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## Methods and approaches to advance soil macroecology

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# 1 Methods and approaches to advance 2 soil macroecology

## 3 Abstract

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

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

17 **Main conclusion:** Soil provides a complex system within which to apply macroecological research,  
18 yet it is this property which itself makes soil macroecology a field ripe for innovative methodologies  
19 and approaches. To achieve this, soil-specific data, spatiotemporal, biotic, and abiotic considerations  
20 are necessary at all stages of research, from sampling design to statistical analyses. Insights into whole  
21 ecosystems and new approaches to link genes, functions and diversity across spatial and temporal  
22 scales, alongside methodologies already applied in aboveground macroecology, invasion ecology and

23 aquatic ecology, will facilitate the investigation of macroecological processes in soil biota, which is  
24 key to understanding the link between biodiversity and ecosystem functioning in terrestrial  
25 ecosystems.

## 26 Introduction

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

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

48 spatial scaling (Schröder, 2008; Decaëns, 2010; Shade et al., 2018). The challenges of soil  
49 macroecology, therefore, arise not only across spatial and temporal scales, but across the  
50 organisational hierarchy of species, communities, and ecosystems.

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

61 Community biodiversity patterns include well-established macroecological relationships, such as the  
62 species-area relationship and latitudinal gradients (e.g. Rosenzweig, 1995), distance-decay curves  
63 (Nekola and White, 1999), as well as models linking biodiversity patterns to environmental variables  
64 such as the species-energy relationship (e.g. Evans et al. 2008). These relationships have formed the  
65 basis of macroecological theory and our knowledge of how diversity is arranged in space and time, at  
66 a range of spatial, temporal, and hierarchical scales. Although community assembly in soil organisms  
67 has been investigated (Caruso et al., 2012; Dirilgen et al. 2018), generalisable spatial and temporal  
68 patterns of soil biodiversity have yet to be determined to the degree that they have above ground (but  
69 see Caruso et al., 2019). For microbes in particular, studies have tended to focus on individual taxa  
70 and metabolic genes, yet it is the emergent properties of communities which influence ecosystem  
71 functioning and services (Ladau and Eloë-Fadroush, 2019), and, therefore, need to be considered if  
72 we are to expand the field of soil macroecology.

73 At the ecosystem level, there have been huge advancements in our ability to model whole ecosystem  
74 functioning, particularly within the context of global change (Allan et al., 2015; De Laender et al.,  
75 2016). The development of measures of functional diversity (the range and variation of ecological  
76 traits present within an area) has facilitated this. Aboveground, these measures have been used to  
77 investigate key conservation issues such as biotic homogenisation (White et al., 2018a). Given the  
78 importance of soil and soil biodiversity in ecosystem functioning and global cycles (Delgado-  
79 Baquerizo et al., 2020), functional traits have much to offer soil macroecology. The measurement of  
80 functional traits is becoming increasingly feasible from a technical perspective (e.g. proteomics and  
81 isotope tracer-enabled analysis of proteins and metabolites, trait database availability), and they can  
82 be directly linked to ecosystem level processes (Hooper et al., 2005). There is a need, therefore, to  
83 continue to develop methods to measure functional diversity and broad scale functioning of soil  
84 organisms, and understand, for example, how these respond to environmental gradients. Applied  
85 properly to soil organisms, macroecological approaches will provide us with another tool to tackle  
86 global challenges related to soil functioning and soil protection.

## 87 Aims and scope of this review

88 To move beyond mapping of soil taxa in space and identify broad, generalisable spatial and temporal  
89 patterns of soil biodiversity and their underlying mechanisms, we need to consider: the biodiversity  
90 data; the spatio-temporal context of the system and mechanisms under investigation; the biotic  
91 components shaping these patterns; and the abiotic components shaping these patterns. We discuss  
92 each of these sets of considerations and review current methods and future directions for each. Our  
93 intention is not to provide a systematic review of macroecological patterns of multiple soil taxa, but  
94 instead, to focus on the specific characteristics of the soil system that have limited soil macroecology,  
95 and review and propose methods that would help address these limitations. To accomplish this, we  
96 use earthworms, mycorrhizal fungi and soil bacteria as focal taxa. These groups have all had their  
97 global biodiversity modelled (earthworms, Phillips et al., 2019; fungi, Kivlin et al., 2011; Tedersoo et  
98 al., 2014; Pärtel et al., 2017; soil bacteria, Delgado-Baquerizo et al., 2018), and they reflect the

99 diversity of taxa which inhabit soil through their variation in body size, life forms and ecology which  
100 leads to differences in the spatial scale at which they perceive and interact with their environment.  
101 They, therefore, provide a range of robust examples of the issues that have hindered soil  
102 macroecological research to date, and the diversity in approaches required to overcome these  
103 difficulties.

