

Soil carbon cycling proxies: Understanding their critical role in predicting climate change feedbacks

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Abstract

The complexity of processes and interactions that drive soil C dynamics necessitate the use of proxy variables to represent soil characteristics that cannot be directly measured (correlative proxies), or that aggregate information about multiple soil characteristics into one variable (integrative proxies). These proxies have proven useful for understanding the soil C cycle, which is highly variable in both space and time, and are now being used to make predictions of the fate and persistence of C under future climate scenarios. However, the C pools and processes that proxies represent must be thoughtfully considered in order to minimize uncertainties in empirical understanding. This is necessary to capture the full value of a proxy in model parameters and in model outcomes. Here, we provide specific examples of proxy variables that could improve decision-making, and modeling skill, while also encouraging continued work on their mechanistic underpinnings. We explore the use of three common soil proxies used to study soil C cycling: metabolic quotient, clay content, and physical fractionation. We also consider how emerging data types, such as genome-sequence data, can serve as proxies for microbial community activities. By examining some broad assumptions in soil C cycling with the proxies already in use, we can develop new hypotheses and specify criteria for new and needed proxies.

KEYWORDS

clay, CUE, models, soil carbon, soil organic matter

1 | INTRODUCTION

To understand and predict how the carbon (C) cycle responds to environmental changes, the underlying ecosystem dynamics that determine net C balance need to be determined. Current efforts to

address this need depend on the exchange of knowledge between empirical research and simulation models. While net primary productivity can be readily measured, and modeled with well-established physical and chemical constraints, the soil C cycle is highly complex and driven by a vast suite of environmental, physical, and biological

factors. Given this complexity, and the limitations to disentangling all the drivers of soil processes, how do we manage, measure, and predict climate change interactions with terrestrial ecosystems?

In the physical and biological sciences, relatively simple proxy variables are often used to substitute for more complex variables or processes. A proxy variable is a measurement of one physical quantity that is used in the place of a different quantity that would be too difficult or expensive to measure directly. Proxies are used extensively in the earth sciences, particularly in attempts to reconstruct past climate, where direct measurements are impossible. For example, oxygen isotopes in benthic foraminifera are commonly used to infer past geologic events such as relative sea-level rise and deep water temperature changes (e.g., Waelbroeck et al., 2002). Both tree ring chronologies (D'arrigo, Wilson, Liepert, & Cherubini, 2008) and marine sediment records (Henderson, 2002) have been used to infer past climate as well. Ljungqvist et al. (2016) used multiple hydroclimate proxy data from ice cores, marine sediments, lake sediments, speleothems, tree rings, and historical documentary data as indicators of hydrological status in order to analyze the spatiotemporal patterns of hydrological anomalies in Northern Hemisphere land areas over the past 12 centuries. These applications of proxies have proven particularly powerful in reconstructing consistent and continuous paleoclimate records, and thus have been well researched and vetted.

Ecologists and biogeochemists, however, have typically been less explicit about using proxies in research, and instead have used proxies to offset the often complex and detailed measurements for processes of interest. Proxies have been used in biogeochemistry and ecology for several different reasons: (1) when direct measurements are not possible, for example, for historic events (similar to paleoclimatology); (2) when direct measurements are not practical due to time, difficulty, and/or cost constraints; (3) when a first-order screening of a complex process can help eliminate measurements or refine hypotheses. For example, an extensive allometry literature uses tree diameter as a proxy for quantities such as biomass and canopy leaf area (Niklas, 1994). In forestry, "site index" is a proxy based on average tree height, an easily measured variable that was developed over a century ago to quantify overall site productivity (Skovsgaard & Vanclay, 2008). The site index proxy is valuable because it encapsulates soil and climate conditions that can be highly variable and are not easily measured. Remotely sensed metrics such as normalized difference vegetation index have been shown to be correlated with plant productivity and biomass, as well as to less-obviously related variables such as herbivore and carnivore species distribution and dynamics (Pettorelli et al., 2011). In soil science, clay content is widely used by both experimentalists (Bernoux, Cerri, Arrouays, Jolivet, & Volkoff, 1998) and modelers (Li, Frolking, & Harriss, 1994) as a proxy for properties such as bulk density, water holding capacity, and soil organic matter. One problem with soil proxies is that they are often based on features that change very slowly (e.g., clay content), so their change in response to a transient disturbance is difficult to ascribe mechanistically. Alternative types of proxies are transient measurements (e.g., NPP) that may be difficult to scale through time and space (Bond-Lamberty et al., 2014).

