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Towards an integrative understanding of soil biodiversity

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ABSTRACT

Soil is one of the most biodiverse terrestrial habitats. Yet, we lack an integrative conceptual framework for understanding the patterns and mechanisms driving soil biodiversity. One of the underlying reasons for our poor understanding of soil

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biodiversity patterns relates to whether key biodiversity theories (historically developed for aboveground and aquatic organisms) are applicable to patterns of soil biodiversity. Here, we present a systematic literature review to investigate whether and how key biodiversity theories (species–energy relationship, theory of island biogeography, metacommunity theory, niche theory and neutral theory) can explain observed patterns of soil biodiversity. We then discuss two spatial compartments nested within soil at which biodiversity theories can be applied to acknowledge the scale-dependent nature of soil biodiversity.

Key words: biodiversity theory, alpha diversity, beta diversity, spatial scale, species–energy relationship, theory of island biogeography, metacommunity theory, niche theory, neutral theory.

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I. INTRODUCTION

Investigations aimed at understanding patterns of biological diversity (hereafter biodiversity) are a popular tradition in modern ecology (Gaston & Spicer, 2004; McGill *et al*., 2015). The results of historic as well as contemporary investigations have led ecologists to develop a number of biodiversity theories that are intended to help us predict biodiversity in a given space and/or time. An important component of biodiversity theories is how variations in spatial and temporal scales influence biodiversity patterns (Levin, 1992; Rosenzweig, 1995). Consequently, there is a growing consensus that biodiversity at any scale is a result of multiple mechanisms that operate from local to regional scales (Ricklefs, 2004; McGill *et al*., 2015). Often, the mechanisms that underlie biodiversity patterns are a result of the interaction of species with their environment and neighbouring species and/or their movement in space and time.

Soil biodiversity is a major component of terrestrial biodiversity (Bardgett & Van Der Putten, 2014), but one that was rarely considered during the historic development of biodiversity theories (Wardle, 2006; Barot *et al*., 2007). Our current understanding of terrestrial biodiversity patterns and underlying interaction- and movement-based mechanisms has mainly relied on studies of aboveground and aquatic organisms. Our aim in this review is to examine biodiversity theories based on interaction- and movement-based mechanisms as applied to soil biodiversity. We provide a systematic review of the literature to determine how some of the key biodiversity theories have been applied to explain soil biodiversity. Subsequently, we present a conceptual framework for an integrative understanding of soil biodiversity, from soil micro- (e.g. bacteria) to macroorganisms (e.g. earthworms), to encompass both interaction- and movement-based mechanisms at varying spatial and temporal scales.

II. SOIL AS A COMPLEX HABITAT

Soil is one of the most complex habitats for life on Earth (Young & Crawford, 2004; Aleklett *et al*., 2018). It represents a highly compact form of three-dimensionally structured habitat featuring fine-scale gradients in physico-chemical characteristics, resource availability, and gas concentrations (Young & Crawford, 2004; Bardgett, 2005). Moreover, biota in the soil have been suggested to be more abundant and extremely species rich compared to most other habitats on Earth (Orgiazzi *et al*., 2016). The body size of soil organisms spans many orders of magnitude (Veresoglou, Halley, & Rillig, 2015), requiring an appropriate choice of spatial scale at which soil biodiversity should be studied (Berg, 2012). We do not claim that this challenge is unique to soil; however, the profound body size variation among soil organisms at a very low gradient of spatial resolution (ranging from μm to cm) increases the likelihood of violating the underlying assumptions of biodiversity theories (Table 1).

Soil ecologists long have investigated the patterns and causes of biodiversity in soils. For instance, Anderson (1975)

Table 1. List of five biodiversity theories reviewed in this study. Details of these theories, such as their key assumptions, predictions and challenges relevant to soil organisms are briefly explained together with their foundational references

Theory	Theory type	Biodiversity type	Underlying mechanisms/ assumptions	Main prediction(s)	Challenges relevant to soil organisms	Foundational references
Species–energy relationships	Species–environment interaction	alpha	(1) Solar energy is the driving force of the productivity gradient. (2) More individuals lead to more species. (3) Species are equivalent in their energy use.	(1) The productivity of an area enhances the number of species, and their population size.	(1) Soil abiotic conditions can alter the strength of productivity–soil biodiversity relationships. (2) Energy conversion depends on environmental stoichiometry. Constraints in environmental stoichiometry are particularly strong in soil. These stoichiometric constraints are overcome by interactions among soil organisms.	Wright (1983); Rosenzweig (1995); Evans, Warren, & Gaston (2005)
Theory of island biogeography	Movement	alpha	(1) Immigration of species from an external pool. (2) Extinctions occur locally, i.e. inside the island. (3) The rates of immigration and extinction in islands reach an equilibrium stage at which the number of island species remains constant. (4) Evolutionary changes are ignored (e.g. speciation). (5) Islands are not connected to each other. (6) Species are assumed to be similar (e.g. in terms of dispersal ability).	(1) Larger and less remote islands contain more species. (2) More (geographically) isolated islands are poorer in species number.	(1) Movement of organisms are constrained at multiple scales in soil. (2) Difficult to define an island/continent within soil (variable across scales).	MacArthur & Wilson (1967)
Metacommunity theory	Movement, species–environment interactions, species–species interactions	alpha, beta	(1) Distinct local communities are connected *via* dispersal of individuals of species.	(1) Local diversity (alpha and beta) depends on dispersal capacity. This relation can be hump-shaped. (2) The persistence of species in sinks depends on species dispersal.	(1) Not easy to estimate dispersal ability. (2) Difficult to define distinct patches (variable across scales).	Wilson (1992); Mouquet & Loreau (2002); Leibold *et al.* (2004)

