

REVIEW SUMMARY

SOIL ECOLOGY

The global soil community and its influence on biogeochemistry

T. W. Crowther*, J. van den Hoogen, J. Wan, M. A. Mayes, A. D. Keiser, L. Mo, C. Averill, D. S. Maynard

BACKGROUND: Soil is the largest repository of organic matter on land, storing ~1500 Gt carbon, which is at least as much as the vegetation (~560 Gt) and atmosphere (~750 Gt) combined. The turnover of this organic material (the rate at which it enters and leaves the soil) is governed by the most diverse community on Earth. By determining the rate and biochemical pathway of organic matter processing, fungi, bacteria, archaea, animals, and protists regulate soil fertility, plant growth, and the climate. Given their roles in regulating the exchanges of elements between terrestrial and atmospheric pools, the effective management of this soil community is among our most powerful weapons in the fight against the global threats of biodiversity loss and climate change. However, despite the critical importance of these organisms, the hyperdiverse nature of local soil communities has traditionally obscured efforts to identify general global patterns. As such, environmental

factors have traditionally been used as proxies to represent the variation in soil functioning across landscapes. But it is the organisms—not only the environment—that directly drive the turnover of organic material. Given that different organisms have varying impacts on elemental cycling, exploring the functional biogeography of soil communities is likely to be critical for improving confidence in global biogeochemical model predictions.

ADVANCES: Over the past decade, a growing body of evidence highlights that regional differences in the soil community drive considerable variation in biogeochemistry. Just as the transition from forests to grasslands drive vast differences in ecosystem functioning, differences in the structure of soil communities can drive enormous variation in elemental cycling. By expanding our horizons to see beyond the complexity of local soil communities, ecologists have begun to identify gen-

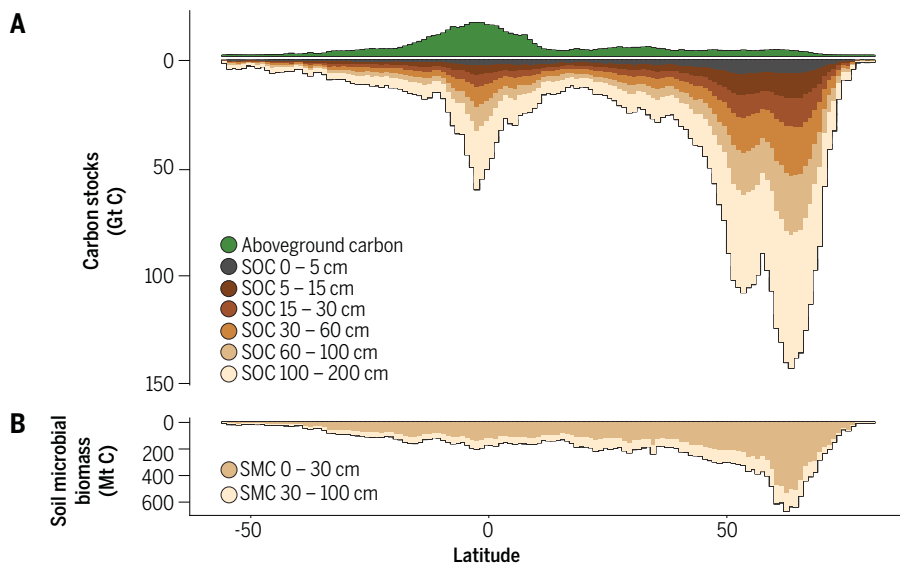
eral patterns in the biomass, composition, and diversity of soil communities. Despite the immense diversity of these organisms, the global soil community appears to be dominated by a manageable number of groups, which are likely to play a prominent role in the regulation of soil biogeochemistry. The metabolic activity and species richness of most

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soil organisms generally increase toward warm, moist tropical regions, where rapid elemental cycling depletes soil carbon relative to the higher latitudes. In addition, the huge accumulation of organic matter stocks in cold Arctic and sub-Arctic regions leads to huge abundances of soil microbes and animals at high latitudes. These global trends reveal key insights into the biological mechanisms that drive the distribution of organic matter on land as well as the vulnerability of different carbon stocks to future global change. Each new layer of global ecological information reveals distinct biogeographic patterns that provide insights into the fundamental distribution and dynamics of organic matter on land.

OUTLOOK: The field of soil ecology continues to uncover critical mechanisms that govern the turnover of organic matter at local scales. But placing these mechanisms into context necessitates that we continue to expand our understanding of the global biogeography of soil organisms. These communities can be viewed at multiple levels of ecological resolution, starting from the biomass of overall communities, which can then be divided into different functional groups, taxa, and functional traits. As we move down this list, we gain mechanistic detail at the expense of predictive understanding. While we continue to refine our detailed understanding of microbial taxa and trait compositions, we also need to step back to characterize the biomass distributions of the major functional groups of soil organisms, which reflect considerable differences in biogeochemical processing rates. As we generate this global ecological data, sensitivity analyses will then be necessary to identify the mechanisms that are most critical for improving biogeochemical model performance. These insights have the potential to improve predictions of soil fertility, plant production, and the climate. Ultimately, this emerging perspective of the most diverse and abundant community on land will provide fundamental insights into the organization of life on Earth. ■



Latitudinal trends in organic matter across terrestrial ecosystems. (A) The latitudinal patterns of terrestrial carbon stocks, both aboveground plant biomass (green) and soil carbon stocks (brown). (B) The same latitudinal trend in soil microbial biomass, revealing similar patterns to that observed in soil carbon. (Data sources are provided in Fig. 2 in the main text.)

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The global soil community and its influence on biogeochemistry

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Soil organisms represent the most biologically diverse community on land and govern the turnover of the largest organic matter pool in the terrestrial biosphere. The highly complex nature of these communities at local scales has traditionally obscured efforts to identify unifying patterns in global soil biodiversity and biogeochemistry. As a result, environmental covariates have generally been used as a proxy to represent the variation in soil community activity in global biogeochemical models. Yet over the past decade, broad-scale studies have begun to see past this local heterogeneity to identify unifying patterns in the biomass, diversity, and composition of certain soil groups across the globe. These unifying patterns provide new insights into the fundamental distribution and dynamics of organic matter on land.

The global soil community is central to the functioning of our planet. The countless species that constitute this community process all terrestrial organic material and influence every aspect of global biogeochemistry (1, 2). By governing the uptake and release of the major elements on land, these organisms govern the fertility of terrestrial ecosystems and the composition of our atmosphere. Changes in the rate of this organic matter processing are a prominent control on the rate of climate change (3, 4). Understanding soil communities across the globe is critical for predicting future changes in plant productivity, atmospheric composition, and the climate.

A detailed understanding of biogeochemical cycling at any location on Earth requires quantitative information about the organisms that drive elemental cycling (humans, plants, and soil organisms) and the environmental conditions (climate, soil physiochemical characteristics, and topography) that regulate their activity. There have been many quantitative models that describe the global variation in all these biotic and abiotic factors, but unifying global patterns in soil organisms have traditionally been obscured by the local variability of soil communities. Yet over the past decade, an explosion of technological advances has begun to facilitate

a global perspective that allows us to see past the apparent idiosyncrasy of local-scale studies (5–8). By providing a predictive understanding of the composition and activity of these communities, this perspective is beginning to transform our understanding of global biogeochemistry under current and future climate scenarios (5–8).