We analyze the use of proxies in the field of soil C dynamics, and suggest ways that the scientific community can use proxies most effectively. We classify types of proxies for the purposes of environmental research and briefly review the historical use of proxies in soil science. To frame the power and limits of proxies, we focus on soil organic matter (SOM) pools that are critical to ecosystem C cycling, exploring three proxies that have been used to capture different aspects of SOM dynamics with different degrees of success, and discuss potential future proxies. Finally, we address potential implications of SOM itself as a proxy for ecosystem services and its use in management and decision-making.

2 | PROXIES AND THEIR HISTORY IN SCIENCE AND LAND MANAGEMENT

For ecological research it is useful to classify proxies into two categories: correlative representations (proxies that reveal insights about covarying factors) and integrative frameworks (summarizing potential pathways and system control points; Figure 1). While both are useful, each has limits on how the data can be interpreted. The thoughtful use of proxies can lead to new hypotheses and experiments to identify causative relationships; the unconsidered use of proxies may result in overweighting of correlations to explain research results and the misrepresentation of mechanisms.

Trade-offs in ease of measurement and predictive value drive the selection and use of proxies in analyses at any spatial scale; an example of this with respect to annual soil respiration is visualized in Figure 2. Some potential proxies of soil respiration are easy to measure but have low explanatory power; some have high explanatory power but are difficult to measure; and a few combine good explanatory power with reasonable ease of measurement. For example, leaf area index (LAI) is a relatively easy, rapid measurement that can inform new hypotheses about terrestrial C fluxes. However, on its own LAI is a poor predictor of soil respiration. In contrast, directly measuring annual heterotrophic respiration is labor-intensive and/or subject to large uncertainties, although it has significant predictive power in this example. We argue that improved understanding of complex systems will follow by formally identifying data types, that is, potential proxies, which are both relatively easy to collect and also useful predictors.

Agriculturalists and other land managers, whose livelihood depends on the productive capacity of soil, have frequently used proxies to assess management effects on soils. For example, total soil organic C is a robust proxy for the potential of processes such as aggregate formation, water retention, or nutrient turnover to support production (Grandy, Porter, & Erich, 2002), although it is an imperfect representation of all the factors that regulate yields, such as precipitation, temperature, and management inputs. In addition, since the Dust Bowl, soil conservation practice has been embodied in concepts that are themselves proxies. For example, the concept of "soil tilth" or "quality" has been used for decades to describe the integrated physical condition of the soil (Karlen, Sadler, & Busscher,