Table 1. Continued

Theory	Theory type	Biodiversity type	Underlying mechanisms/ assumptions	Main prediction(s)	Challenges relevant to soil organisms	Foundational references
Niche theory	Species–environment interaction, species–species interaction	alpha, beta	(1) Species are at their equilibrium population. (2) Feedback of diversity on diversity through the creation of new niches is ignored. (3) Demographic stochasticity and ecological drift are ignored.	(1) For two or more species to coexist in an environment, they must occupy different niches or at least avoid niche overlap among them as far as possible. The greater the number of limiting factors (both biotic and abiotic), the greater the biodiversity (more heterogeneity leads to greater biodiversity). (2) Species abundance distribution depends on resource partionining. (3) Species similarity decays with difference in environmental variables.	(1) Ecosystem engineering by soil organisms generates strong feedback on soil biodiversity. (2) The equilibrium is a matter of scale, and soil represents a system with cross-scale interactions. (3) Selection of the right environmental variable.	Hutchinson (1959); MacArthur (1972)
Neutral theory	Species–species interaction, movement	alpha, beta	(1) All individuals within a community have the same chances of reproduction and death. (2) Habitat is entirely saturated with individuals. (3) Demographic stochasticity is the dominant process, and everything else is ignored.	(1) Species abundance distribution depends on spatial structure. (2) Species similarity decays with spatial distance.	(1) Strong simplification and ignores many processes.	Hubbell (2001); Bell (2001)

Table 2. Glossary of terms

Alpha diversity	Species diversity or richness of a local community.
Beta diversity	Differences in diversity associated with variations in habitat or spatial scale.
Metacommunity	Set of local communities interlinked by the dispersal of multiple species which also interact with each other.
Equalizing processes	Processes that lead multiple species to be equal (or close to equal) in their fitness.
Stabilizing processes	Processes that cause species to limit their population size more than they limit other neighbouring species.
Grain	The first level of spatial resolution possible in a given data set or the spatial unit of sampling.
Extent	Total area of study.
Self-organization	A process in which global-level patterns of a system emerge from numerous interactions among lower-level components of the system.

highlighted that greater diversity of soil organisms is due to their lack of trophic specialization combined with widespread micro-scale abiotic heterogeneity. In recent years, however, the key research agenda of soil biodiversity studies has shifted to highlighting their crucial roles as drivers of ecosystem functions and ecosystem services that influence human well-being (Bardgett & Van Der Putten, 2014; Nielsen, Wall, & Six, 2015; Wall, Nielsen, & Six, 2015). These studies have yielded important insights on how our well-being is closely related to healthy soils with high biodiversity (Wall *et al.*, 2015; Orgiazzi *et al.*, 2016). In addition, recent methodological advances such as high-throughput sequencing have enabled investigations of soil biodiversity with greater precision and have promoted insights on patterns of soil biodiversity at varying spatial scales (Bahram *et al.*, 2018; Geisen *et al.*, 2018; Ramirez *et al.*, 2018; Potapov, Tiunov, & Scheu, 2019). Yet, only a few studies have tested contemporary biodiversity theories using patterns of soil biodiversity.

Here, we consider five biodiversity theories: (i) species–energy relationships, (ii) theory of island biogeography, (iii) metacommunity theory, (iv) niche theory, and (v) neutral theory. We selected these based on their ability to generate clear predictions of species diversity (see Tables 1 and 2), as well as their known prominence in the aboveground and aquatic biodiversity literature. We acknowledge that there are many other ecological theories that might explain patterns of biodiversity. However, we limit this review to theories that make predictions for alpha and/or beta diversity, and which mainly rely on movement- and interaction-based mechanisms (Table 1). The five chosen theories also overlap to varying degrees. For instance, metacommunity theory extends several components of theory of island biogeography, specifically mechanisms associated with colonization and extinction processes (Hanski & Gilpin, 1991), while neutral theory is often used as a null model for niche theory (Alonso, Etienne, & McKane, 2006; McGill, Maurer, & Weiser, 2006). We provide a general overview of these five theories in Table 1.

III. SYSTEMATIC LITERATURE SEARCH

The literature search was performed on 21 June 2019 in ISI *Web of Science*. We performed an initial search focused on the five theories examined herein using the following search terms: 'island biogeography'; 'metacommunity' OR 'meta−community'; 'species−energy relations*' OR 'species energy relations*' OR 'productivity gradient' OR 'productivity−diversity relations*' OR 'productivity diversity relations*'; and 'neutral theory' OR 'Hubbell's neutral theory' OR 'the unified neutral theory of biodiversity' OR 'niche theory' OR 'competitive exclusion principle'. The total number of results for each search was used as an indication of the number of papers investigating a given biodiversity theory. To identify the research conducted on these biodiversity theories in belowground systems, the search was then repeated using the same search terms, plus the following additional soil-specific search terms: (('soil' OR 'belowground' OR 'below−ground') AND ('biota' OR 'fauna' OR 'microfauna' OR 'macrofauna' OR 'mesofauna' OR 'arthropod*' OR 'rotifer*' OR 'nematod*' OR 'hypha*' OR 'oligochaet*' OR 'protozoa*' OR 'protist*' OR 'microb*' OR 'bacteria' OR 'fung*' OR 'mite*' OR 'acari' OR 'amoeba*' OR 'flagellate*' OR 'archae*' OR 'annelid*') OR ('collembol*' OR 'springtail*' OR 'earthworm*' OR 'micro−arthropod*' OR 'microarthropod*' OR 'mycorrhiza*' OR 'enchytrae*' OR 'ciliate*' OR 'lumbricid*')).

The total number of results from these searches was then used as an indication of how many papers discussed each specific biodiversity theory in relation to soil biodiversity. However, because papers identified in our search may have mentioned soil but not have included an actual test of the biodiversity theories with soil organisms, we also screened all soil-specific papers in detail. Papers were excluded if they did not test the biodiversity theories using a soil organism.

Where papers tested a biodiversity theory with a soil organism, we assessed whether the results supported the biodiversity theory or rejected it, based on the main predictions outlined in Table 1. Our assessment was based on information given within graphs, tables or results/discussion text in these papers.