Here, we review the recent advances in our understanding of global soil communities and their role in governing the biogeochemistry of our planet. First, we describe the dominant drivers of the variation in soil community functioning, which determine the patterns of soil organic matter (SOM) turnover across the globe. Second, we summarize the hierarchy of approaches that have emerged to characterize global soil communities, each of which provides fundamental insights into the structure of life on Earth. Third, we discuss the different approaches by which soil ecological information is currently being incorporated into biogeochemical models, and we outline how these modeling approaches can alter our understanding of SOM turnover. Last, we synthesize this information to highlight the future research avenues that are urgently needed to enhance our understanding of global soil biogeography and biochemistry.

Functioning of global soil communities

Soil stores the majority of organic matter in the terrestrial biosphere, with more carbon than vegetation and the atmosphere combined (9). Plants are responsible for fixing this carbon from the atmosphere, but heterotrophic soil organisms—including bacteria, fungi, archaea, protists, and animals—determine the turnover of this organic matter pool. The turnover of SOM is governed by an array of ecological processes that are responsible for the uptake and release of carbon and nutrients in various different forms. These include many specialist

functions such as the production and uptake of methane (methanogenesis and methanotrophy) or different nitrogen-containing compounds (such as nitrification, denitrification, and nitrogen fixation) that can only be performed by certain microbial groups. It also includes generalist functions such as the mineralization of carbon into inorganic forms (primarily CO₂), which is performed by all organisms across the globe (Fig. 1A). Generating a predictive understanding of the global variation in these soil ecological functions is critical for parameterizing global biogeochemical models to predict future climate conditions.

Extrinsic drivers of soil metabolic activity

The traditional paradigm of SOM turnover states that the functioning of soil communities is governed primarily by climate conditions, which regulate the metabolic activity of soil communities, and by plant characteristics, which determine the amount and quality (or chemical composition) of organic matter inputs (10, 11). Despite ongoing debate about the relative importance of climate and plant traits in governing variation in SOM turnover rates across landscapes and continents (10, 12), contemporary temperature and moisture consistently emerge as prominent predictors of carbon and nitrogen mineralization at the global scale (13–15). Specifically, the highest activity levels are consistently found in warm, moist regions, with limited carbon and nitrogen mineralization rates in cold or dry ecosystems (13, 15). These patterns are similar for terrestrial nutrient uptake, with increased rates of carbon fixation (by plants) (16) and nitrogen fixation (by soil microbes) (17) in warm, moist regions. Yet, the increased rates of organic matter turnover in these regions leads to the depletion of organic matter in most warm, tropical ecosystems, relative to those higher latitudes (Fig. 2A). The global variation in turnover rates determine the fundamental distribution of organic material on land. Because cold or waterlogged conditions restrict respiratory carbon losses to a greater extent than primary production, the greatest accumulation of soil carbon stocks occurs in wetlands and in Arctic and sub-Arctic soils (Fig. 2A) (18).

In combination, the full range of contemporary climate, plant, and soil characteristics explain ~20 to 50% of the variation in nitrogen and carbon mineralization rates across terrestrial ecosystems (13–15), revealing patterns that match the global variation in litter mass loss and decomposition (Fig. 2B) (19). The strength of these relationships is both a blessing and a curse for our efforts to represent soil community functioning in global biogeochemical models. By characterizing the global Q_{10} (temperature coefficient) sensitivity of soil respiration, which is generally found to be between 1.4 and 2 (20, 21), we can use temperature as a proxy to represent much of the variation in SOM turnover rates in global biogeochemical models. However, this reliance on these broad-scale environmental correlations may have obscured efforts to represent

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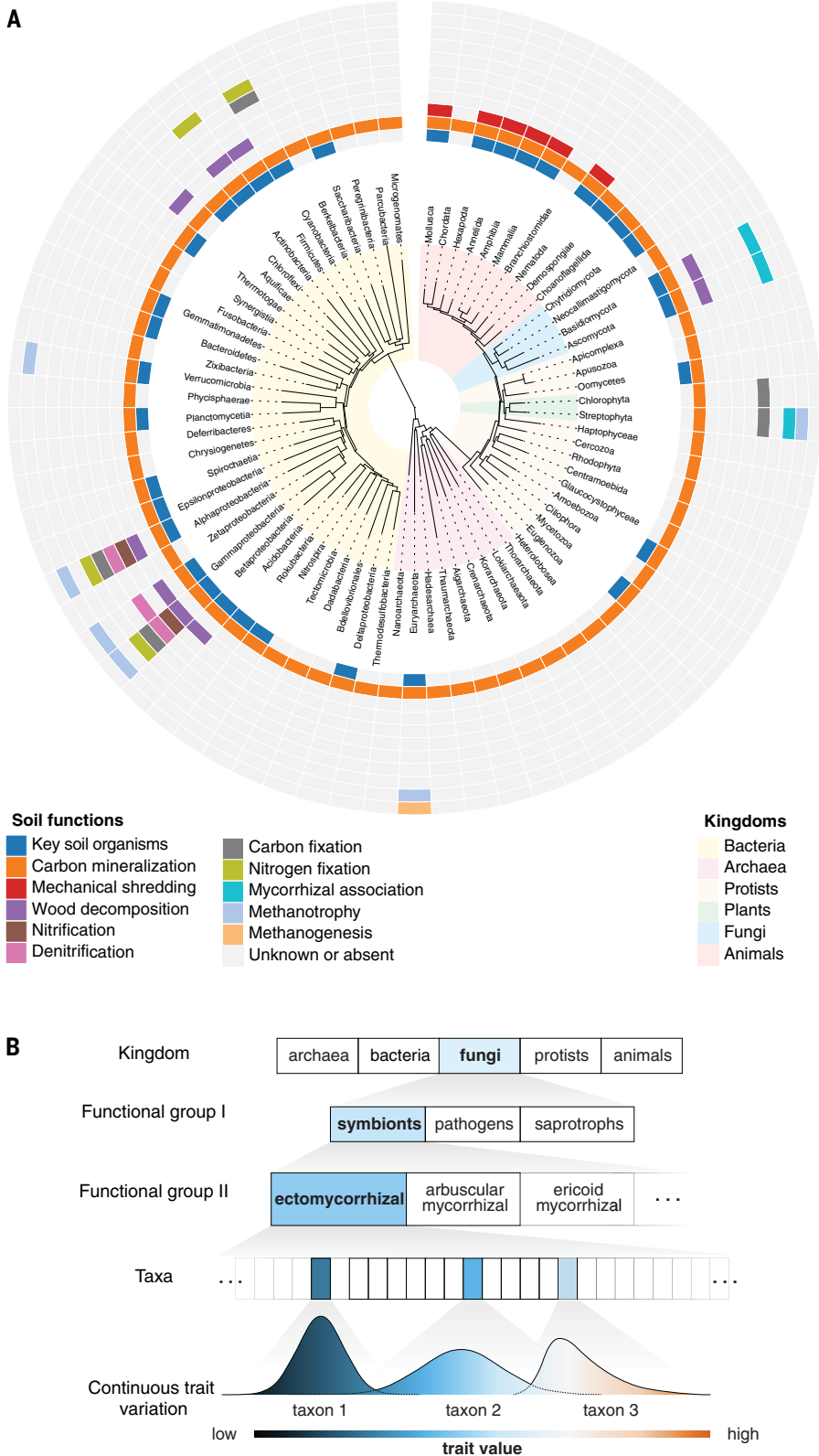


Fig. 1. The functioning of soil biota. Soil organisms span all domains of life. (A) The phylogenetic distribution of 12 common functions that are performed by soil organisms. Colored blocks indicate the performance of a particular function by at least one species in the respective taxonomic group. Colors on the branches of the phylogenetic tree indicate the different kingdoms. Phylogenetic relationships are according to Hug *et al.* (113). (B) A hierarchy of approaches used by ecologists to characterize soil communities. Here, fungi are used as the example, but the same hierarchy exists for all soil organism groups.

the structure and function of the soil community, which is expected to account for a substantial amount of unexplained variation in elemental processing rates across the globe (11, 22).