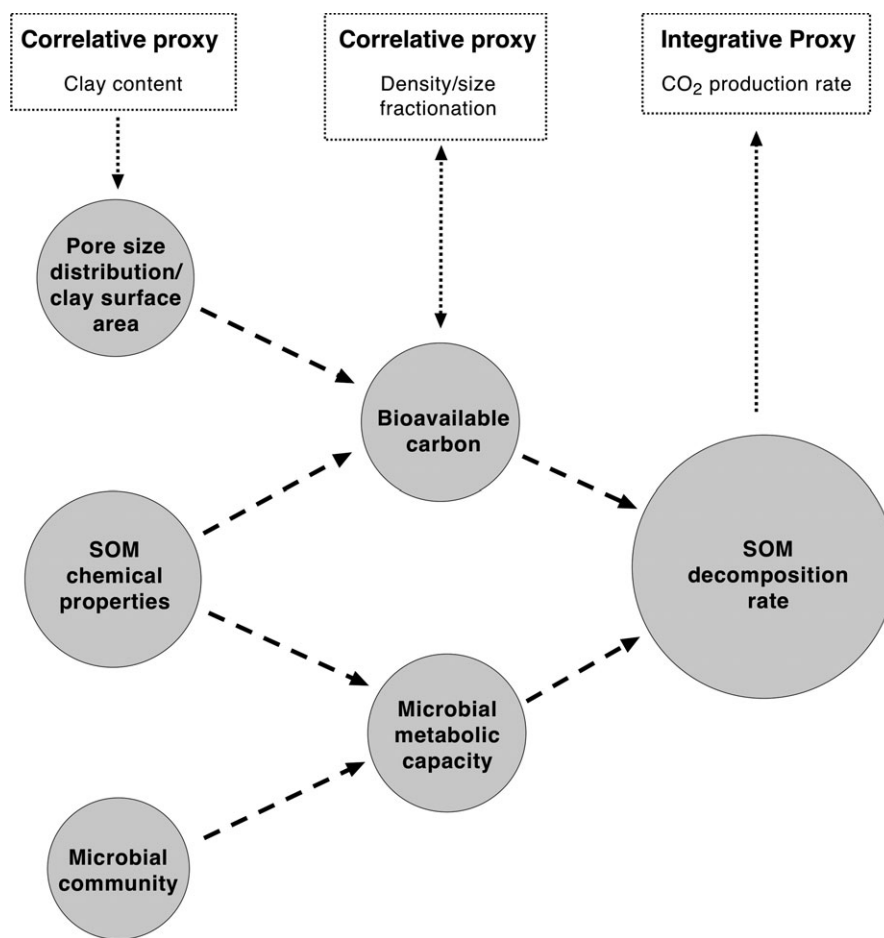


FIGURE 1 Proxies can be considered correlative or integrative. Here, we show a simplified network of interactions between processes and related proxies relevant to the examples presented in this paper. Correlative proxies may not be directly causative of the process/feature of interest, however, the relationship between a proxy and the feature of interest can suggest new hypotheses and refine other analyses needed. Integrative processes are measurements that reflect a collection of features, and how they work as a system. These can be valuable for high-level inferences, but extracting mechanistic understanding from integrative proxies may be difficult

1990), and is a proxy for specific measurements of aggregate structure, water infiltration, and porosity.

Modelers, empirical scientists, and practitioners all use proxies, yet, it is important to note that their specific goals, and thus the types of proxies they may depend upon, frequently diverge. Empiricists typically want to understand underlying mechanisms, and thus tend toward reductionist approaches, using proxies only when absolutely necessary. Modelers recognize the necessity of proxies for tractable models (i.e., models that are parameterizable and characterized by only as much complexity as is necessary). Land managers are even less likely to be interested in the details and fidelity of representation, and are typically interested in highly integrative and immediately useful proxies. These divergent goals result in inconsistent use and acceptance of proxies in environmental, soil, and climate change sciences and management.

3 | OPERATIONAL MEASUREMENTS AND PROXIES IN SOIL ORGANIC MATTER RESEARCH

The formation, transformation, and persistence of SOM are difficult to study and predict. SOM is chemically diverse, spatially heterogeneous, and its fate is driven by a suite of chemical reactions and

physical interactions that occur in soil microsites. We lack the sensitivity and resolution to capture these changes in real time, and it is only over significant time scales (e.g., decades) that we detect the overall direction of change to the abundance and nature of SOM. A further difficulty is separating inherent characteristics of SOM from the environmental factors influencing its cycling (Davidson, 2015; Schmidt et al., 2011). Given the complex drivers of SOM dynamics, scientists rely heavily on proxies (Table 1), although direct measurements of SOM stability do exist. Perhaps the most direct measure we have of SOM stability is its radiocarbon signature. Radiocarbon has been used to estimate SOM mean residence time in simple steady-state models (Gaudinski, Trumbore, Davidson, & Zheng, 2000), as well as highly complex models which take into account variation in inputs and decay over time (Sierra, Müller, & Trumbore, 2012), and can provide significant constraints on model formulation and results (He et al., 2016). Other direct measurements include the resistance of SOM to microbial degradation in laboratory incubations, or to hydrolysis by strong acids.

Despite these direct measures of SOM stability, many other soil measurements are proxies rather than direct measurements. In order to illuminate common issues with widely used proxies, we discuss in depth three that are commonly used in different areas of soil science. These relate to microbial dynamics and soil C cycling (*Metabolic quotient*), soil texture and physical properties that control SOM