For each of the papers testing biodiversity theories with a soil organism, we recorded the taxon studied. For the analysis, these taxa were placed into four categories commonly used in soil ecology (Decaëns, 2010;Briones, 2014 ; Veresoglou *et al.*, 2015): microorganisms (e.g. fungi, bacteria), microfauna (e.g. nematodes, amoebae), mesofauna (e.g. springtails, mites), and macrofauna (earthworms,

Table 3. Number of studies providing support (Yes or No) for each of the five biodiversity theories (see Appendix S1 for a list of the studies included). N is the total number of cases. Support is also listed for the four categories of body size (microorganisms, microfauna, mesofauna and macrofauna, see Section III). The minimum and maximum grain and extent investigated for each theory are shown. The data presented in this table include all cases (note that there is some overlap of studies between niche and neutral theories) including those where the grain or extent was not provided, and thus these data differ from those plotted in Fig. 1

	Species–energy relationships		Theory of island biogeography		Metacommunity theory		Niche theory		Neutral theory	
Theory support	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
N	5	4	16	7	17	1	16	8	12	13
Microorganisms	4	3	7	0	6	1	8	8	9	7
Microfauna	0	0	1	2	1	0	0	0	1	0
Mesofauna	0	0	7	5	9	0	3	0	2	3
Macrofauna	2	0	1	0	1	0	5	0	0	3
Minimum extent	100 m	1 km	1 km	1 km	10 m	100 km	10 m	10 m	1 m	10 m
Maximum extent	1000 km	1000 km	100 km	100 km	100 km	100 km	global	global	global	global
Minimum grain	10 cm	10 cm	1 cm	1 cm	1 cm	10 cm	1 cm	10 cm	1 cm	1 cm
Maximum grain	10 m	10 cm	10 cm	10 cm	10 cm	10 cm	10 m	10 m	10 m	10 m

arthropods) (Briones, 2014; Veresoglou *et al.*, 2015). We also recorded the spatial scale of each study, including the grain size which was defined as the size of the smallest sampling unit, and the extent which was defined as the total area of the study encompassed by all sampling units (Turner *et al.*, 1989). The grain and extent size were assigned to categories closest to their actual value (1 cm, 10 cm, 1 m, 10 m, 100 m, 1 km, 10 km, 100 km, 1000 km).

We further recorded the temporal scale (ranging from one time point to 5 years of sampling), the ecosystem type, the country, and whether the study was experimental (i.e. included manipulations or treatments) or observational (i.e. using naturally occurring contrasts) (see online Supporting Information, Appendix S1). A single paper often contained more than one test of a biodiversity theory, for example, with different taxon groups, or at different spatial extents. Additionally, some papers tested multiple biodiversity theories. Every test was recorded separately, so a single paper could provide more than one case of support and/or no support.

IV. RESULTS

Our literature search showed that soil biodiversity was mentioned in a minority of articles for each theory. Only 3.2% of articles on theory of island biogeography mentioned soil organisms, 0.2% of articles investigating niche and neutral theories tested soil organisms, while 5.8% of articles on species–energy relationships mentioned soil organisms.

In total, we found 99 explicit tests of the predictions of the five biodiversity theories that used soil organisms from 56 published articles (Table 3, identified with asterisks in the reference list, Appendix S1). Species–energy relationships, theory of island biogeography, niche theory, and metacommunity theory received support in over 50% of studies (56, 70, 67, and 91%, respectively). Neutral theory was the least-supported biodiversity theory (48%) (Table 1). Given the low number of tests with soil organisms for some of the biodiversity theories (e.g. species–energy relationships), it is not possible yet to conclude which of these theories best predicts patterns of soil biodiversity. Further, we advocate pluralistic approaches rather than using a single biodiversity theory in future studies investigating patterns of soil biodiversity. Below, we extend these ideas in a proposed conceptual framework.

Soil microorganisms and soil macrofauna were the best-represented groups in studies involving the five biodiversity theories (Fig. 1). The reasonable level of support for these theories with a wide range of soil organisms indicates that both interaction- and movement-based mechanisms apply to soil organisms. However, the spatial scale at which these theories were applied successfully to soil organisms is central to an integrative understanding of soil biodiversity. The spatial extent (the distance over which the entire study was conducted) (Turner *et al.*, 1989) of the study areas ranged from 1 m to global, whereas the spatial grain of the studies (the smallest sampling unit) (Turner *et al.*, 1989) varied from 1 cm to 10 m, with the range in these values broadly consistent among tests of the five theories (Fig. 1). Most studies used a spatial grain range of 1–10 cm, as expected given standard protocols for sampling soil organisms, although the spatial grain range was higher (10 cm–1 m) in tests of species–energy relationships (Fig. 1). Spatial extents were also consistent among studies of the five theories across soil organism groups (Table 1, Fig. 1).

V. AN INTEGRATIVE FRAMEWORK FOR SOIL BIODIVERSITY

As outlined in Table 1, soil as a system presents several challenges with the application of any biodiversity theory. An emerging consensus among soil ecologists is to acknowledge that patterns of soil biodiversity vary at different spatial