Intrinsic capacity of the soil community

Although the contemporary climate determines the physiological activity of soil organisms, the functional potential is ultimately determined by the composition of those soil communities (23, 24). Shaped by distinct combinations of environmental and historical events, this “soil community context dependency” can explain a considerable proportion of the variation in soil functioning (23, 24). Different soil communities process organic matter at very different rates and can fundamentally change the relationship between extrinsic environmental drivers and soil community functioning (Fig. 3C) (11, 25, 26). For example, the moisture sensitivity of communities assembled under wet tropical environments can be two to four times higher than in communities from drier conditions, when assayed under identical conditions (26, 27). Similarly, under identical conditions, communities assembled under historically warm, tropical conditions have a higher temperature sensitivity than those from temperate or boreal regions (Fig. 3) (28). These predictable functional legacies are tied to the abundance and composition of selected microbial taxa (27, 29); communities selected for under “optimal” growing conditions are selected for high functional performance rather than stress tolerance or survival mechanisms that are widespread in harsh environments (29).

Predictable environmental legacies are not only shaped by the historical climate but also by changes in the ecosystem structure. After changes in vegetation type—through land conversion (30), invasive species (31), or natural disturbance events (32)—soil communities can retain the functional characteristics of former ecosystems. How long these legacies can persist remains an important research question because long-term experiments are relatively rare. But the few long-term reciprocal transplant experiments suggest that soil microbial community composition and function can persist for several years (26), and even decades (33), although such long-term effects are certainly not universal (34). This knowledge of the soil community context is now being applied in an agricultural context by selecting microbial communities that can promote nitrogen mineralization and plant productivity (35). In addition, the introduction of entire soil communities from natural ecosystems can also promote the successful restoration of native vegetation in degraded regions, with high specificity to steer the plant community development toward different target communities (36). Although these soil community attributes cannot explain all of the variation in soil functioning, the signal of soil community effects appears to be consistently detectable across soils. This highlights that the functioning of terrestrial soils is governed not only by the contemporary environmental conditions but

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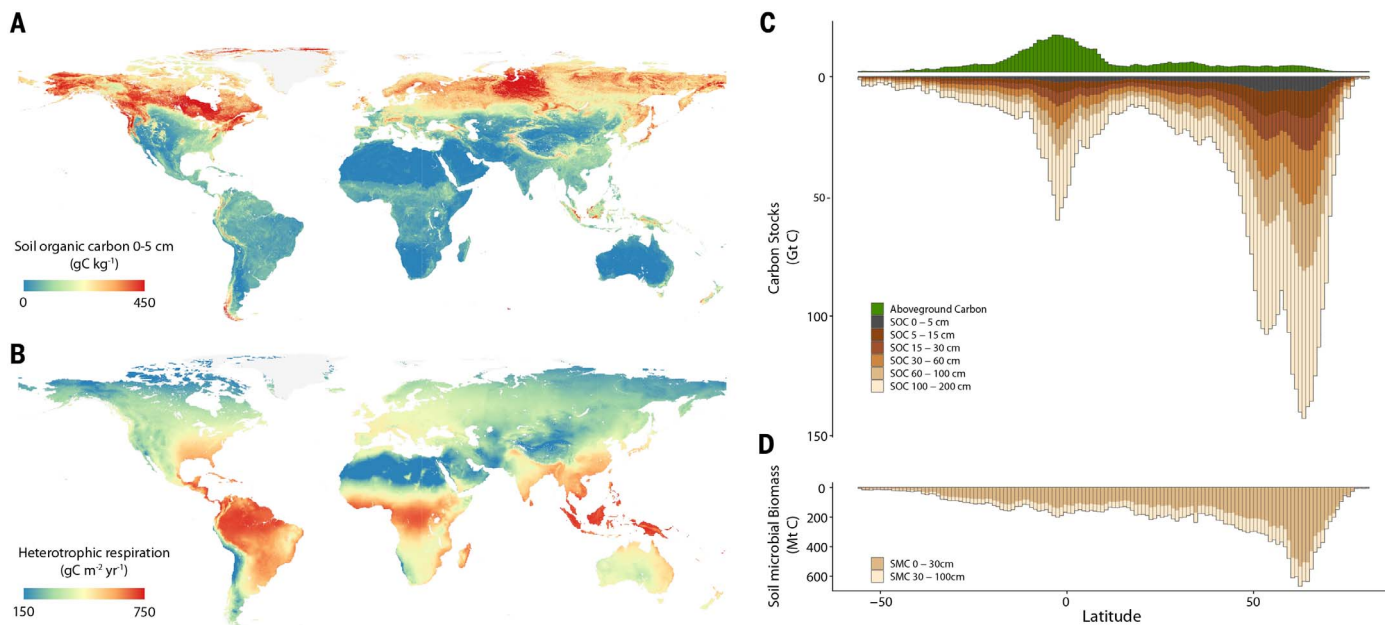


Fig. 2. Bulk soil community functioning. (A and B) The global patterns of (A) soil carbon storage [data from Hengl *et al.* (18)] and (B) heterotrophic respiration [data from Hashimoto *et al.* (14)]. Generally opposing latitudinal trends highlight that carbon stocks in soil are high in regions with slow carbon mineralization by heterotrophic organisms. (C) The resulting latitudinal patterns of terrestrial carbon stocks, both aboveground living plant biomass (green) [data from Gibbs *et al.* (114)] and soil carbon stocks (brown) [data from Hengl *et al.* (18)]. (D) The same latitudinal trend in soil microbial biomass, revealing similar patterns to that observed in soil carbon [data from Xu *et al.* (41)]. Although this dataset is expected to over-represent the scale of total carbon stocks in some regions, the SoilGrids data accurately describe the spatial distribution of soil carbon across the globe.

also by the intrinsic properties of the soil community that has been assembled in that location.

Characterizing the global soil community

To generate a predictive understanding of the soil context dependency, ecologists have begun to characterize the patterns of soil communities across the globe. Given their relevance for governing global biogeochemistry, characterizing these communities has the potential to explain much of the uncaptured variation in SOM turnover rates across the globe. Four distinct research areas have emerged to characterize global soil communities, describing patterns in (i) biomass and abundance, (ii) functional group composition, (iii) taxonomic diversity and composition, and (iv) functional trait expression. We discuss how each of these four categories yield complementary insight into the functional biogeography of global soil communities.

Biomass and abundance of soil community

At the highest level of ecological organization, the total abundance of biological cells in a region ultimately places a fundamental limit on the rate of SOM turnover in soil (37, 38). The biomass or abundance of important soil organisms can thus provide initial insights into the baseline functional potential of a soil community. In terms of biomass, fungi dominate global soil communities, with an approximate global biomass of 12 Gt carbon (C) (39). This value is nearly double that of soil bacteria (7 Gt C), with

soil animals and archaea storing ~2 and 0.5 Gt C, respectively (39). Although these groups vary in their processing rates, the spatial distribution of this biomass is a critical ecosystem characteristic that places a biophysical constraint on the rates of SOM turnover across the globe.