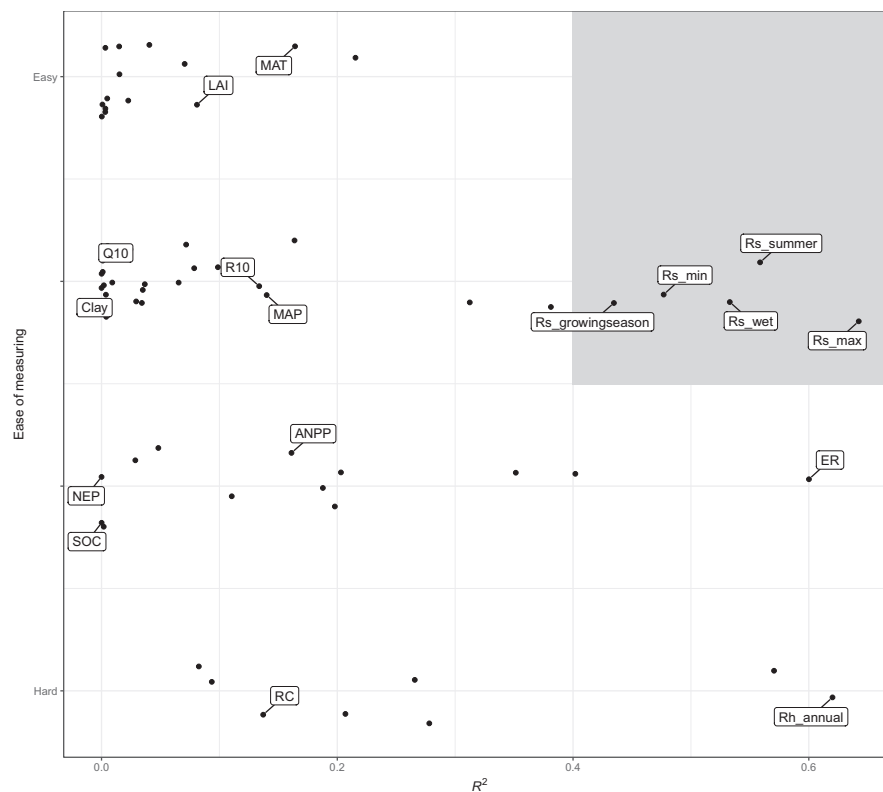


FIGURE 2 The balance between ease of measurement and the predictive power of a measurement often drives the selection of analyses for a given experiment. This plot combines a *quantitative* measure (how well various ancillary data or proxies are correlated with total annual soil respiration, x axis) with a *qualitative* one (roughly how easy each proxy is to measure as judged by the authors, y axis). For clarity, only a subset of points is labeled. For example, some potential proxies of soil respiration are easy to measure but have low explanatory power (e.g., leaf area index, LAI, and mean annual temperature, MAT, in upper left), while some have high explanatory power but are difficult to measure (e.g., annual heterotrophic respiration, Rh_annual, in lower right). Five variables labeled in upper right combined good explanatory power with reasonable ease of measurement: summer and growing season soil respiration (Rs_summer and Rs_growingseason), minimum and maximum annual soil respiration (Rs_min and Rs_max), and tropical wet season soil respiration (Rs_wet). Other labeled points on the graph include ecosystem respiration (ER), aboveground net primary production (ANPP), net ecosystem production (NEP), soil organic carbon (SOC), mean annual precipitation (MAP), respiration at 10 C (R10), clay content (Clay), and root contribution to respiration (RC). By explicitly considering this value assessment, proxies can be identified that serve both the research goals while staying within time- and cost constraints. Data are from the SRDB database (Bond-Lamberty & Thomson, 2010)

stabilization (*Clay content*), and bioavailability of SOM (*Soil physical fractions*).

3.1 | Metabolic quotient as a proxy for CUE

The metabolic quotient is the ratio of respiration to microbial biomass C, and has been broadly used to describe the constraints placed on soil microbes by substrate quality (Wardle & Ghani, 1995). Similarly, C utilization efficiency (CUE), the ratio of microbial biomass C to microbial biomass plus CO₂-C, is used to describe the efficiency of organic matter conversion into microbial products relative to CO₂ released via respiration (Sinsabaugh, Manzoni, Moorhead, & Richter, 2013). Although these indices are used near-interchangeably based on their close relationship with one another (Dilly & Munch, 1996), they derive from different measurements. Recent studies provide a rigorous review of these indices, and focus on the constraints posed by the ecosystem and fundamental thermodynamics on microbial growth, the limitations of available research tools for measuring

microbial growth, and how these features can be used to represent microbial growth in ecological models (Geyer, Kyker-Snowman, Grandy, & Frey, 2016; Sinsabaugh et al., 2013).

