methods (Mathieu, Caro, & Dupont, 2018). Using these newer technologies to determine active and passive dispersal of soil organisms will allow movement-based theories of ecology to be tested (Thakur et al., 2019) that contribute to spatial and temporal biodiversity patterns across scales (Dirilgen et al., 2018; Gumiere et al., 2016).

5.2 | Interactions

Microbiota, including soil fungi and bacteria, are almost always sampled at scales larger than that at which individuals interact, therefore, lumping together sets of taxa that partition different resources, or occupy different microhabitats (Bach et al., 2018; Fierer & Lennon, 2011). This can greatly influence observed macroecological patterns, such as the species–abundance distribution (Shoemaker, Locey, & Lennon, 2017). Multiscale sampling is recommended to provide novel insights into the processes and mechanisms underlying spatial organization of communities of soil taxa of various body sizes. Using soil aggregate isolation techniques when sampling, for example, will help characterize biodiversity of soil microbes relevant

to the spatial scale at which individuals interact and use resources (Bach et al., 2018).

Network analyses based on Spearman's rank correlations have been used to determine co-occurrences of soil bacteria (Barberán et al., 2012), but due to the complex 3-D structure of soil, these networks may not always be indicative of real species interactions (Morriën, 2016). The simulation approach used by Raynaud and Nunan (2014), for example, shows that interspecific interactions between bacterial species are substantially lower than what you may expect given the bacterial diversity frequently measured in soil samples (see Dimensionality section above). For earthworms, stable isotopes have been used to determine interactions between invasive species of earthworms within a 2-km² area in the USA (Zhang et al., 2010), providing a sophisticated tool to address the challenge of non-transparency of the soil medium in identifying biotic interactions where they cannot easily be observed.

There is a momentum to improve aboveground models of species distributions by incorporating biotic interactions (e.g., Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017). While challenging, this research track is promising for soil macroecology. Indeed, the particular importance of addressing this challenge for soils is highlighted by the substantial contribution of biotic interactions in shaping soil organisms' distributions (Bahram et al., 2018; Raymond, Wharton, & Marshall, 2013), and the complex aboveground–belowground interactions that have been observed globally (De Deyn & Van der Putten, 2005). Joint SDMs account for species interactions via correlation matrices of co-occurrence (Pollock et al., 2014) and can disentangle species interactions from environmental correlates in large multispecies data sets (Warton et al., 2015), holding promise for soil macroecological studies.

Aboveground and belowground systems are linked by food web interactions and nutrient fluxes through plant litter decomposition (de Vries et al., 2013; Wardle et al., 2004), modulation of soil physical properties by plant diversity (Gould, Quinton, Weigelt, De Deyn, & Bardgett, 2016), and direct species–species interactions (Bardgett & Wardle, 2010). Soil biodiversity data, therefore, can be extremely powerful when used in conjunction with aboveground community data (Ramirez et al., 2015). This is particularly true for mycorrhizal fungi, which form mutualisms with plants, and for which host specificity is an important geographical constraint on species distributions (Sato, Tsujino, Kurita, Yokoyama, & Agata, 2012). Hence, studies of community structure and biogeographical patterns of soil fungi are significantly improved when data on plant diversity and distributions are included within their models (Koyama, Maherali, & Antunes, 2019; Pellissier et al., 2014; Vályi, Mardhiah, Rillig, & Hempel, 2016). To this end, the FungalRoot database (Soudzilovskaia et al., 2020) provides key data on mycorrhizal associations with which to study the macroecology and biogeography of these interactions.

Feedbacks between the aboveground and belowground systems, however, are difficult to predict at large scales, as species interactions are complex (De Deyn & Van der Putten, 2005; Wardle et al., 2004), vary along latitudinal gradients of biodiversity (De Deyn & Van der Putten, 2005) and operate over a hierarchy of temporal

scales (Bardgett et al., 2005). Small spatial and temporal scale experimental manipulations (e.g., Gould et al., 2016; León-Sánchez et al., 2018), therefore, may not truly capture the complexities or multifunctionality of aboveground–belowground processes (De Deyn & Van der Putten, 2005), which also pose a challenge to traditional modelling approaches.