Although the distribution of most aboveground metazoan biomass is governed primarily by climate conditions, the distribution of belowground microbial biomass is shaped primarily by edaphic characteristics. At the global scale, both fungal and bacterial biomass generally increase in regions with high SOM content and lower pH (Fig. 4A) (8). Both show the opposite trend to aboveground plant biomass, with the greatest abundances in Arctic and sub-Arctic regions (Fig. 4A) (40, 41). Following this trend, the most abundant soil animals—nematodes—also show the highest abundances at high latitudes, where cold conditions have caused the accumulation of huge SOM stocks (42). Regional contingencies in these patterns contrast with these general latitudinal trends and lend support for the mechanisms driving these broad-scale patterns. For example, the accumulation of organic matter in waterlogged tropical peatlands (for example, Peruvian Amazon and Bornean rain forest) or in high-altitude soils (for example, the Rocky Mountains or Himalayan Plateau) can lead to high microbial and animal biomass in certain low-latitude regions (Fig. 4A).

The general trend of increasing soil organism biomass with latitude seems paradoxical, highlighting the negative relationship between biomass and SOM turnover rates at a global scale

(Fig. 4). This trend contradicts the results from local-scale studies, which consistently highlight the positive influence of microbial biomass on nutrient decomposition and respiration rates (37, 38). Yet, the negative global-scale relationship is likely to be mediated by global variation in heterotrophic organisms in cold regions drives the accumulation of large organic matter stocks, which support high abundances of soil biota with slow metabolic rates (42). Thus, although the relationship between soil community biomass and SOM turnover is negative at a global scale, this relationship flips when controlling for the effects of temperature and soil moisture (Fig. 4B). That is, under equivalent environmental conditions, larger communities generally drive faster SOM turnover, a pattern that underpins much of the soil community's context dependency at a global scale (Fig. 4B).

Composition of functional groups

To generate a more detailed understanding of soil functioning, we can identify how soil community biomass is partitioned between different functional groups. Given their particular trait combinations, different functional groups (or guilds) are often filtered into distinct environments that characterize the biochemical cycling in those regions (Fig. 1B). This is especially apparent within specialized microbial communities that define the biogeochemical processing in certain ecosystems, such as the methanogenic archaea that dominate wetland soils. Despite covering less than 6% of the land surface, these

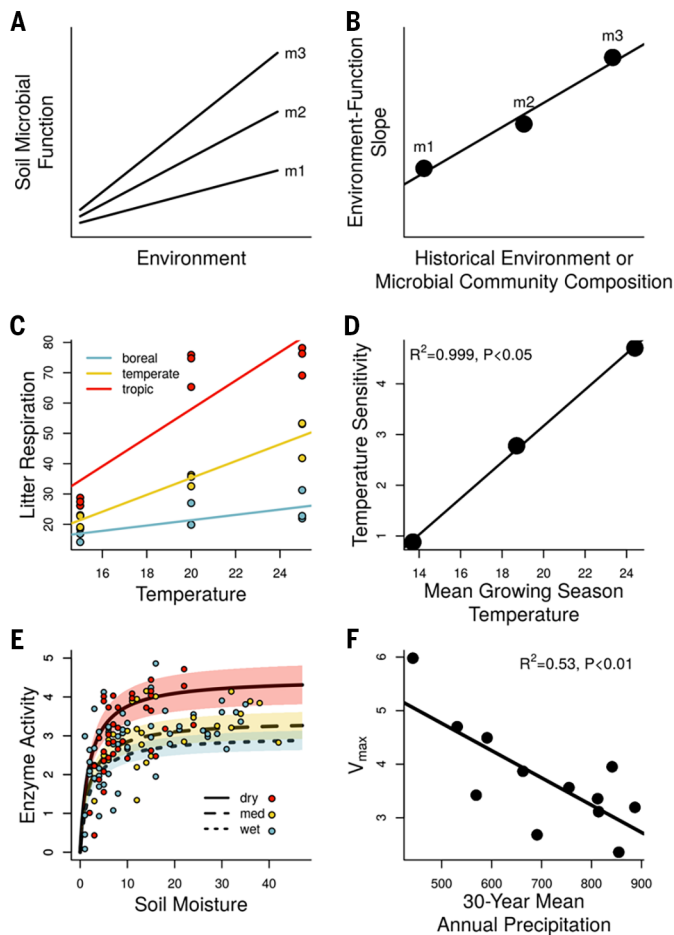


Fig. 3. Historical context determines the nature of the relationship between climate and soil function. Context dependency of soil community function can be explained by historical environment, which may be standing in for differences in microbial community composition. (A and B) How different soil communities can exhibit different sensitivities to the environment and how this may be linked to historical environmental conditions, potentially standing in for difference in microbial community composition. (C) An example of this phenomenon, in which litter respiration is differentially sensitive to temperature across a latitudinal gradient. (D) Variation in the slope of the temperature-respiration relationship (temperature sensitivity) can be explained by differences in historical climate (24). (E) The response of soil enzyme activity (natural log transformed) to soil moisture across a historical precipitation gradient in central Texas, USA. (F) The maximum activity parameter, referred to as V_{max} , at the site level is linked to historical rainfall [Averill *et al.* (52)].

anaerobic soils contribute 30 to 40% of the global methane emissions ($0.2 \text{ Gt CH}_4 \text{ year}^{-1}$) (43). These ecosystems also support the largest global communities of methanotrophic archaea, which consume a large fraction of these emissions (9). As such, these soil communities make wetland ecosystems functionally and biochemically distinct from other terrestrial soils.

In contrast to the specialist processes, many generalist functions such as carbon and nitrogen mineralization are broadly distributed across all taxa in all terrestrial soils (Fig. 1A). Yet given the structural, morphological, and biochemical differences between the major kingdoms of soil organisms (Fig. 1B), fungi, bacteria, archaea, protists, and animals vary considerably in their impacts on SOM turnover rates. As the most abundant soil organisms in soil, the relative

biomass of fungi versus bacteria (F:B ratio) has received considerable attention at broad spatial scales. Fungi-dominated systems are generally associated with slow decomposition of more chemically recalcitrant organic matter (8, 44), supporting the growth of slow-growing plants (such as trees). By contrast, grasslands are typically dominated by bacteria, which drive rapid nutrient cycling that promotes the existence of fast-growing, nutrient-rich plant species. Even within these ecosystem types, the F:B ratio increases with the C:N ratio of soil. Therefore, the proportion of fungi is likely to increase with soil C storage (45) and lower gross nitrogen mineralization rates (46), driving a general trend of increasing fungal dominance toward the high-latitude regions with larger SOM stocks (8). Despite considerable research efforts to

disentangle the drivers of F:B ratios across landscapes, we still lack a spatially explicit characterization of these different functional groups at a global scale.