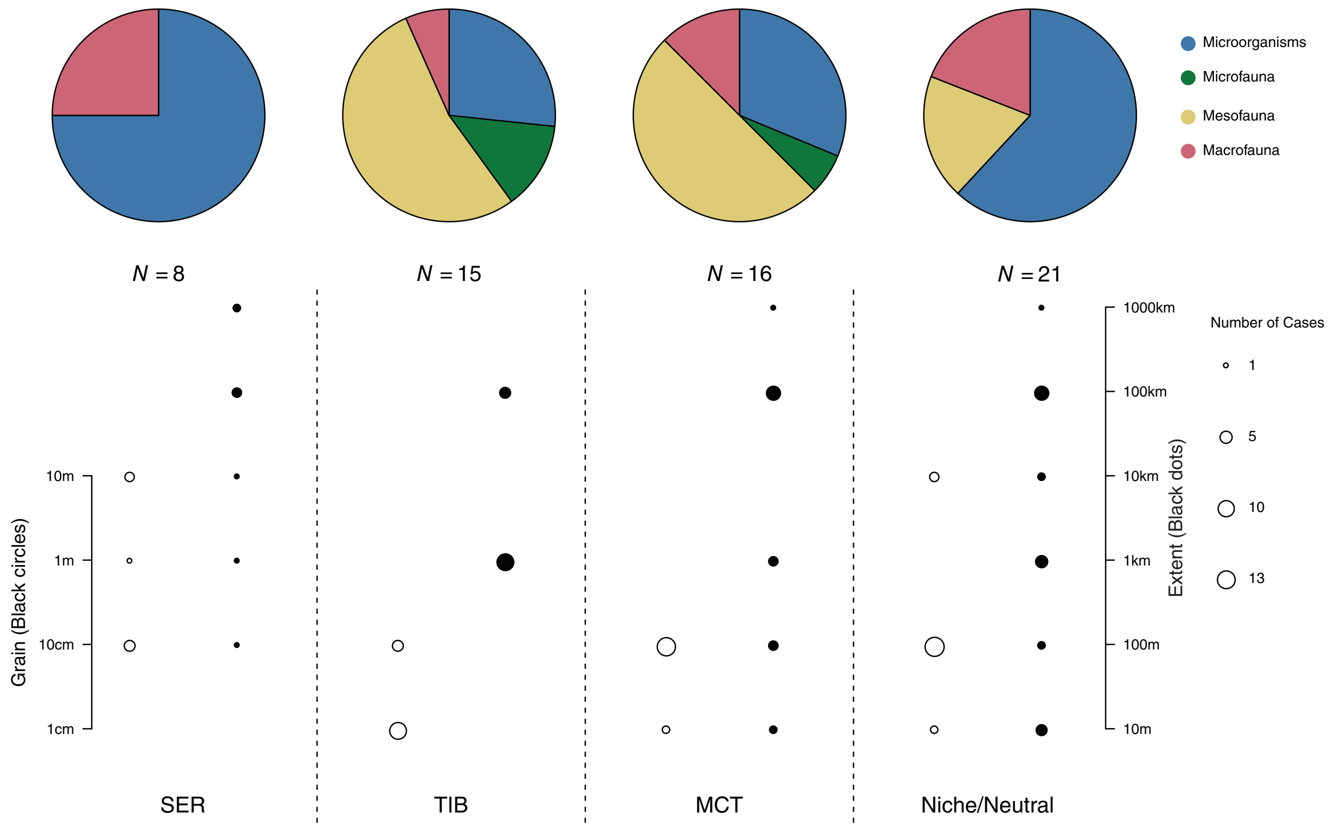

Fig. 1. Pie charts (top row) documenting the representation of different groups of soil organisms in studies of the five biodiversity theories considered herein. Soil organism categories are based on Decaëns (2010) and Veresoglou *et al.* (2015). *N* is the number of studies testing each theory. Below the pie charts, the range of grain and extent sizes reported in the studies are shown, with the size of the point indicating the number of cases. Studies were omitted from this figure if they did not report either the grain or the extent size. Studies on niche and neutral theory are combined as both theories were tested together in some studies, with the rejection of diversity patterns proposed by neutral theory (null hypothesis) considered as support for an alternative pattern proposed by niche theory. MCT, metacommunity theory; SER, species–energy relationships; TIB, theory of island biogeography.

scales within the soil (Ettema & Wardle, 2002; Berg, 2012). Accordingly, previous authors have advocated the integration of spatial hierarchies of different soil habitats to allow a better understanding of the (spatial) scale-sensitive diversity patterns of soil organisms (Giller, 1995; Ettema & Wardle, 2002; Decaëns, 2010; Berg, 2012). We here build upon these previous ideas and propose an integrative framework for understanding soil biodiversity at multiple spatial scales.

Our conceptual framework is based on dividing soil (S) into two spatial compartments (Fig. 2): soil hotspots (S′) and soil microsites (S″). Soil microsites are nested in soil hotspots and soil hotspots are nested in the soil (S). These compartments represent the grain size at which soil biodiversity can be studied. The extent of these three different spatial scales can vary from local (e.g. a few 100 m) to global.

Soil (S) is the coarsest scale in our framework and the most commonly used in soil biodiversity studies (Table 3). At this spatial scale, both bulk and rhizosphere soil are present, and all size groups of soil organisms can be sampled.

Soil can be divided into soil hotspots (S′), or functional domains, which could be the rhizosphere, drilosphere or even the litter layer (Fig. 2). Within this compartment, the biodiversity of intermediate-sized soil organisms, such as soil meso- and microfauna are mainly studied. Often the study of soil microarthropods and their resources are carried out at this spatial scale.

Within soil hotspots, soil microsites (S″) represent another spatial compartment, and this is the finest spatial scale at which biodiversity can be studied in the soil. Soil microsites could range from a tip of a plant root to even a single aggregate (μm to mm) in the soil (Bailey *et al.*, 2013). The study of soil biodiversity at this spatial scale focuses primarily on the diversity of microorganisms and their primary predators (Fig. 2).