## 104 Data considerations

### 105 Data availability

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

118 The Global Soil Biodiversity Initiative and Ramirez et al. (2015), on the other hand, aim to maximise  
119 the potential of existing data by establishing global platforms that combine databases of all types of  
120 soil biodiversity data, including molecular, taxonomic, and morphological measurements and traits.  
121 Assembling data from multiple sources is complicated due to variability in taxonomic resolutions,  
122 unresolved taxonomies (Cameron, Decaëns, Lapied, Porco & Eisenhauer, 2016) and lack of

123 standardisation of sampling techniques that cause technical factors (e.g. sampling protocol, primer and  
124 sequencing platform) to be an important source of inter-study variability (Ramirez et al., 2018). Some  
125 studies choose to only include data collected using specific methodologies to reduce inter-study  
126 variability (e.g. European earthworm diversity maps, Rutgers et al., 2016; 2019), yet, non-  
127 standardised datasets can still provide important global insights into the ecological preferences and  
128 geographical ranges of species (Ramirez et al., 2015). These data will complement standardised  
129 sampling protocols when analysed appropriately, for example using meta-analytical or machine  
130 learning approaches (Hendershot, Read, Henning, Sanders & Classen, 2017; Ramirez et al. 2018).  
131 Substantial geographic gaps in sampling, however, need to be addressed (Cameron et al., 2018) if we  
132 are to determine generalisable patterns of biodiversity, and model predictions should be refined and  
133 updated as empirical datasets become increasingly available.

## 134 Measuring and defining soil biodiversity

135 To study many macroecological patterns such as species-abundance distributions, species-area  
136 relationships and latitudinal gradients, we first need to identify the species. However, challenges  
137 remain with identification of many soil taxa (Soininen, 2012); the huge diversity of soil organisms  
138 combined with their small size (Schaefer et al., 2010), has led to a distinct lack of taxonomic  
139 knowledge of soil biodiversity (Decaëns, Lavelle & Jiménez, 2008; Phillips et al., 2017).  
140 Biogeographic realms at multiple spatial scales, therefore, exist, where every new place sampled,  
141 especially remote locations, can give huge volumes of undescribed species or sequences that cannot  
142 be matched to any known species or genus-level taxon (Decaëns, 2010; Fierer, 2017). Indeed, even  
143 urban systems such as Central Park in New York City, can harbour large volumes of undescribed soil  
144 biodiversity (Ramirez et al. 2014), and earthworms, a comparatively well-studied group with  
145 relatively low diversity, have had a large number of cryptic species revealed through DNA barcoding  
146 (King, Tibble & Symondson, 2008).

147 Gene-based diversity assessments of environmental DNA (eDNA) are a promising toolset for  
148 facilitating large scale sampling of soil diversity (Bik et al., 2012; Deiner et al., 2017). Species can be

149 identified using short metabarcodes and small samples of soil (e.g. earthworms, Bienert et al., 2012).  
150 eDNA has already furthered macroecological research, for example, through the detection of  
151 earthworm diversity at the landscape-scale, revealing impacts of abiotic factors not detected using  
152 traditional survey methods (Pansu et al., 2015). Nevertheless, the degree to which eDNA-based  
153 diversity estimates capture the living soil biota (rather ‘relic’ DNA) is unclear (Lennon et al., 2018;  
154 Ruppert, Kline and Rahman, 2019). Furthermore, this technique can vary with soil organic matter  
155 content and type, complicating the comparison of biodiversity patterns across environments and  
156 highlighting the continued, pressing need for the standardization of methodologies (Philippot et al.,  
157 2012; Geisen et al., 2019).

158 In particular, many molecular studies use targeted sequencing of specific marker genes or gene  
159 regions, which serve as ‘barcodes’. Sequence differences within the “variable regions” of the marker  
160 genes are used to identify operational taxonomic units (OTUs), which may serve to delineate taxa  
161 below the genus level (e.g. earthworms, Pansu et al., 2015; fungi, Pellissier et al., 2014; Tedersoo et  
162 al., 2014). However, there is no universal threshold for an eukaryotic OTU, and this may well be  
163 clade-specific, and dependent on the barcode length and region of choice (Mysara et al.,  
164 2017). Despite recent technological advances in sequencing and bioinformatic pipelines to process  
165 high-throughput amplicon sequences, considerable challenges remain when using gene-based  
166 methodologies (Nesme et al., 2016). Errors or biases can arise from different DNA extraction methods  
167 (Inceoğlu, Hoogwout, Hill & van Elsas, 2010), primer specificity, sequencing chemistries (i.e. short  
168 read length, Tedersoo et al., 2015; Tremblay et al., 2015), and bioinformatic processing, as well as  
169 difficulties with OTU delimitation and chimeras (Orgiazzi, Dunbar, Panagos, de Groot & Lemanceau,  
170 2015), and lack of matching current database entries (e.g. fungi; Tedersoo et al., 2014, bacteria;  
171 Ramirez et al., 2014; Thompson et al., 2017). These can confound diversity estimates in cross-study  
172 comparisons (Fierer, 2017; Thompson et al., 2017). Recent developments in clustering algorithms, i.e.  
173 a reference-free approach to resolve sequence variants at a single nucleotide resolution (Callahan,  
174 McMurdie & Holmes, 2017; e.g. Deblur, Amir et al., 2017), could offer stable identifiers across  
175 different studies (Thompson et al., 2017), facilitating data reusability and integration of multiple data