Metabolic quotients typically integrate a number of different properties: substrate quality, metabolic rates, and decomposition products. Metabolic quotients correlate weakly but significantly with microbial stoichiometries such as C:P (Hartman & Richardson, 2013), a relationship that was consistent across a wide range of soils across the globe. However, the stronger association ($r^2 = 0.44$) was with the availability of inorganic phosphorus, attributed to a stimulation of C cycling by P, even in N-limited soils (Hartman & Richardson, 2013). When well defined, such correlations can be useful surrogates for microbial activities, but as noted, these are still proxies, and the soil properties they encompass are complex integrative processes with many controlling variables that are difficult to resolve.

Similarly, CUE emerges from a complex suite of integrative processes (Geyer et al., 2016). Empirically, CUE has been used to represent a number of soil traits, and itself, has been inferred from fungal:

bacterial ratio (Thiet, Frey, & Six, 2006) and net microbial growth (Blagodatskaya, Blagodatsky, Anderson, & Kuzyakov, 2014). CUE can be a proxy used in lieu of measuring community structure with respect to biomass or activity ratios (Bailey, Smith, & Bolton, 2002), or microbial uptake and metabolism of substrates (Blagodatskaya et al., 2014); such proxies are used to identify high-level changes in the microbial community. Relating CUE to shifts in F:B (Thiet et al., 2006) or growth kinetics actually targets a high-level physiological change in the soil. In such cases, it is the outcome (net C emissions) that is being explained by an integrative proxy, CUE. We can then use CUE and the assumption that fungi and bacteria fundamentally differ in their metabolism of C (Wang et al., 2012) to represent microbial community shifts in ecological models. Similarly, we can use the assumption that balanced growth in a soil comes from a suite of microbial communities for which all catabolic and anabolic processes are balanced.

From a modeling perspective CUE is frequently defined as the ratio of uptake C to amount of C incorporated into biomass and is subtly different from the experimental CUE mentioned above (Manzoni, Taylor, Richter, Porporato, & Agren, 2012). It is important to note that there can be other biological CO₂ emissions in many of these models including basal or maintenance respiration, and adaptive costs (i.e., thermophilic metabolism, extracellular enzyme production, substrate-specific consumption). Thus, modeling CUE is not necessarily directly comparable to the empirically measured CUE described above. This is an excellent example of modelers and experimentalists using the same name to refer to similar, but not identical, proxies; care must be taken to ensure that the experiments (both empirical and modeling) are comparable.

3.2 | Clay content as a proxy for mineralogy and physicochemical properties

Soil texture, specifically clay content (% clay), is widely used as both a correlative and integrative proxy for soil physical properties in the context of ecosystem models (Sulman, Phillips, Oishi, Shevliakova, & Pacala, 2014; Wieder, Grandy, Kallenbach, & Bonan, 2014). Typically, % clay is estimated by separating soil mineral particles by size and defining clay as the smallest particle size class, regardless of the mineral phases present. Soil properties inferred based on the % clay correlative proxy include hydrology-related properties such as porosity and pore size distribution, and parameters related to the formation and mean residence time of mineral-associated and microaggregated organic matter. As an integrative proxy, clay accumulation is the direct result of mineral weathering occurring over time, and therefore soils with high clay contents can reflect the soil-forming factors over time and are presumed to have properties consistent with older, more weathered soils. Increases in soil clay content across chronosequences have shown correlations with mean annual soil temperature and the clay content of the parent material (Bockheim, 1980), indicating that clay content may additionally be accounting for some SOM variance associated with geology and climate.

Clay content is favored as a proxy for larger scale, more generalized models (Lawrence & Slater, 2008; Milly et al., 2014; Sulman et al., 2014; Wieder, Grandy, Kallenbach, Taylor, & Bonan, 2015) due to the ease of its measurement and the availability of data at appropriate spatial scales consistent with the predictions desired—important criteria for an effective proxy. The analysis of specific mineralogy is time consuming, requires specialized equipment, and produces results that can be challenging to interpret. Similarly, the analysis of specific surface area is both difficult to perform and complex to interpret, and aggregate formation can confound the relationship between mineralogy, specific surface area, and C stabilization in soils (e.g., Fernández-Ugalde et al., 2016). Thus, regional-scale analyses of C sequestration (e.g., Jobbágy & Jackson, 2000), would be impossible without the simple proxy of % clay, which, through various combinations of the correlations above, can exhibit significant relationships with soil C stabilization for many soils (Balabane & Plante, 2004; Jobbágy & Jackson, 2000; Kirchmann, Haberhauer, Kandeler, Sessitsch, & Gerzabek, 2004; Wiesmeier et al., 2015).