The key drivers of biodiversity patterns at each of these spatial compartments (within which temporal scales will also differ, Fig. 2) vary significantly (e.g. Bach *et al.*, 2018) and it is thus important that they are considered when testing empirically the predictions of any biodiversity theory. In addition, spatial compartmentalization allows better integration of the variability in body size of soil organisms. For instance, the S compartment contains the highest range in body size of soil organisms, and biodiversity at this scale

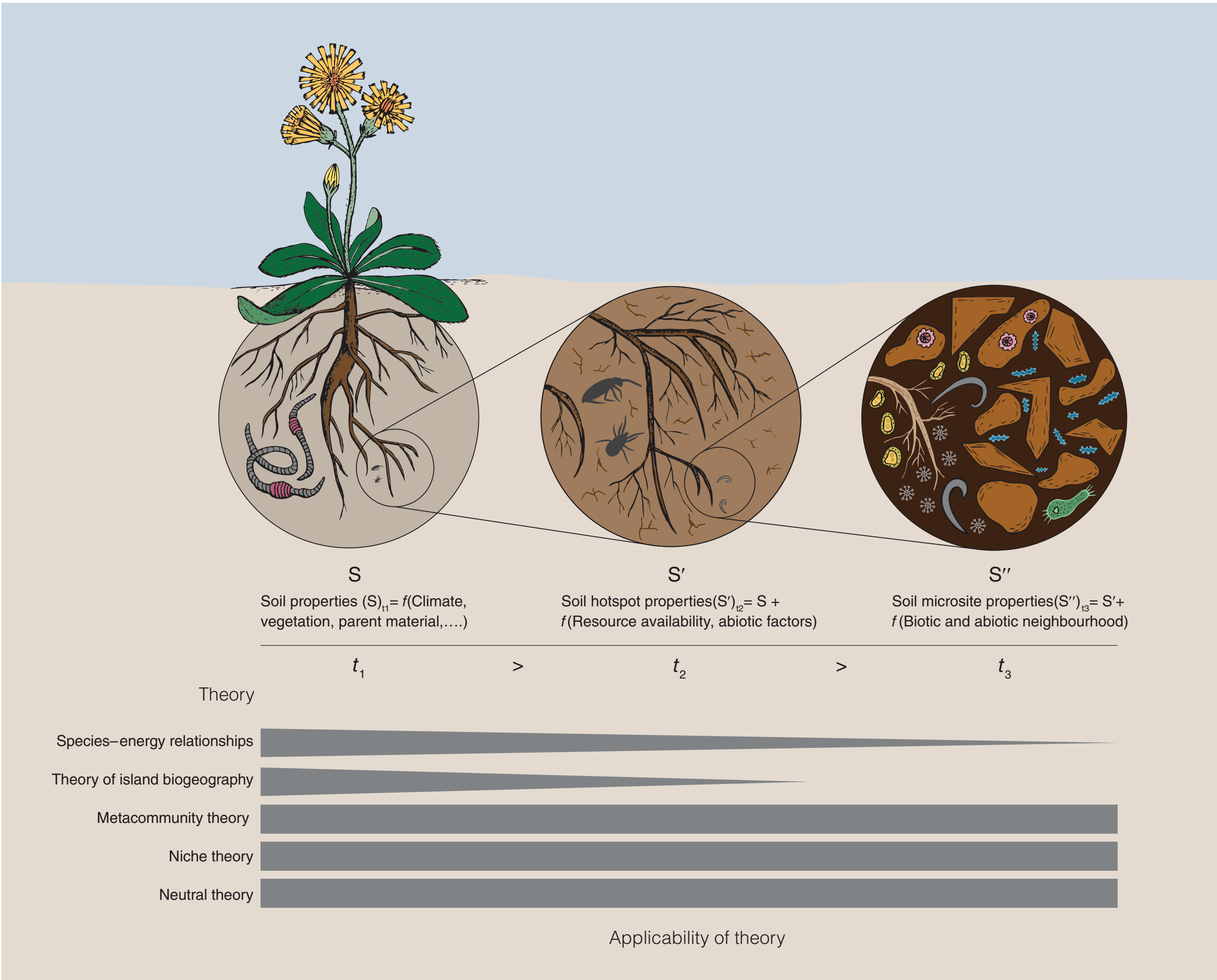

Fig. 2. Illustration of spatial compartments in the soil for studying soil biodiversity from micro- to macroorganisms. The properties of each compartment that potentially affect the respective biodiversity pattern are listed below the compartments. As we begin to zoom in from soil (S) to soil microsites (S″), the applicability of some biodiversity theories may also change (indicated by thickness of grey bars below the figure). Soil micro-aggregates are coloured light brown in the S″ compartment; all organisms in S″ are either microorganisms or their predators (e.g. nematodes and protists). Note that microorganisms also can colonize micro-aggregates as illustrated in S″. Since the temporal scale (t) also co-varies with spatial scale (Wolkovich *et al.*, 2014), the figure presents three different temporal scales ($t1-t3$) corresponding to the three spatial scales. f, function.

is more likely to be explained by factors such as climate and vegetation of a site. On the other hand, when we attempt to understand soil biodiversity at finer spatial scales, such as at S′ and S″, we require information on additional factors such as resource availability and soil abiotic properties (Fig. 2).

VI. APPLICABILITY OF BIODIVERSITY THEORIES ACROSS THE THREE COMPARTMENTS

Violation of the assumptions of some of the five biodiversity theories considered herein are most likely at the microsite compartment (S″) in our conceptual scheme (Fig. 2). For instance, in the application of theory of island biogeography at the S″ scale, issues will arise relating to the definition of a true mainland (or an external source) from which soil microorganisms and their primary consumers (e.g. protists and nematodes) can colonize a S″ island (Fig. 2). Such issues of habitat definition at the S″ scale could be resolved using the framework of metacommunity theory. While the theory of island biogeography only considers colonization from a mainland to an island, metacommunity theory incorporates colonization of organisms both between and within a mainland and islands (Hanski & Gilpin, 1991; Mouquet & Loreau, 2002; Leibold *et al.*, 2004). Further, metacommunity theory allows the incorporation of both interaction- and movement-based mechanisms, both of which might be relevant at this scale. For example, microorganisms can move in soil *via* processes involving diffusion or water transport (Dechesne, Pallaud, & Grundmann, 2007), which may determine their rate of encounters with potential competitors or predators. A recent conceptual study highlighted that soil aggregate formation at the microsite scale could affect the evolutionary trajectories of microorganisms, such as bacteria, by causing isolation (Rillig, Muller, & Lehmann, 2017). Hence, the S″ compartment in our framework could be suited to the study of eco-evolutionary dynamics of soil microorganisms and their primary predators with subsequent effects on biodiversity at this scale.