176 sets (Amir et al., 2017), thus maximising the potential of gene-based surveys in soil macroecology  
177 (Geisen et al., 2019). Alternatively, DNA-targeted enrichment (bait capture) allows more efficient  
178 recovery of sequence information, not relying on sequence affinity as strongly as PCR (Dowle et al.  
179 2016). DNA enrichment can be applied to a range of different sample sources, in individual or pooled  
180 samples and can be used for recovering exogenous DNA present in environmental samples (Shokralla  
181 et al. 2016).

182 Many studies now focus on alternative dimensions of biodiversity to taxonomic diversity. Functional  
183 diversity, which measures the diversity and range of traits within a community, can be closely linked  
184 to ecosystem functioning (Heemsbergen et al., 2004; Hooper et al., 2005). Shifting from taxonomic to  
185 functional information can provide a way to unify the study of soil macroecology: the units are no  
186 longer species, or taxa, but functions and the diversity of functions expressed, which are relevant  
187 across taxonomic groups. Macroecological patterns that emerge from traits include trait-area and -  
188 time relationships (e.g. White et al., 2018b), and functional diversity gradients (e.g. Meynard et al.,  
189 2011), which further our knowledge on the spatial, temporal and environmental structuring of  
190 ecological traits and ecosystem functioning (Violle et al., 2014), and provide new insights into  
191 community assembly theory (Smith et al., 2013). Due to the key ecosystem functions that soil  
192 biodiversity provides (Heemsbergen et al., 2004), we advocate a concerted shift towards functional  
193 approaches within soil macroecology through the following methodological and data options.

194 Trait databases facilitate the investigation of trait composition of soil communities. Morphological,  
195 physiological and phenological traits are present in the literature for many soil invertebrates due to  
196 their relative ease of measurement (e.g. carabid beetles, Barbaro & van Halder, 2009; earthworms,  
197 Hedde et al., 2012; collembola, Martins da Silva et al., 2016; Bonfanti et al., 2018: ants, Bishop et al.,  
198 2016). For soil bacteria and fungi, on the other hand, characterisation of morphological, physiological  
199 and phenological traits can be more challenging since isolation of individual species for trait  
200 measurements is not feasible in most cases (Krause et al., 2014, Zanne et al., *in press*). Two recently  
201 published, large global databases, FungalRoot (Soudzilovskaia et al. 2020) and the Fungal Functional  
202 Database (FUNfun, Zanne et al. 2020) however, will facilitate better understanding of trait

203 composition of fungal communities, their interactions with plants, and their effects on worldwide on  
204 ecosystem functioning (Powell & Rillig 2018). However, as with many taxa, fungal trait databases are  
205 often incomplete (Zanne et al. 2020). There has also been a concerted effort to quantify microbial  
206 functions in soil due to their importance for key ecosystem functions (Aguilar-Trigueros et al. 2015;  
207 Zanne et al. 2020) through standardized ‘omics’ and enzymatic approaches (Dawson et al., 2019), as  
208 well as the measure of climate tolerances to investigate life history trait trade offs at large spatial  
209 scales (Maynard et al., 2019).

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

223 Despite limitations (i.e., transcriptomics may reveal potential, rather than fulfilled functions, Prosser,  
224 2015), elucidating the underlying molecular mechanisms supporting functions could help to unlock  
225 the functional networks that interact to sustain soil properties (e.g. Bonfante and Genre, 2010). Semi-  
226 controlled experiments can build novel bridges with complex natural systems. For example, we  
227 recommend mesocosm experiments coupled with “omics” approaches designed to identify  
228 longitudinal biological responses of soil biota to microbiomes (e.g. soil and rhizosphere) and plants,  
229 although destructive sampling is a limitation. Further still, defining a global transcriptome-based

230 delineation of functional entities, and obtaining a landscape of their similarities and differences based  
231 on differential expression of genes across different combinations of hierarchical levels and abiotic  
232 factors, for example, could help to derive the sets of genes involved in specific ecological processes  
233 that could be targeted in the field using metagenomics as a ground-truthing approach. Integrating  
234 multiple “omic” approaches, therefore, into community studies will lead to a rapid transformation in  
235 our empirical understanding of soil functioning and interactions (Swenson and Jones, 2017), and  
236 complementary approaches to DNA sequencing remain a priority for soil biodiversity research  
237 (Eisenhauer et al., 2017) as they will reveal new information on the mechanisms underlying  
238 ecosystem processes.