Within these broad organismal groups, soil organisms can be delineated into key functional groups (or guilds) that drive independent soil functioning (Fig. 1B). One major functional group distinction that has received attention at the global scale is that between the dominant types of symbiotic fungi. Mycorrhizal fungi are a ubiquitous component of the soil microbiome, forming symbiotic associations with the roots of most plants (47). Two major types of mycorrhizal fungi—arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi—dominate most terrestrial soils. Because AM fungi rely on inorganic forms of nitrogen that have been mineralized by free-living decomposers (48), plants that form AM symbioses tend to dominate “fast” nitrogen-cycling ecosystems. By contrast, the larger networks of EM fungi can degrade and acquire organic forms of nitrogen directly (49, 50) and are predicted to dominate “slow” nitrogen-cycling ecosystems with low levels of inorganic nutrients (47, 48). With slow rates of SOM turnover, the proportion of AM fungi in soil is expected to increase the turnover of organic matter stocks across the global forest system (51–53). Structural differences between these mycorrhizal groups also influence the ecosystem-level responses to global change because EM-dominated plants exhibit more sustained increases in productivity under elevated CO_2 (54). By taking advantage of the associations between mycorrhizal types and symbiotic tree species, Steidinger *et al.* (55) generated quantitative global maps of mycorrhizal association type across the global forest system. This revealed that although AM fungi dominate ~95% of tree species, these communities are restricted to lower-latitude tropical and subtropical soils, with EM dominating a larger proportion of trees in temperate and boreal regions with slower SOM turnover (55). Given differences in the nutrient processing rates of EM and AM fungi, these quantitative relationships can provide direct insights into the spatial patterns of SOM processing across the globe (Fig. 4) (55).

By characterizing the proportional representation of broad kingdoms (such as fungi versus bacteria) or functional groups (such as EM versus AM fungi) across terrestrial soils, ecologists can reveal valuable mechanistic insights into the functioning of entire ecosystems. Both examples (F:B and AM:EM) represent differences between fast and slow cycling, which can reflect the relative differences in fast and slow energy channels within the soil community (45). The importance of distinct fast versus slow energy channels has been recognized for decades in soil ecology (56, 57), providing critical insights into the stability of soil communities and the turnover SOM at local scales. Generating spatially explicit data to reflect the relative abundances of different functional groups across the globe can allow the incorporation of such mechanisms into global-scale models (55). Yet despite

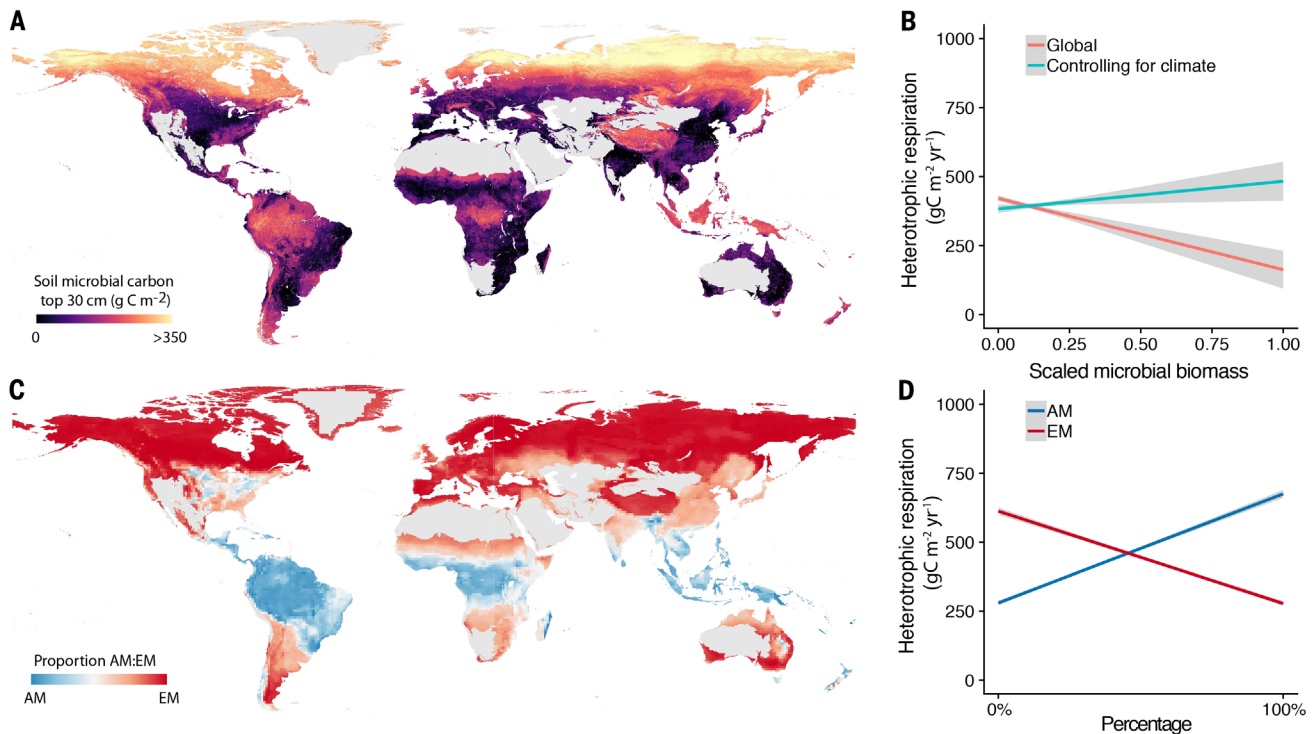


Fig. 4. Quantitative global maps of soil biota and functional group composition can help us to contextualize our understanding of global carbon turnover. (A) The global patterns in soil microbial carbon [data from Xu *et al.* (41)]. (B) The negative correlation for this microbial biomass and soil heterotrophic respiration at a global scale (red line), an effect that flips when controlling for the effects of climate (light blue) [respiration data from Hashimoto *et al.* (14)]. (C) The

global patterns in the ratio of arbuscular versus ectomycorrhizal (AM:EM) fungi [data from Steidinger *et al.* (55)]. (D) The positive correlation between soil respiration and the proportion of AM fungi that dominate tropical regions, an effect that is reversed for the EM fungi that dominate in higher latitudes. It should be highlighted that these correlations are not causative, but they highlight the context-dependency of soil communities across the globe.

the explanatory power of these functional group descriptions, few studies have attempted to explore the relative abundances of other major soil organisms (animals versus protists versus archaea) at the global scale. In addition, each of these kingdoms can be further divided into functional groups according to differences in body size (such as microinvertebrates versus macroinvertebrates), trophic status (such as predatory versus herbivorous invertebrates), successional stage (such as early versus late-stage wood decomposers), biochemical pathway (such as nitrifying versus denitrifying bacteria), or resource use (such as litter versus wood decomposing fungi) (Fig. 1B). Generating quantitative, spatially explicit information about the relative abundances of these major functional groups at a global scale will be critical for characterizing the ecological status of terrestrial soils.

Taxonomic composition

Different species within functional groups can vary widely in their rates of SOM processing. Hence, dividing the biomass of these functional groups into different taxa can provide a more refined understanding of soil community functioning. DNA metabarcoding is now the most widely adopted strategy to categorize the relative abundance of different taxa in soil (7, 8). In

species richness, the prokaryotes (bacteria and archaea) are the most diverse components of the soil community, followed by fungi, and then protists and animals, although the majority of all groups remain uncharacterized (58). Generally, it has been assumed that the global richness of most soil taxa follows the same trend as aboveground taxa, with increasing richness toward warm, moist tropical regions (6, 59–61). However, recent studies suggest that this latitudinal trend may not be as consistent as in plants; bacterial richness may peak in midlatitude soils with approximately neutral pH and relatively high soil carbon:nitrogen ratio (8). These diversity trends may also differ for functional groups that are biogeographically separated. For example, the richness of EM fungi peaks in high-latitude forests that support the greatest proportion of EM trees (60), whereas AM diversity peaks in tropical regions where this functional group is most prevalent (62). Untangling the interacting drivers of soil community diversity can reveal how soil diversity influences the structure and functioning of terrestrial ecosystems at a global scale (63).