To overcome the challenge of integrating network ecology research into macroecology, we encourage the use of modelling approaches that facilitate complex interactions and pathways between multiple variable types (Kissling & Schleuning, 2015). For soil systems in particular, it is important to develop methods, such as correlation networks and structural equation models (SEMs), that emphasize biotic interactions, and also include environmental effects, for example, through latent and composite variables, to study causal mechanisms involving variables that are difficult to measure at a spatial scale relevant for soil organisms, or themselves exhibit complex interactions (e.g., as seen for soil fertility in Siciliano et al., 2014). SEMs are a useful correlative approach that can be easily implemented and characterize complex pathways at the ecosystem level, including the complex interaction networks and feedback loops observed in soil-to-aboveground systems (Eisenhauer, Bowker, Grace & Powell, 2015). Grace, Anderson, Han, and Scheiner (2010) present SEMs as an approach to address the challenge of eliciting generalizable patterns, such as those sought in macroecology, from heterogeneous system components. For example, SEMs have been used to partition causal influences and determine the direct and indirect relationships between geographical variables, soil characteristics, plant productivity/diversity and soil diversity at both the continental and global scale for soil bacteria and fungi (Delgado-Baquerizo et al., 2017; Tedersoo et al., 2014), as well as to determine the causal mechanisms underlying ecosystem functioning (Eisenhauer, Reich, & Isbell, 2012) and food web stability (de Vries et al., 2012). They, therefore, provide a useful tool for soil scientists and macroecologists to combine biotic and abiotic factors into studies of causal patterns of soil diversity and functioning.

6 | ABIOTIC CONSIDERATIONS

6.1 | Climate and microclimate

Fine-scale spatial structuring of soil species may occur where the macroscopic environment appears uniform (Caruso et al., 2012; Nielsen et al., 2010). For example, the spatial structure of grass tussocks in pasture alter the microclimate of the soil, which impacts earthworm diversity (Mathieu et al., 2009). To model soil biodiversity, therefore, measurement of environmental heterogeneity is required at fine scales (e.g., measuring and modelling microclimates). Microclimate modelling can be expanded to the macro-scale by using gridded continental-scale soil and weather data to accurately predict hourly local microclimates at multiple soil depths using a mechanistic modelling framework (Kearney et al., 2014). Microclimate

modelling has become more accessible through advances in remote sensing, for example, light detection and ranging (LiDAR), to quantify environmental covariates at high resolutions (Lembrechts, Nijs, & Lenoir, 2019), and development of freely available software and code, for example, the R package *microclima* (Maclean, Mosedale, & Bennie, 2019). Furthermore, combining microclimate modelling frameworks with soil moisture simulation algorithms can provide accurate, high resolution soil moisture estimates for entire continents (Kearney & Maino, 2018). Moving beyond simple correlative models towards mechanistic modelling is being encouraged within the SDM literature (Buckley et al., 2010) and offers a promising alternative for predicting distributions of soil organisms in particular, where small-scale spatial and temporal heterogeneity of the environment is often more important than large-scale climatic variables (Dauber et al., 2005; Kearney et al., 2014).

6.2 | Geodiversity and pedodiversity

Environmental factors other than climate are likely to be particularly ecologically relevant determinants of species distributions belowground, and geological as well as biological resources should be considered (Ibáñez, Krasilnikov, & Saldaña, 2012). The incorporation of soil types, texture and geochemistry (i.e., pedodiversity)

into analyses of soil biodiversity has been encouraged (Parker, 2010) and carried out at the local scale (e.g., earthworms, Decaëns & Rossi, 2008; Solomou, Sfougaris, Vavoulidou, & Csuzdi, 2013; bacteria, Ranjard et al., 2010), as well as larger scales for earthworms (Rutgers et al., 2016). Integration of point level soil characteristics data, such as the land use and coverage area frame survey (LUCAS) data set (Orgiazzi, Ballabio, Panagos, Jones, & Fernández-Ugalde, 2018), can provide environmental information at coarse resolutions (2 km × 2 km) but large geographical extents, that is, continental, whilst machine learning techniques combining soil and earth observation data can provide global gridded soil information at a resolution of 250 m × 250 m (Hengl et al., 2017). The latter has recently been incorporated into models of global earthworm diversity, but did not appear important in shaping community diversity, likely due to the scale of the study (Phillips et al., 2019). Diversity of geophysical properties (i.e., geodiversity) and pedodiversity provide opportunities to scale up soil biodiversity analyses. Spatial soil information science has become particularly advanced and sophisticated statistical tools to predict spatial patterns of soil properties (including salinity, soil moisture content and soil bulk density) offer novel opportunities to obtain predictor variables of soil organism distributions and diversity (Padarian, Minasny, & McBratney, 2020). We may expect an obvious link between geodiversity or pedodiversity variables and soil biodiversity; however, incorporation of these factors