239

## 240 Spatio-temporal considerations

### 241 Scale and structure

242 Intra- and interspecific aggregations (Ettema & Wardle, 2002), which result from the microscale  
243 heterogeneity of the soil system and limited dispersal of organisms, structure soil communities across  
244 spatial scales (Noguez et al. 2005; Decaëns, 2010; Bach et al., 2018; Thakur et al., 2019). In a  
245 Brazilian agricultural system, for example, geographical distance explained nearly 18-times more  
246 variance in soil fungal community composition than environmental factors such as soil and climate  
247 characteristics (Gumiere, Durrer, Bohannan & Andreote, 2016). Biogeography of soil bacteria has  
248 been investigated at a range of scales from continental and global scales (e.g. Fierer & Jackson, 2006;  
249 Barberán et al., 2012; Bahram et al., 2018) to the landscape scale (Bru et al., 2011; Pasternak et al.,  
250 2013), and even at the centimeter scale (O’Brien et al., 2016). By taking multiple soil cores separated  
251 by only a few centimetres at sampling plots spaced 6 m apart, O’Brien et al. (2016) showed that there  
252 was extreme patchiness in community structure at the centimetre scale, but more general patterns in  
253 diversity, linked to fertilisation, were observed at the plot-level. This scale-dependent heterogeneity  
254 arises from the operating scale of mechanisms underlying community assembly. This needs to be

255 accounted for in sampling design for investigations of spatial patterns of soil diversity with multiscale  
256 sampling protocols (e.g. Rasmussen et al., 2018). Additionally, macroecological analyses of soil  
257 diversity need to use techniques that model space, such as autoregressive models (Beale, Lennon,  
258 Yearsley, Brewer & Elston, 2010), to address the strong spatial structuring in soil ecosystems, as  
259 demonstrated by spatial analyses of earthworm abundance, biomass and diversity (Joschko et al.  
260 2006), and ectomycorrhizal fungi (Pickles, 2010). Similarly, techniques such as Principal Coordinates  
261 of Neighbourhood Matrices (PCNM) are useful in differentiating between spatial and environmental  
262 structuring of communities at different spatial scales (e.g. Columbian earthworm communities,  
263 Jiménez, Decaëns, Lavelle and Rossi, 2014).

264 The scale at which similar processes act varies between taxonomic groups due to variation in body  
265 size and life history, and is an important consideration when studying spatial patterns of soil  
266 communities (Montagna et al., 2018). When studying landscape scale processes, Jackson and Fahrig  
267 (2012) highlight the concept of the ‘scale of effect’ (the scale at which an ecological response is best  
268 predicted by the habitat structure) and recommend sampling areas far enough apart to ensure sample  
269 points are independent (i.e. taxa in one sample point do not directly interact with those in others).  
270 Thakur et al. (2019) present a conceptual framework splitting soil into spatial compartments at which  
271 different nested groups of soil organisms can be studied to test biodiversity theories: soil, where all  
272 size groups of organisms can be sampled; hotspots (rhizosphere and drilosphere), where meso- and  
273 micro-fauna can be sampled; and microsites (root tips and aggregates), where micro-fauna can be  
274 sampled. This compartmentalisation allows integration of body size into the investigation of classical  
275 ecological theory. Beyond simply considering ‘scales of effect’ and spatial compartmentalisation, we  
276 suggest researchers further draw upon work on investigating scaling issues in complex landscapes to  
277 build on the conceptual framework of Thakur et al. (2019) and inform sampling designs. For example,  
278 the problem of "coarse-graining" occurs when fine-scale information is aggregated to larger scales to  
279 reduce model complexity (Newman et al. 2019). By tracking how this leads to loss of information  
280 explicitly and investigating scaling relationships, corrections for statistical biases may be possible  
281 (Wu, 2004; Newman et al. 2019).