Rather than focusing on the number of species, efforts to understand the relative abundance of taxa in soil can provide greater insights by identifying which taxa dominate the soil com-

munity. Given the overwhelming number of soil-dwelling species, this has been a daunting challenge. Growing evidence now suggests that soil communities are highly uneven and dominated by a few cosmopolitan species that characterize the global community. In a global analysis of bacterial communities, only 500 species were found to dominate the global soils, most of which fell into the Proteobacteria, Actinobacteria, Acidobacteria, and Planctomyces (7). By clustering the dominant bacterial taxa, Delgado-Baquerizo *et al.* (7) were able to visualize the spatial patterns of four major types of bacterial community that characterize different ecoregions across the globe. Similar levels of hyperdominance have been detected in broad-scale communities of mycorrhizal fungi (64), archaea (65), and invertebrates (66). Once the functional capacity of these dominant taxa has been characterized, these cosmopolitan species may provide a valuable research avenue for characterizing the functional biogeography of soil communities (7).

The soil community includes many rare and endemic species, and there has been a focus on describing the “dissimilarity” in the relative abundance of taxa across soils. Predicting global patterns in this beta diversity remains highly challenging because levels of endemism are high among soil fauna (67). However, at higher

phylogenetic levels (such as at the family or phylum levels), there is enough representation across samples to detect continuous spatial variation. Edaphic and biotic characteristics consistently emerge as dominant factors that shape the composition of bacterial communities at broad spatial scales (7, 8, 44, 68–70). Soil pH consistently explains a large proportion of the variation in bacterial phyla across studies, with increasing pH corresponding with a greater proportion of Actinobacteria and Bacteroides and the relative loss of Acidobacteria species (68). In addition, as we continue to generate global maps of vegetation indices (16), we are beginning to recognize the dominant role of plant biomass and ecosystem type (grassland or forest) in shaping the distribution of dominant taxa (7, 71). Yet, the signal of climate is still apparent, particularly in arid conditions, which give rise to taxonomically distinct communities, promoting *α-Proteobacteria* and reducing Acidobacteria and Verrucomicrobia (70). In contrast to the prokaryotes, the signal of environmental filtering in shaping patterns of eukaryotic communities may be slightly weaker (67, 72) because spatial distance alone explains >30% of the dissimilarity in fungal community composition at broad scales (67, 72). Yet with enough samples across the globe, the patterns of niche filtering are beginning to emerge (8), as environmental variables including evapotranspiration and soil C:N drive consistent variation in fungal community composition (6, 8). Reflecting these differences in edaphic characteristics, the signal biotic filtering is particularly apparent in fungal communities because the shift from grasslands to forest ecosystems drives a strong increase in the abundance of *Basidiomycota*, relative to *Ascomycota* (71). Similarly, the composition of soil animals (58, 66) and protists (73) appear to be structured primarily by soil moisture, C:N concentrations, and vegetation types, driving fundamentally different biogeographic trends than those observed in soil bacteria (73). With so many species across all groups, we do not yet have a clear synthesis to describe the taxa existing at any given location. But conceptual advances in this field have the potential to transform our understanding of SOM turnover if we can characterize the functional potential of those taxa. A key challenge is to generate quantitative information, which will require scaling this relative abundance information with estimates of total biomass at each location.

Functional traits

At the finest level of understanding, soil communities can be characterized on a truly continuous scale by examining the expression of functional traits (Fig. 1B). The functioning of a community is ultimately governed by the traits expressed by individuals and not their taxonomic identity per se. Functional traits can include structural, morphological, biochemical, or genetic characteristics of organisms, which determine the performance of individuals in time or space. Soil ecology has been founded on the

measurement of countless organismal characteristics that describe the functioning of individuals in simplified communities. Over the past decade, there has been a resurgence in these trait-based approaches to characterize the coexistence and functioning of individuals within complex communities (74–76). As such, the emergence of trait-based approaches at the global scale can provide tangible linkages between the biogeography and functioning of global soil communities (74–76).

Molecular approaches—such as metagenomics (estimating microbial composition and genomic capacity), metatranscriptomics (estimating gene expression), and metaproteomics (estimating protein synthesis)—can provide insights into the functional profile of entire soil communities. Few studies have begun to characterize the global trends in these community-level traits, and our global understanding is coarse. The expression of most functional genes in soil differs between biomes, driven by interactive effects of climate and edaphic characteristics (77, 78). In particular, communities in arid environments tend to exhibit distinct functional characteristics (77) because genes related to carbohydrate, iron, and phosphorus metabolism tend to be underrepresented in deserts relative to forests and grasslands (78). As the most abundant components of the soil, fungi and bacteria also appear to dominate the functional profile of most soils. For fungi, these broad-scale patterns in functional trait expression are predominantly linked to differences in soil carbon-to-nitrogen ratio and soil moisture (8, 67). By contrast, the presence (not necessarily expression) of bacterial functional is predominantly governed by soil pH (8, 77), so that bacterial functioning largely mirrors global patterns in richness and community composition. Yet despite the prominent control of edaphic characteristics in shaping the composition of functional genes at a global scale, the abundance of bacterial proteins appears to match the global patterns in climate, with higher abundance of most proteins in warm, moist regions with rapid SOM turnover (79). Similar to the “bulk soil community functions,” these community-level estimates are beginning to reveal broad-scale patterns in the functional potential of entire communities but do not enable the direct measurement of individual-level traits that are necessary for a mechanistic understanding of soil community assembly.

At the finest level of mechanistic understanding, the direct measurement of traits expressed by individual organisms can highlight the trade-offs that underpin soil community coexistence and performance in any given region (74). Broad-scale trait measurements on individuals have begun to reveal basic mechanisms that hold across fungi and bacteria, in which trade-offs in the expression of traits associated with stress tolerance and competitive dominance determine the relative activity levels of taxa across broad environmental gradients (76, 80). Moving from tropical moist regions toward cold or dry ones,

traits associated with stress tolerance are expressed at the expense of competitive traits, a mechanism that gives rise to clear functional biogeographic patterns across continents (80). These physiological traits also underpin the nutrient processing rates of microbes because stress-tolerance traits that are abundant in cold or dry regions are expressed at the expense of fast decomposition rates (75). These biogeographic patterns in functional trait expression can provide fundamental insights into the variation in SOM turnover rates across varying environmental gradients.

Biogeochemical modeling

Beyond providing insight into the structure of the biosphere, a comprehensive understanding of global soil communities will improve accuracy in global biogeochemical model predictions (7). Although microbial processes are still largely absent from global Earth system models, the past decade has revealed that incorporating even the simplest of microbial features into biogeochemical models can fundamentally alter long-term projections of SOM turnover and C storage. However, scaling such inference to the globe hinges on our ability to first enhance the confidence and precision in these projections, requiring improved global-scale understanding of the distribution and abundance of soil biota. Here, we focus on outlining the different approaches currently being used to model soil processes, and given the ongoing nature of such efforts, we provide a simplified overview of the different model structures that would be readily informed by global-scale soil ecological data.