The assumptions of species–energy relationship models are also prone to violation at the microsite scale. A positive species–energy relationship (e.g. productivity–diversity relationship) has been shown to be susceptible to fluctuations in resource availability (Rosenzweig, 1995; Waide *et al.*, 1999; Chase & Leibold, 2002). For the S″ compartment, the temporal variability of resource availability is likely to be much more dynamic than at the spatial scales of the S and S′ compartments, which will undermine predictions of species–energy relationship models (Wright, Currie, & Maurer, 1993). For example, plant root exudates are one of the major determinants of biotic and abiotic conditions at the microsite scale (Bais *et al.*, 2006; Bardgett, Mommer, & De Vries, 2014; Reinhold-Hurek *et al.*, 2015). Temporal variability in root exudation profiles is usually very high (due to root growth) and thus resource quality and quantity of soil microsites are likely to be highly dynamic (Badri & Vivanco, 2009; York *et al.*, 2016). Temporal variability of resources in the S and S′ compartments can also be high, but this will take place over longer time scales compared to the S″ compartment, making the assumptions of species–energy relationships relatively robust at coarser scales (Fig. 2).

The inapplicability of theories of island biogeography and species–energy relationships to the microsite scale does not mean that microorganisms and their primary consumers could not be used in tests of these theories. Our systematic literature search showed that such tests have been made with soil microorganisms but at coarser scales. For instance, Vannette, Leopold, & Fukami (2016) applied the theory of island biogeography to root-associated fungi of a single plant present in 18 different forest patches isolated by volcanic lava to estimate the effects of isolation on fungal diversity. Although this study was carried out on a single oceanic island, the isolation of forest fragments by old volcanic lava made them a proxy for islands (Vannette *et al.*, 2016). Studies on other island-like habitats (e.g. epiphytes on treetops) have confirmed that larger islands usually support greater numbers of soil organisms like microarthropods (Wardle *et al.*, 2003). The quality of resources in islands also affects the diversity of microarthropods irrespective of island size, as shown by post-fire chronosequence studies in islands in Swedish lakes (Bokhorst, Berg, & Wardle, 2017). The spatial compartments used in these studies resemble the coarser scales (e.g. S or S′) of our framework.

We suggest that neutral theory, niche theory and metacommunity theory apply to all three spatial compartments of our conceptual framework. Neutral theory of biodiversity assumes ecological drift in communities, i.e. that populations of member species within a community fluctuate at random due to their equal probabilities of reproduction and/or mortality independent of their identity (Rosindell, Hubbell, & Etienne, 2011) (Table 1). Although this assumption has several ecological limitations and has been criticised (Purves & Turnbull, 2010; Clark, 2012), the neutral theory of biodiversity remains a powerful test of biodiversity patterns, mainly due to this simplistic assumption of species equivalence (McGill *et al.*, 2006; Missa, Dytham, & Morlon, 2016). Accordingly, several studies have used the neutral theory of biodiversity as a useful null model (McGill *et al.*, 2006; Rosindell *et al.*, 2012). When species abundance distribution patterns fit a zero-sum multinomial distribution as opposed to a log-normal distribution, biodiversity patterns are assumed to be driven by neutral processes (McGill *et al.*, 2006; Caruso *et al.*, 2012*a*). The species abundance distribution can be analysed for all three spatial compartments of our framework. This allows a test of the relative importance of niche *versus* neutral-based mechanisms operating at different spatial scales. However, the shape of the species abundance distribution may not be an adequate test for niche *versus* neutral processes given its aggregated nature, inherent to which is a loss of information on whether communities are driven by deterministic (niche) or stochastic (neutral) processes (Clark, 2012; Matthews & Whittaker, 2014). Several recent studies have called for an integrative framework, combining niche and neutral perspectives, to explain biodiversity patterns, suggesting that this will improve our ability to test the relative importance of deterministic and stochastic processes in communities (Tilman, 2004; Adler, HilleRisLambers & Levine, 2007; Vellend, 2010; Haegeman & Loreau, 2011; Scheffer, van Nes, & Vergnon, 2018).

Metacommunity theory allows the incorporation of both niche and neutral perspectives by incorporating processes at local and regional scales simultaneously (Mouquet & Loreau, 2002). According to metacommunity theory, the key determinant of biodiversity is the ability of species to move from one patch to another, which may differ according to environmental conditions. Metacommunity theory could thus be applied to all three proposed spatial compartments in our conceptual framework. Moreover, Leibold *et al.* (2004) emphasized four perspectives upon which movement and interaction-based mechanisms operate within a metacommunity. Predominantly homogeneous environments are characterized by patch dynamics and by the neutral perspective, whereas heterogeneous environments exhibit source–sink dynamics (or mass effects) and a species-sorting perspective (Mittelbach, 2012). However, neutral processes may not be restricted only to homogeneous environments (Leibold & Chase, 2018). For instance, one study carried out in temperate forest soils at a coarse soil scale (equivalent to the S scale in our framework) reported that variations in fungal diversity were explained marginally by environmental selection and dispersal limitation despite the presence of environmental heterogeneity in the study soils (Bahram *et al.*, 2016).

There are other theoretical frameworks that attempt to combine both niche and neutral perspectives to explain biodiversity patterns. Chesson (2000) and Adler, Hillerislambers, & Levine (2007) proposed a combination of equalizing mechanisms (neutral-based assumptions), such as those related to fitness similarity among the interacting species, and stabilizing mechanisms (niche-based assumptions), which relate to interspecific relative to intraspecific competition, as the major driving force behind the coexistence of interacting species. Although this integrative niche-neutral framework (also referred as modern coexistence theory) has been tested mostly using annual plants (Kraft, Godoy, & Levine, 2015), there is potential to test this framework using a range of soil organisms, particularly those with relatively short generation times. Importantly, this framework also makes assumptions regarding low levels of environmental fluctuations and a lower number of resources than that of consumer species (Barabás, D'Andrea, & Stump, 2018). Application of any theoretical framework to the understanding and prediction of soil biodiversity pattern thus requires a meticulous examination of the underlying assumptions (Table 1).