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

294 As well as accumulation in space, temporal accumulation of species is an important part of  
295 macroecology, and community turnover and can be investigated using the species-time relationship.  
296 In aboveground literature, the species-time relationship has been studied far less frequently than the  
297 species-area relationship (White et al., 2006), and belowground, this lack of studies is even more  
298 pronounced (Ladau and Eloe-Fadrosh, 2019). The temporal component of soil biodiversity, however,  
299 is critical to consider. As well as hot spots of diversity, Kuzyakov and Blagodatskaya (2015) highlight  
300 ‘hot moments’ of soil microbial diversity which can occur either occasionally or regularly as a  
301 component of periodic processes within a system, often dependent on the temporally dynamic input of  
302 C into soil. Additionally, species interactions operate at multiple temporal scales and vary within and  
303 between taxa. For example, the connectivity of soil networks on abandoned arable land varies  
304 temporally during restoration (Morriën et al. 2017). Hence, for temporal questions, sampling is  
305 required at temporal scales relevant for the organisms of interest and the ecosystem properties with  
306 which they interact (Ettema & Wardle, 2002; Bardgett et al., 2005; De Deyn & Van der Putten, 2005).  
307 However, the appropriate scale remains an outstanding question in temporal biodiversity change of  
308 most soil organism groups (Eisenhauer et al., 2017; Shade et al., 2018). We, therefore, recommend

309 sampling at multiple time scales depending on the question at hand to determine the temporal scales at  
310 which soil biodiversity varies, from macroevolutionary investigations (e.g. Schaefer and Caruso,  
311 2019) to short-term dynamics (Kuzyakov and Blagodatskaya, 2015).

## 312 Dimensionality

313 To date macroecological patterns have been primarily conceptualised in a 2D context (e.g. species-  
314 area relationships, distance-decay relationships in geographic space, latitudinal gradients). However,  
315 where depth and/or height have a strong influence on the biodiversity estimates and community  
316 dissimilarity (e.g. marine systems, tropical forests and soils), there is much to be gained by explicitly  
317 extending these macroecological concepts to a third dimension. Given that soil community  
318 composition varies strongly with soil depth (e.g. fungi and bacteria, Fierer et al., 2003; Eilers et al.,  
319 2012; ants, Wong and Guénard, 2017; microfauna, Pausch et al., 2018), and key ecosystem processes  
320 are reliant on sub-soil fauna at different depths (Rumpel & Kogel-Knabner, 2011; Ward, 2016), the  
321 integration of depth as a third dimension into macroecological theory is a key area to which soil  
322 ecologists can contribute. Expanding soil macroecology into this third dimension will be particularly  
323 important for obtaining comparable estimates of true soil diversity, for example through extension of  
324 species accumulation curves to depth profiles. Furthermore, it will enhance our understanding of  
325 species-environment relationships, and provide insights into interaction dynamics in 3D space. In  
326 order to do so, state-of-the-art sampling designs and modelling approaches will be required.

327 To address these questions it is essential that both soil biota and abiotic properties be sampled across  
328 depth profiles. For macrofauna, sampling must involve multiple methods (e.g. pitfall trapping, direct  
329 sampling, Berlese extraction, subterranean baiting) as each is known to capture different species (Fig.  
330 1). For example, in a review of sampling methods Wong and Guénard (2017) identified seven studies  
331 in which more than 10% (range 12.3 to 44.4%) of all ant species recorded were unique to  
332 subterranean samples; and would have been missed with conventional sampling methods. For smaller  
333 macro-organisms, such as collembolans and arthropods, core samples provide samples from across  
334 the depth profile, but these must be carefully sorted to maintain information on sample depths as

335 combining multiple soil depths into a single sample can homogenize microscale variation  
336 (Grundmann et al., 2001). For microbial organisms, microsampling of smaller soil quantities across  
337 the depth profile is advised (e.g. Dechesne et al., 2003), or 2D images of soil thin sections at multiple  
338 depths can be used to count bacterial cell distributions and construct 3D distributions (Raynaud and  
339 Nunan, 2014). Sampling of root-associated species such as mycorrhizal fungi, may be facilitated by  
340 incorporating information on the depth distribution of roots (e.g. Sosa-Hernandez et al., 2018). Depth  
341 distributions of many taxa can vary seasonally, for example, some earthworm species aestivate in  
342 lower soil layers during the summer (Gerard, 1967). Therefore, where feasible, sampling should be  
343 conducted seasonally to capture the full breadth of species depth distributions (e.g. Martay & Pearce-  
344 Higgins, 2018).