Recent history of decomposition models

Despite the hypercomplexity of soil communities, their representation in many Earth system models is relatively simple, in part because of a lack of global-scale data, which is needed to build and parameterize more complex models. Organic matter decomposition in nearly all Earth system models thus relies on linear, first-order decay models (RothC, Yasso, Century, or similar approaches) (74, 75). In general, these models have three or four SOM “pools,” each corresponding to conceptual categories of organic material by fitting to decay curves observed in laboratory- and field-based experiments, which are adequate to fit decay curves observed in laboratory-based experiments. Empirical decomposition rates are then modified by environmental parameters such as temperature, moisture, and clay content, often leading to successful site-level modeling of SOM stocks.

At the Earth system scale, model-based predictions of C dynamics are characterized by large uncertainty, with a sixfold difference in predicted SOM stocks in the fifth Coupled Model Intercomparison Project (CMIP5) (81). Because first-order models lack explicit representation of the soil organisms that regulate the size of SOM pools, these models typically suggest that increased carbon inputs will lead to increased SOM formation. Yet, long-term

empirical studies demonstrate that concurrent changes in microbial populations can negate SOM accumulation under increased C inputs (82, 83). This phenomenon is more easily captured with nonlinear models without needing to invoke additional biogeochemical assumptions, some of which have weak empirical support (1). As such, explicitly representing different microbial pools that regulate the processing of this organic matter has emerged as a research focus in the past decade, with the potential to transform soil biogeochemical modeling. Nevertheless, the flexibility of nonlinear models comes at the expense of model simplicity because these more complex models demand more precise empirical data to avoid overfitting and ensure reliable long-term projections (84).

Representing microbes in models

Nonlinear models with explicit microbial pools are intended to represent the context-dependency of different microbial communities. In many ways, these models are similar to nonlinear consumer-resource models, which have a long history in ecology. Although a variety of modeling approaches exist for quantifying microbial C dynamics, most assume that decay rates depend on both SOM substrate and the catalyst pool concentrations, which are proportional to microbial biomass or enzyme activity (Fig. 5) (85). Many of these global-scale microbial models are motivated by Michaelis-Menten kinetics (86), in which microbial decomposition rates saturate as substrate availability or enzyme concentrations rise (known as “forward” and “reverse” kinetics, respectively) (87). Building on this framework, Earth system models are incorporating increasing levels of microbial complexity by explicitly representing various aspects of microbial physiology (such as carbon-use efficiency, substrate affinity, or microbial stoichiometry) that determine the rate of C mineralization or assimilation (88–90).

To further account for the complexity of the soil C cycle, Earth system models have begun to incorporate nonlinear microbial mediated SOM feedbacks, which can better capture variation in bulk soil functioning relative to single-pool, first-order decomposition frameworks (1, 91–97). For example, the latitudinal trend in microbial biomass was captured by Wang *et al.* (96) to improve estimates of global SOC dynamics. Yet even in such approaches, the microbial community is still typically represented as a single, homogeneous pool, largely because of a lack of broad-scale data linking compositional differences to functioning. Some local-scale models distinguish between different microbial components—such as active versus dormant biomass (98), fast versus slow cycling (99), and resource specialists versus generalists (100)—and these approaches appear to improve predictions of microbial C dynamics. By relating these distinct microbial pools to empirically defined functional groups, these models have the potential to better capture patterns in SOM formation across broad spatial scales. For example,

Sulman *et al.* (94) accounted for the strikingly different C turnover rates between AM and EM fungi by coupling mycorrhizal function with vegetative nitrogen demand (97). Along a gradient of slower cycling EM trees and faster cycling AM ecosystems, labile C additions stimulated the EM communities to decompose unprotected SOM pools and mine for N to a greater extent as compared with the AM communities (94). Thus, SOC losses were greater in the EM communities under elevated CO₂ conditions, highlighting how functional group information can help Earth system models represent complex environmental feedbacks. Extending such approaches to free-living microbial groups that reflect differences in organic matter processing rates is an important challenge.

The next generation—Representing continuous variation in traits

As model frameworks are developed to represent the functionally distinct impacts of different components of the soil community, the direct incorporation of microbial trait information represents the forefront of biogeochemical modeling (Fig. 5). Most developments in this field are occurring at the scale of process models rather than Earth system models. The most common method for incorporating microbial traits uses

taxonomic information to characterize specialist functions such as nitrogen fixation, nitrate reduction, sulfate reduction, methanogenesis, and methanotrophy (101). For example, the N cycle is relatively tractable because the thermodynamic geochemical reaction pathways and the microbial taxa that perform them are well described (102, 103). There are examples with other microbial functional groups—notably, separation of iron and sulfate reducers and acetogenic and hydrogenotrophic methanogens (104, 105)—but there remain sparse empirical data to parametrize or test these models. Increasingly, studies are using a mixture of -omics approach and traditional trait-based assays to quantify how aggregate-level traits such as functional gene expression, carbon use efficiency, and enzyme production vary in response to changing environmental conditions (1, 106–109). By combining these experimental data with theoretical and empirical information about microbial physiology, trait-based microbial models are beginning to provide tangible predictions of how microbial-mediated ecosystem processes, such as decomposition or respiration, vary through time and space (90, 110, 111).

As data on direct individual-level trait patterns becomes available at the global scale, we will be able to represent important new mechanisms

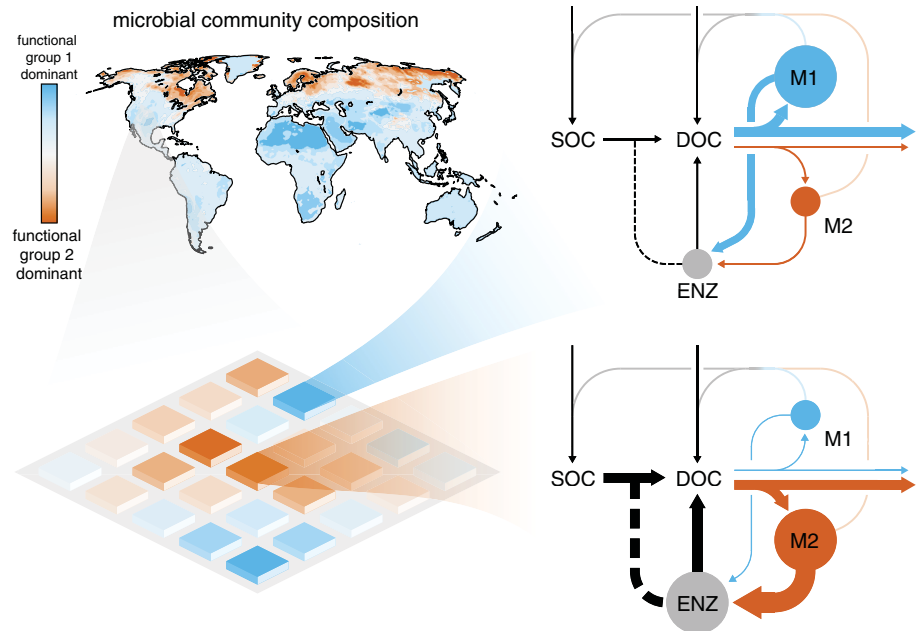


Fig. 5. Representing functional groups in spatially explicit biogeochemical models. In this conceptual figure, we illustrate how global-scale functional information can be used to more accurately model the different roles of soil organisms in governing biogeochemical processes. In this example, a global map of the relative abundance of two functional groups of microbes (red versus blue) is used to parameterize a spatially explicit model of soil carbon turnover. At each location, the functional composition determines the relative sizes of two microbial biomass pools (for example, AM versus EM fungi) that differ in their allocation to different enzymes (ENZ). Incorporating functional data allows a single model to predict microbe-driven differences in the breakdown of soil organic matter (SOM) into dissolved organic carbon (DOC) and in overall soil respiration (rightmost arrows).

that govern global SOM dynamics. However, somewhat paradoxically, the incorporation of microbial processes into biochemical models can also increase uncertainty in model estimates owing to corresponding uncertainty in the microbial derived model parameters (84). As we increase the complexity of models, there will always be a trade-off between model flexibility and simplicity. Until we can be sure that new ecological mechanisms are necessary to capture a significant proportion of unexplained variation, increasing model complexity is always likely to compromise overall performance. Especially when these mechanisms have limited empirical support at the global scale, this extra complexity can increase the risk of overparameterization and misrepresentation of complex processes, which can seriously hinder model performance. This fact highlights the urgent need for model sensitivity analyses, to identify the level of ecological information that is necessary to maximize model performance.