VII. CURRENT CHALLENGES AND FUTURE DIRECTIONS

A long tradition in soil biodiversity research has been to consider interaction-based mechanisms to be the main driving forces of soil biodiversity (Anderson, 1975; Bardgett, 2002; Nielsen *et al.*, 2010). For example, Wardle (2006) highlighted biotic interactions in the form of competition, facilitation and predation as the key determinants of soil biodiversity at finer spatial scales. Recent soil food web studies based on gut content and fatty acid analyses of soil invertebrates have further highlighted that soil food webs usually lack trophic specialization due to a greater number of omnivorous and cannibalistic interactions (Brose & Scheu, 2014; Thakur & Geisen, 2019) and systematically lower predator–prey body mass ratios (Brose *et al.*, 2019). While these recent findings concur with the classical soil biodiversity paradigm that complex soil structures prevent trophic specialization in the soil by constraining movements (Anderson, 1975), it remains unclear how this may vary spatially and temporally in the soil (Ettema & Wardle, 2002; Quist *et al.*, 2017). For instance, interaction strengths among soil organisms were recently shown to increase progressively from early to mid- and late-successional stages of restored semi-natural grasslands on former arable land, indicating that biotic interactions in the soil varied on a temporal scale while affecting, and being affected by, ecosystem development (Morrien *et al.*, 2017). We may also expect greater trophic specialization at the microsite scale due to specialized interactions between plant and soil pathogens (e.g. pathogenic fungi and oomycetes) (Mommer *et al.*, 2018), and mutualistic interactions are also likely to be stronger in microsites (Werner & Kiers, 2015). Whether the number and strengths of interactions differ in our proposed spatial compartments remains an important challenge for future studies aimed at understanding the scale-variant nature of soil biodiversity (Table 4).

Niche-based explanations further relate to how plant diversity relates to soil biodiversity by providing a variety of plant-derived resources, upon which soil organisms primarily depend (Lavelle *et al.*, 1995; Hooper *et al.*, 2000; Zak *et al.*, 2003). A higher diversity of resources from plants increases niche dimensionality, thus enhancing the probability that soil organisms can partition resources and coexist (Hooper *et al.*, 2000). However, this relationship depends on the extent to which plant diversity contributes to heterogeneity in soil physical conditions (Wardle, 2006). Accordingly, positive relationships between plant diversity and soil biodiversity are not always found. One cross-continental study showed that plant diversity was not related to alpha diversity of soil microorganisms but instead was associated closely with microbial beta diversity (Prober *et al.*, 2015). The authors reported that compositional differences between microbial communities increased with increasing plant diversity (Prober *et al.*, 2015). The influence of plant biodiversity on soil biodiversity is likely to vary in our proposed spatial compartments and future investigations should attempt to understand context-dependent plant–soil biodiversity relationships.

Table 4. Ten open questions in soil biodiversity research

(1)	Why are soils a hyperdiverse habitat and how is this biodiversity spatially and temporally organized in soils?
(2)	How does movement of soil organisms play a role in maintaining soil biodiversity?
(3)	How do active and passive dispersal of soil organisms differ among spatial compartments?
(4)	What biotic and abiotic factors link spatial compartments in soils?
(5)	How do interactions among spatial compartments depend on time?
(6)	How does specialization in symbiotic relationships among soil organisms and plants change with spatial compartments?
(7)	How do disturbances like land use change and climate change affect soil biodiversity in different spatial compartments?
(8)	How does climate change such as drought affect soil biodiversity *via* its effects on the passive dispersal of soil organisms?
(9)	How do stabilizing and equalizing processes work in soils and how does their relative importance change with spatial compartments?
(10)	Can spatial compartment approaches be applied to other habitats than soils to embrace the scale-dependent nature of biodiversity?

Movement-related processes in the soil are relatively poorly studied compared with interaction-based processes. This may reflect the limited (active) dispersal capacity of soil organisms compared with organisms living aboveground or in aquatic systems (Anderson, 1975; Van der Putten *et al.*, 2001; Wardle, 2002; Decaëns, 2010). With a limited capacity to disperse actively (larger soil organisms being an exception), passive dispersal is common in soil organisms (Nemergut *et al.*, 2013; Schuppenhauer, Lehmitz, & Xylander, 2019; Zinger *et al.*, 2019). For example, meso-fauna living in the S′ compartment, including collembolans and soil micro-arthropods are poor active dispersers but are often passively dispersed in the soil (Ettema & Wardle, 2002; Türke, Lange, & Eisenhauer, 2018; Schuppenhauer *et al.*, 2019). Long-term studies with better temporal resolution could unravel the importance of passive dispersal of slow-moving soil organisms for predicting their biodiversity patterns (Dirilgen *et al.*, 2018).

Soil microorganisms and their primary consumers in the S″ compartment can move within the water microfilm (*via* passive dispersal), but narrower windows of aqueous phases and higher viscosity may impose formidable challenges to movement in the S″ compartment (Tecon & Or, 2017). Nevertheless, large-scale dispersal (from m to km) of soil microorganisms is a common phenomenon regulated mostly *via* rainfall and wind events and also by human-mediated dispersal (Vos *et al.*, 2013; Thakur *et al.*, 2019). Although the dispersal ability of soil organisms will vary among different spatial compartments, it is important to note that species traits and soil structure will both impose challenges on the dispersal of soil organisms. The diversity of larger soil organisms may be related to active dispersal potential, whereas that of smaller organisms may be more affected by passive dispersal (Bahram *et al.*, 2016; Zinger *et al.*, 2019).