345 A final opportunity for macro-ecological approaches related to dimensionality arises from the  
346 existence of soil communities *ex situ*, i.e. in soil micro-habitats above the soil proper. For example,  
347 true soil-dwelling invertebrates including springtails and mites occur in suspended soil at various  
348 heights (up to 35 m) in canopies of subtropical and temperate rainforests (Rodgers and Kitching,  
349 1998; Lindo and Winchester, 2006). In Canadian Western redcedar trees, 18 of the 53 springtail  
350 (Collembola) species recorded from suspended soils did not occur in the forest floor (Lindo and  
351 Winchester, 2006). In Indonesian oil palm plantations, suspended soil in frond axils of palm oil trunks  
352 supported much higher densities and biomasses of soil microfauna and mesofauna than belowground  
353 soil, with suspended soils contributing an estimated 28% of the overall soil fauna metabolism in  
354 plantations (Potapov et al., 2020). These contributions of suspended soils to overall diversity and  
355 community turnover, suggest that there is much to be gained by extending soil sampling above-  
356 ground in forest ecosystems (Fig. 1).

357 Information from vertical sampling may be integrated into the investigation of  
358 important macroecological patterns through the explicit incorporation of depth/height as a parameter  
359 standard macroecological approaches e.g. Does community similarity decay more rapidly with depth  
360 than horizontal distance?. However, more complex models will be required to investigate species-  
361 environment relationships in 3D domains. For such applications, it may useful to turn to the marine

362 literature where development of SDM techniques for 3D systems is already underway (e.g. Duffy &  
363 Chown, 2017; Pérez-Costas 2019). Similarly, investigations into the scaling of interaction strengths  
364 within species networks can differ between two- and three-dimensional systems in terrestrial and  
365 marine realms, where advanced non-linear statistical approaches, 3D statistical point pattern models,  
366 and 3D agent based modelling have been successfully applied (see Raynaud and Nunan 2014;  
367 Barrios-O'Neill et al., 2019; Pawar et al., 2019).

368

## 369 Biotic considerations

### 370 Dispersal

371 The dispersal capacity of many soil biota, and thus the environment in which soil communities  
372 develop and interact, is often at a much finer resolution than the scale at which environmental  
373 variables are commonly measured (Grundmann & Debouzie, 2000; Hendershot et al., 2017), and  
374 varies tremendously between and within different soil taxa (e.g. microbes, dispersing as spores, can  
375 generally disperse at larger scales than most soil animals). However, dispersal syndromes vary at  
376 multiple phylogenetic scales (e.g., fungi *vs.* bacteria and phylotypes within bacteria in Archer et al.  
377 2019). Therefore, sudden environmental changes that favour specific dispersal modes, may then  
378 favour certain taxa and so drive community structure through an intensified propagule pressure of  
379 those taxa, thus dictating macroecological patterns. This process, as well as others, may operate at  
380 multiple scales. For example, some biogeographical 'rules' that apply to the distribution of vertebrates  
381 at the continental scale, e.g. range size-frequency distributions, can be detected in prokaryotes within  
382 an 8 m x 8 m quadrat (Noguez et al. 2005), conflicting with the traditional idea that soil microbes are  
383 not limited by dispersal (Finlay, 2002). Overall, it is now well established that dispersal limitation is  
384 central to explain the distribution of all soil organisms, and that dispersal may differ at different  
385 phylogenetic levels (Davison et al., 2015; Archer et al., 2019). It is, therefore, crucial to include  
386 dispersal capacity into models of belowground species and to take into account the fact that



387 dispersal capacity varies greatly with size, ecology and life stage of the organism (Ettema & Wardle,  
388 2002; Soininen, McDonald & Hillebrand, 2007).

389 Dispersal kernels are a frequently used tool in invasion ecology that can be used to incorporate  
390 dispersal into species distribution models (Meentemeyer, Anacker, Mark & Rizzo, 2008). These  
391 describe the probability distribution of the distance travelled by an individual from a parent source  
392 and can be used to estimate the probability of colonisation (Franklin, 2010). Novel tools for  
393 implementing cellular automata models into SDMs which map accessibility from source cells are  
394 another promising recent development (Nobis & Normand, 2014). Although implementing such  
395 models can be challenging as the dispersal characteristics of many soil organisms remain largely  
396 unknown (Schröder, 2008), molecular techniques provide tools to measure whole community  
397 dispersal of microbial systems (Peay, Garbelotto & Bruns, 2010; Peay, Schubert, Nguyen & Bruns,  
398 2012). For example, within a biogeographical framework of plant host ‘islands’, Peay et al. (2012) use  
399 next-generation sequencing of propagules to demonstrate a dispersal limitation of one kilometre  
400 across a whole ectomycorrhizal fungal community. For earthworms on the other hand, visual tagging  
401 methods (Butt and Lowe, 2007) and X-ray scanning have been used to measure dispersal in addition  
402 to molecular methods (Mathieu, Caro & Dupont, 2018). Using these newer technologies to determine  
403 active and passive dispersal of soil organisms will allow movement-based theories of ecology to be  
404 tested (Thakur et al., 2019) that contribute to spatial and temporal biodiversity patterns across scales  
405 (Gumiere et al., 2016; Dirilgen et al., 2018).