Pathways forward

With an ever-expanding technological toolkit, the field of soil ecology continues to uncover mechanisms that govern the biodiversity and functioning of soil communities. But placing these local findings into a broader context and understanding the relevance of these mechanisms require that we build on recent advances to characterize the global biogeography of soil communities. Only when we know the abundance and metabolic activity of those organisms in any location can we truly realize the relevance of any process. After decades of pioneering soil ecological research, we now have the ecological data and statistical tools to generate a global perspective of this integral, but previously uncharacterized, component of the terrestrial biosphere. Ultimately, in order to build a consistent global perspective, the major challenge for soil ecologists will be to find simplicity and generality in this highly complex belowground community. As we move through the levels of ecological detail (biomass, functional groups, taxa, and traits), we gain mechanistic insight at the expense of predictive clarity. With so many studies operating at the level of taxonomic and trait-based detail, this Review emphasizes the need to also step back to characterize the global biomass patterns of the major functional groups of soil organisms. Not only can this biomass information explain much of the variation in community-level functioning, it is also necessary to scale and contextualize the relative abundance of information collected in more detailed taxonomic and trait-based analyses. Much of the contemporary theory in soil ecology is built on the compartmentalization of different energy channels, which can improve our understanding of ecosystem stability and organic matter turnover (56, 57). Identifying the relative abundance of the major organismal groups (such as fungi, bacteria, animals, protists, and archaea), with distinct biogeochemical processing pathways and rates, can be the first step toward reflecting the relative contribution

of different energy pathways across global soils. Just as differences between major plant functional types (forests and grasslands) continue to improve our understanding of terrestrial ecosystems, it is likely that major differences in soil organisms can improve our understanding of terrestrial functioning across the globe. Once we have characterized these highest levels of soil community information, dividing these biomass pools into further functional groupings—which can be defined by using taxonomic or trait-based approaches—may then refine our insights into the functioning of ecosystems across the globe.

To find this generality across broad spatial scales, it is critical that we can see past the limitations that have traditionally obscured advances in soil ecology. Comparing soil community information across samples is challenging because different methods are often used to characterize different taxa. Even when using the same standardized methods to identify soil organisms (for example, metagenomic sequencing or phospholipid fatty acid extraction), differences in the efficiency of extraction, identification, or quantification of different groups can mean that entirely unbiased comparison is rarely possible (112). However, similar sampling limitations exist in the characterization of above-ground organisms but has not precluded the detection of broad-scale trends in plant biomass, diversity, and functional composition. As long as the identification of different groups is not consistently biased, these random sampling errors simply contribute to statistical noise, which can only be overcome with large sampling efforts. As we continue to increase the scale of our observations across wider environmental gradients, we will have a greater power to detect the true drivers of soil ecological patterns through the statistical noise. We do not need a detailed comparison of all species in every region. Instead, we need to identify which regions are statistically more likely to support different organisms across a wide biogeographic range.

From a biogeochemical modeling perspective, a major goal is to generate standardized modeling frameworks for the consistent representation of major ecological processes that regulate SOM turnover. To achieve this, a critical remaining challenge is that we do not yet know the appropriate level of ecological resolution that best captures the variation in soil community functioning. Although the incorporation of high-level microbial biomass appears to improve model performance (96), it remains unclear to what extent we should separate this biomass into the different functional or taxonomic groups to represent distinct mechanisms. For example, quantifying spatial patterns of specialist groups with distinct biogeochemical pathways (such as nitrogen fixers and methanogens) should be key to understanding broad-scale SOM dynamics (102, 103), whereas the importance of generalist pathways (such as N and C mineralization) may be more useful for capturing differences in processing rates, reflecting fast and slow cycling

energy pools (56, 57). As we divide these pools into more refined functional groups with different attributes, there will necessarily be a trade-off between capturing important new mechanisms and introducing unnecessary complexity that will compromise model performance. Model sensitivity analyses will be critical for identifying which level of ecological detail is optimal for improving predictive power without compromising model simplicity. These efforts can then guide empiricists to generate the quantitative global information at the ecological resolution that can have the greatest impact on model performance.

Conclusions

The vast majority of soil-dwelling species remain to be characterized, and this taxonomic deficit is likely greater than 90% (58). Combined with the immense fine-scale variability of soil communities, this makes it highly challenging to identify unifying patterns in the global distribution of soil-dwelling species. However, by expanding our horizons beyond local-scale analyses and focusing on broader organism groups that characterize community-level functioning, soil ecologists have begun to identify general patterns that provide a simplified perspective. By exploring the general patterns in soil organisms across thousands of locations, these efforts have begun to reveal that the global soil community is dominated by a manageable number of taxa (7, 65), with consistent global patterns of abundance (40, 42) and diversity (6, 8). As we expand this global perspective, every new level of global ecological information will enable us to ask increasingly complex questions about the fundamental organization of life on land. Shaped by complex mixtures of climate, edaphic, and topographic factors, as well as biotic interactions, each of these soil biogeographic patterns is unique and provides insights into the fundamental distribution and dynamics of terrestrial organic matter.

As the largest terrestrial repository of both biodiversity and carbon, the effective management of soil at a global scale is among our most powerful weapons in the fight against the combined threats of climate change and biodiversity loss (4). We are now at an exciting time because decades of pioneering local-scale analyses have provided the data and tools to characterize this integral component of the biosphere. As we strive to understand this global resource, we cannot continue to ask “whether” the identity of soil communities influences global biogeochemistry. Given the weight of evidence from the past decade, we must now continue to ask “how” global soil communities drive global biogeochemistry. Expanding our perspective of global soil communities will enable us to test critical hypotheses about the distribution of organic matter on land and its dynamics under future climate change scenarios. But ultimately, this emerging perspective of the most diverse and abundant community on land will provide insights into the fundamental organization of life on Earth.

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The global soil community and its influence on biogeochemistry

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Microbes' role in soil decomposition

Soils harbor a rich diversity of invertebrate and microbial life, which drives biogeochemical processes from local to global scales. Relating the biodiversity patterns of soil ecological communities to soil biogeochemistry remains an important challenge for ecologists and earth system modelers. Crowther *et al.* review the state of science relating soil organisms to biogeochemical processes, focusing particularly on the importance of microbial community variation on decomposition and turnover of soil organic matter. Although there is variation in soil communities across the globe, ecologists are beginning to identify general patterns that may contribute to predicting biogeochemical dynamics under future climate change.

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