Future studies using newer technologies (e.g. molecular techniques and visual tracking techniques) to measure movement of soil animals may help to quantify constraints on the movement of soil organisms that affect the relative importance of niche- and neutral-based processes at the microsite scale (Nunan *et al.*, 2003; Aleklett *et al.*, 2018). Hovatter *et al.* (2011) showed that dispersal limitation (independent of soil environmental factors) in soil bacterial communities (i.e. neutral processes) was the main factor driving their diversity but only in the presence of host plants. In the absence of host plants, soil bacterial diversity was explained mainly by environmental factors (Hovatter *et al.*, 2011). Soil animal movement around the plant root zones (S′ compartment) can also affect fitness. A study on cyst nematodes demonstrated that individuals performed better when they were able to move towards newer root zones of their host plants compared to those that were unable to migrate (Van der Stoel & Van der Putten, 2006). Larger soil organisms such as earthworms can contribute to the passive dispersal of soil microorganisms which is likely to affect microbial biodiversity patterns across spatial compartments (Lavelle *et al.*, 2016; Yang & van Elsas, 2018). Our understanding of soil biodiversity will improve once we begin to understand what factors limit such movement and thus dispersal in soil across the spatial compartments.

A key challenge to the development of an integrative understanding of soil biodiversity is how biodiversity in the three spatial compartments affect each other's dynamics. Predators could link these compartments (Fig. 2) by feeding on prey from other compartments, hence linking energy flow across spatial compartments, as has been shown in soil food web studies (Digel *et al.*, 2014; Morrien *et al.*, 2017). Past research has shown that connectance in soil food web networks *via* feeding interactions is critical for the maintenance of soil biodiversity (de Ruiter, Neutel, & Moore, 1995; Neutel *et al.*, 2007) and its stability (Neutel *et al.*, 2007; Rooney & McCann, 2012). For example, increasing frequency of omnivory links in soil food webs over time, such as along successional gradients, acts as a source of weak interactions in food webs that contribute to soil food web stability (McCann, 2000; Neutel *et al.*, 2007). In addition, understanding factors facilitating or constraining predator–prey interactions in the soil will be crucial for understanding soil biodiversity patterns at multiple scales. For example, plant root and microbial volatiles acting as chemical cues may facilitate movement of predators from coarser scale S to S′ and S″, in turn regulating the microbial population in the S″ compartment (Schulz-Bohm *et al.*, 2017; Turlings & Erb, 2018).

In addition to trophic interactions across compartments, non-trophic interactions also occur in soil, mainly due to ecosystem engineers increasing soil structural complexity and thereby constraining direct encounters between predators and prey (Wardle, 2006; Schwarzmüller, Eisenhauer, & Brose, 2015). These ecosystem engineers (e.g. earthworms, ants, termites) also create resource patches for soil organisms, whilst potentially both facilitating and constraining the interactions and movements of soil animals (Jouquet *et al.*, 2006). Soil organisms contribute to the formation of soil aggregates *via* a variety of biological activities (Lehmann, Zheng, & Rillig, 2017). Hence, the physical complexity of soils is an emerging property that results partly from the biological activity of soil organisms, which is likely to feed back to soil biodiversity as well as to plant diversity patterns. Life in soil is likely to follow the principles of self-organization at multiple organismic scales ranging from soil micro- to macroorganisms mainly *via* engineering activities of soil organisms (Lavelle *et al.*, 2016). Self-organization in the soil operates *via* organismic interactions at discrete scales, nested within each other in a hierarchical design, from scales of a few microns (e.g. S″), to tens of microns (S″ and S′), and from millimetres to centimetres (S′ and S). This may eventually result in the emergence of patterns ranging from physical structures in the soil to spatially structured soil biodiversity. Research programs to quantify the nature of feedbacks among spatial compartments will no doubt provide newer insights into the causes underlying the enormous diversity of soil.

VIII. CONCLUSIONS

(1) Advances in the understanding of biodiversity patterns depend on our ability to accurately predict biodiversity in space and time. This review evaluates the extent to which common biodiversity theories, originally developed for aboveground biodiversity, may apply to soils. While these theories appear to be able to predict some aspects of soil biodiversity (Fig. 1, Table 3), we highlight the importance of a greater awareness of scale-related biodiversity variations in soils (Fig. 2) echoing recent recommendations for increasing scale awareness in ecology (Chase *et al.*, 2018; Estes *et al.*, 2018; Galiana *et al.*, 2018).

(2) Scale awareness is further important for systems where community structure is characterized by a steep body-size gradient of organisms at a very small spatial scale. Soil represents a system with an unparalleled fine-scale structural complexity. We believe that a better understanding of drivers of soil biodiversity at multiple scales will be gained by explicit recognition of the three spatial compartments present in soils (Fig. 1), within each of which different factors may be crucial for maintaining biodiversity.

(3) Soil biodiversity research should also aim to investigate ecological feedbacks among the proposed spatial compartments to allow us to develop an integrative understanding of soil biodiversity, which will be key to embracing the scale-dependent nature of soil biodiversity. Moreover, we advocate frameworks that incorporate multiple biodiversity theories, as exemplified by metacommunity theory. The roles of movement of soil organisms by both active and passive dispersal also need greater attention in order to understand soil biodiversity patterns (Hirt *et al.*, 2018; Mathieu, Caro, & Dupont, 2018).

(4) We advocate the extension of a spatial compartmentalization approach to other systems, particularly when multi-scale understanding of biodiversity is necessary. For instance, in aboveground systems, a compartmental framework could be applied to scale biodiversity from phyllosphere microorganisms to larger invertebrates and on to vertebrates. Indeed, the challenge to the use of such spatial approaches is whether the assumptions of any given biodiversity theory remain robust across multiple spatial scales.

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X. AUTHOR CONTRIBUTIONS

M.P.T., H.R.P.P. and E.K.C. conceived the initial ideas, which were substantially developed by the theory working group of sWorm (U.B., F.T.D.V., P.L., M.L., J.M., C.M., W.H.V.d.P., M.C.R., D.A.W.). E.K.C., N.E. and M.P.T. obtained the grant for the workshop. M.P.T., H.R.P.P. and E.K.C. wrote the manuscript with major contributions from the theory working group of sWorm. All authors contributed to the revision of the manuscript.

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XII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Appendix S1. List of studies included in the systematic literature analysis.

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