## 406 Interactions

407 Microbiota, including soil fungi and bacteria, are almost always sampled at scales larger than that at  
408 which individuals interact, therefore lumping together sets of taxa that partition different resources, or  
409 occupy different microhabitats (Fierer & Lennon, 2011; Bach, Williams, Hargreaves, Yang &  
410 Hofmockel, 2018). This can greatly influence observed macroecological patterns, such as the species-  
411 abundance distribution (Shoemaker et al., 2017). Multiscale sampling is recommended to provide  
412 novel insights into the processes and mechanisms underlying spatial organisation of communities of

413 soil taxa of various body sizes. Using soil aggregate isolation techniques when sampling, for example,  
414 will help characterise biodiversity of soil microbes relevant to the spatial scale at which individuals  
415 interact and use resources (Bach et al., 2018).

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

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

436 Aboveground and belowground systems are linked by food web interactions and nutrient fluxes  
437 through plant litter decomposition (Wardle et al., 2004; de Vries et al., 2013), modulation of soil  
438 physical properties by plant diversity (Gould, Quinton, Weigelt, De Deyn & Bardgett, 2016), and

439 direct species-species interactions (Bardgett & Wardle, 2010). Soil biodiversity data, therefore, can be  
440 extremely powerful when used in conjunction with aboveground community data (Ramirez et al.,  
441 2015). This is particularly true for mycorrhizal fungi, which form mutualisms with plants, and for  
442 which host specificity is an important geographical constraint on species distributions (Sato et al.,  
443 2012). Hence, studies of community structure and biogeographic patterns of soil fungi are  
444 significantly improved when data on plant diversity and distributions are included within their models  
445 (Pellissier et al., 2014; Vályi et al., 2016; Koyama, Maherli and Antunes, 2019). To this end, the  
446 FungalRoot database (Soudzilovskaia et al., 2020) provides key data on mycorrhizal associations with  
447 which to study the macroecology and biogeography of these interactions.

448 Feedbacks between the aboveground and belowground systems, however, are difficult to predict at  
449 large scales, as species interactions are complex (Wardle et al., 2004; De Deyn & Van der Putten,  
450 2005), vary along latitudinal gradients of biodiversity (De Deyn & Van der Putten, 2005) and operate  
451 over a hierarchy of temporal scales (Bardgett, Bowman, Kaufmann & Schmidt, 2005). Small spatial  
452 and temporal scale experimental manipulations (e.g. Gould et al., 2016; León-Sánchez et al., 2018),  
453 therefore, may not truly capture the complexities or multifunctionality of aboveground-belowground  
454 processes (De Deyn & Van der Putten, 2005), which also pose a challenge to traditional modelling  
455 approaches.

456 To overcome the challenge of integrating network ecology research into macroecology, we encourage  
457 the use of modelling approaches that facilitate complex interactions and pathways between multiple  
458 variable types (Kissling & Schleuning, 2015). For soil systems in particular, it is important to develop  
459 methods, such as correlation networks and structural equation models (SEMs), that emphasise biotic  
460 interactions but also include environmental effects, e.g. through latent and composite variables, to  
461 study causal mechanisms involving variables that are difficult to measure at a spatial scale relevant for  
462 soil organisms, or themselves exhibit complex interactions (e.g. as seen for soil fertility in Siciliano et  
463 al., 2014). SEMs are a useful correlative approach that can be easily implemented and characterise  
464 complex pathways at the ecosystem level, including the complex interaction networks and feedback  
465 loops observed in soil-to-aboveground systems (Eisenhauer, Bowker, Grace & Powell., 2015). Grace

466 et al. (2010) present SEMs as an approach to address the challenge of eliciting generalisable patterns,  
467 such as those sought in macroecology, from heterogeneous system components. For example, SEMs  
468 have been used to partition causal influences and determine the direct and indirect relationships  
469 between geographic variables, soil characteristics, plant productivity/diversity and soil diversity at  
470 both the continental and global scale for soil bacteria and fungi (Tedersoo et al., 2014; Delgado-  
471 Baquerizo, Powell et al., 2017), as well as to determine the causal mechanisms underlying ecosystem  
472 functioning (Eisenhauer, Reich & Isbell, 2012) and food web stability (De Vries et al., 2012). They,  
473 therefore, provide a useful tool for soil scientists and macroecologists to combine biotic and abiotic  
474 factors into studies of causal patterns of soil diversity and functioning.