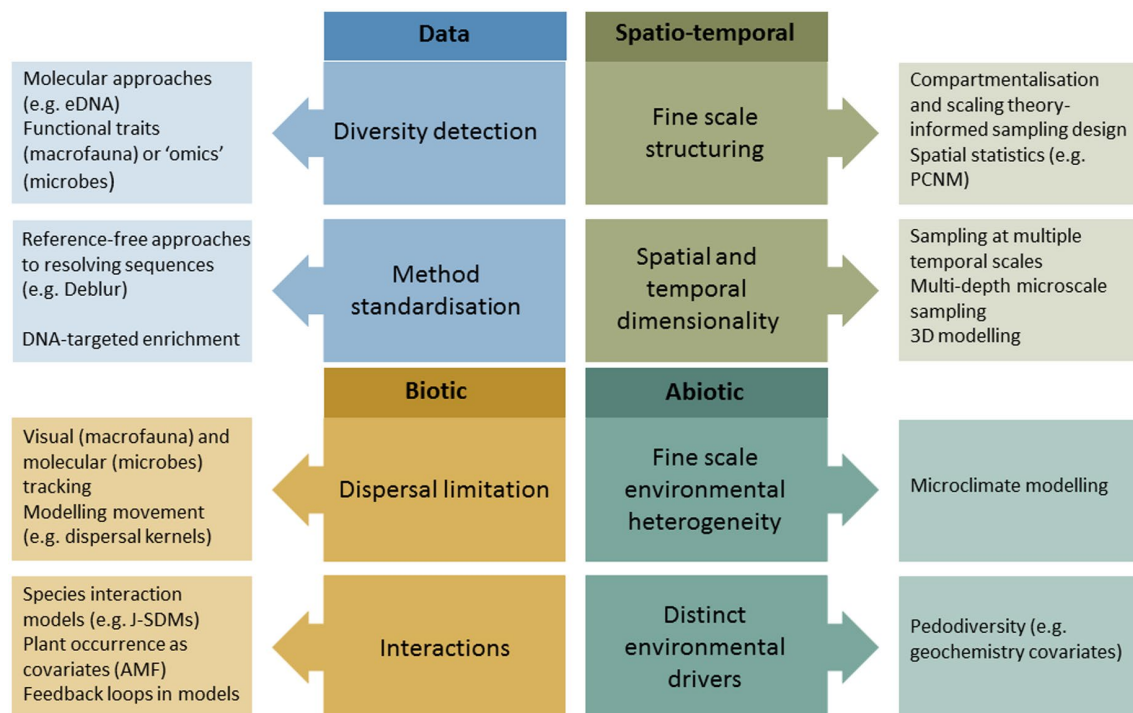


FIGURE 2 The challenges associated with the belowground system that contributed to a lack of soil macroecological research, and potential approaches to address them. These challenges can be separated into four sets of necessary considerations: data; spatio-temporal; biotic; and abiotic. Challenges for each solution are highlighted in central darker boxes whilst example approaches to address these challenges are shown in the surrounding, lighter boxes. eDNA = environmental DNA; J-SDMs = joint species distribution models; AMF = arbuscular mycorrhizal fungi; PCNM = principal coordinates of neighbourhood matrices [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

into models has often been restricted to plants (e.g., Bailey, Boyd, & Field, 2018; Tukiainen et al., 2017), although geochemical variables including salinity and soil nitrate variables have been linked to nematode abundances in Antarctica (Poage et al., 2008), and global soil bacteria richness peaks in neutral soils (Fierer & Jackson, 2006). Pedodiversity analyses, therefore, offer an exciting opportunity to overcome a severe gap in soil macroecological research.

7 | RECOMMENDATIONS AND FUTURE PERSPECTIVES

Although there has been a recent surge in broad scale papers mapping soil biodiversity, the field of soil macroecology needs to be advanced by emphasizing process over pattern (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012). Soils differ from aboveground systems in ways that have been challenging for the generalizations dear to macroecology: they are characterized by high heterogeneity making data collection and analysis difficult, and are inhabited by organisms that are incredibly variable in size and trophic roles, while being poorly known taxonomically. We have discussed how recent methods and data management initiatives might help soil ecologists and macroecologists to collaborate more often. We demonstrate that methodological considerations need to be made at all stages of investigation spanning delimitation and quantification of diversity, spatial and temporal context, biotic considerations and abiotic properties, and propose multiple approaches to deal with challenges within each of these sets of considerations (Figure 2). Most of these methods are applicable (and some already applied) aboveground, but are particularly suited to address the incredible spatial and temporal variability of biotic and abiotic conditions, combined with the scarcity of data, in soils. When these are overcome, we expect that new rules may emerge from macroecological analysis of soils.

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