## 475 Abiotic considerations

### 476 Climate and microclimate

477 Fine-scale spatial structuring of soil species may occur where the macroscopic environment appears  
478 uniform (Nielsen et al., 2010; Caruso, Taormina & Migliorini, 2012). For example, the spatial  
479 structure of grass tussocks in pasture alter the microclimate of the soil which impacts earthworm  
480 diversity (Mathieu et al., 2009). To model soil biodiversity, therefore, measurement of environmental  
481 heterogeneity is required at fine scales (e.g. measuring and modelling microclimates). Microclimate  
482 modelling can be expanded to the macro-scale by using gridded continental-scale soil and weather  
483 data to accurately predict hourly local microclimates at multiple soil depths using a mechanistic  
484 modelling framework (Kearney et al. 2014). Microclimate modelling has become more accessible  
485 through advances in remote sensing, e.g. LiDAR, to quantify environmental covariates at high  
486 resolutions (Lembrechts, Nijs & Lenoir, 2019), and development of freely available software and  
487 code, e.g. the R package *microclima* (Maclean et al. 2019). Furthermore, combining microclimate  
488 modelling frameworks with soil moisture simulation algorithms can provide accurate, high resolution  
489 soil moisture estimates for entire continents (Kearney & Maino, 2018). Moving beyond simple  
490 correlative models towards mechanistic modelling is being encouraged within the SDM literature

491 (Buckley et al., 2010) and offers a promising alternative for predicting distributions of soil organisms  
492 in particular, where small-scale spatial and temporal heterogeneity of the environment is often more  
493 important than large-scale climatic variables (Dauber et al., 2005; Kearney et al., 2014).

## 494 Geodiversity and pedodiversity

495 Environmental factors other than climate are likely to be particularly ecologically relevant  
496 determinants of species distributions belowground, and geological as well as biological resources  
497 should be considered (Ibáñez, Krasilnikov and Saldaña, 2012). The incorporation of soil types, texture  
498 and geochemistry (i.e. pedodiversity) into analyses of soil biodiversity has been encouraged (Parker,  
499 2010) and carried out at the local scale (e.g. earthworms, Decaëns & Rossi, 2008; Solomou et al.,  
500 2013; bacteria, Ranjard et al., 2010), as well as larger scales for earthworms (Rutgers et al., 2016).  
501 Integration of point level soil characteristics data, such as the LUCAS dataset (Orgiazzi, Ballabio,  
502 Panagos, Jones & Fernández-Ugalde, 2018), can provide environmental information at coarse  
503 resolutions (2 km x 2 km) but large geographical extents, i.e. continental, whilst machine learning  
504 techniques combining soil and earth observation data can provide global gridded soil information at a  
505 resolution of 250 m x 250 m (Hengl et al. 2017). The latter has recently been incorporated into models  
506 of global earthworm diversity, but did not appear important in shaping community diversity, likely  
507 due to the scale of the study (Phillips et al. 2019). Diversity of geophysical properties (i.e.  
508 geodiversity) and pedodiversity provide opportunities to scale up soil biodiversity analyses. Spatial  
509 soil information science has become particularly advanced and sophisticated statistical tools to predict  
510 spatial patterns of soil properties (including salinity, soil moisture content and soil bulk density) offer  
511 novel opportunities to obtain predictor variables of soil organism distributions and diversity (Padarian  
512 et al., 2020). We may expect an obvious link between geodiversity or pedodiversity variables and soil  
513 biodiversity, however, incorporation of these factors into models has often been restricted to plants  
514 (e.g. Tukiainen et al., 2017; Bailey et al., 2018), although geochemical variables including salinity and  
515 soil nitrate variables have been linked to nematode abundances in Antarctica (Poage et al., 2008), and

516 global soil bacteria richness peaks in neutral soils (Fierer & Jackson, 2006). Pedodiversity analyses,  
517 therefore, offer an exciting opportunity to overcome a severe gap in soil macroecological research.

## 518 Recommendations and Future Perspectives

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

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**Table 1** Examples of existing databases that include soil biodiversity or distribution data.

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

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1052 **Figure Legends**

1053 **Figure 1.** Considering different soil habitats and corresponding sampling methods adds  
1054 dimensionality to macroecological approaches.

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1056 **Figure 2.** The challenges associated with the belowground system which contributed to a lack of soil  
1057 macroecological research, and potential approaches to address them. These challenges can be  
1058 separated into four sets of necessary considerations: data; spatio-temporal; biotic; and abiotic.  
1059 Challenges for each solution are highlighted in central darker boxes whilst example approaches to  
1060 address these challenges are shown in the surrounding, lighter boxes. J-SDMs = joint species  
1061 distribution models; AMF = arbuscular mycorrhizal fungi; PCNM = Principal Coordinates of  
1062 Neighbourhood Matrices.

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