Percent clay may, however, fail as an effective proxy for key soil properties affecting C sequestration, due to the widely ranging surface chemistry and surface area of these different mineral phases. Simple clay percentages do not capture variation in mineral composition. This is important as extensive research has confirmed the importance of mineral composition in C sequestration in soils, including the specific mineral phases present and their relative abundance (Kramer, Sanderman, Chadwick, Chorover, & Vitousek, 2012; Lawrence, Harden, Xu, Schulz, & Trumbore, 2015; Rasmussen, Torn, & Southard, 2005). The critical role of specific surface area and chemistry of minerals, particularly that of iron and aluminum oxyhydroxide species, has also been recognized (Kaiser & Guggenberger, 2003; Spielvogel, Prietzel, & Kögel-Knabner, 2008) although see (Vogel et al., 2015). For example, an Inceptisol and an Andisol from neighboring sites may have similar total clay contents, but vastly different SOM contents due differences in specific clay minerals: allophane and ferrihydrite in the Andisol have a higher SOM sorption capacity compared to the mica clay phases found in the Inceptisol (Parfitt, Theng, Whitton, & Shepherd, 1997). Clay can also be a poor predictor of specific surface area (Farrar & Coleman, 1967; Ross, 1978) and therefore does a poor conceptual job of representing factors relating to available sorptive area. Specific surface area values (post-SOM removal) may be a more effective proxy for variation in soil mineralogical properties such as shrink-swell potential (Ross, 1978), cation exchange capacity (Farrar & Coleman, 1967), and availability of SOM sorption sites (Parfitt et al., 1997).

Clay content is thus a powerful integrative proxy because it is intimately associated with both the conditions that shaped the soil, and the current physicochemical conditions in the soil. However, the use of clay content as a proxy variable in mechanistic models may be unwise, since clay content is not directly linked to the surface area or reactivity of different minerals. Therefore, model development and application studies should consider whether % clay is being used as a correlative or integrative proxy, and recognize the

potential mismatch between the effective scales of the model and the proxy.

3.3 | Physical soil C fractions as proxies for bioavailability

Recent studies have suggested that the vulnerability of soil organic matter to microbial decomposition is largely a function of OM accessibility within the soil matrix and interactions between organic compounds and mineral surfaces (Dungait et al., 2012; Kleber et al., 2011; Schmidt et al., 2011). Although these factors interact with organic matter properties to create a continuum of SOM turnover times, empiricists typically separate SOM into categories of pools with different turnover times and functions. Likewise, widely used soil biogeochemical models such as the CENTURY family of models define SOM pools primarily based on turnover rates ranging from seasonal to millennial time scales (Kelly et al., 2000). While these rate-defined pools facilitate the precise modeling of CO₂ production and changes in total C stocks over time, they represent combinations of SOM fractions stabilized through different chemical and physical processes (Parton, 1996) and can be difficult to relate directly to physically measurable soil fractions, leading to widespread use of proxies representing soil carbon fractions with varying stabilities.

Soil organic matter scientists have studied for decades how to connect SOM pools with different turnover times to physically measurable soil fractions (e.g., Christensen, 1996; Motavalli, Palm, Parton, Elliott, & Frey, 1994; Skjemstad, Spouncer, Cowie, & Swift, 2004; Sohi et al., 2001; Stewart, Plante, Paustian, Conant, & Six, 2008), with the majority of recent analyses using size and/or density fractionation. For example, a nest of sieves can be used to separate soil into different aggregate size classes, which can be used as a proxy for SOM pools with different degrees of physical protection. Alternately, a high-density liquid can be used to separate soil into a light fraction composed of unprotected organic matter and heavier or occluded fractions composed of organic matter trapped in aggregates or bonded onto mineral particles. Within small soil aggregates, a portion of organic matter can be sequestered within pores too small for microbes or their enzymes to access (Bailey, Smith, Tfaily, Fansler, & Bond-Lamberty, 2017; Six, Conant, Paul, & Paustian, 2002).

Recently, a new cohort of soil biogeochemical models has attempted to use a more mechanistic approach to simulating SOM formation and decomposition by explicitly representing microbial dynamics and physically defined, mineral-associated organic matter pools (Sulman et al., 2014; Tang & Riley, 2015; Wang et al., 2015; Wieder et al., 2014). A key factor in this push for increased mechanistic representation has been the explicit simulation of mineral-associated and microaggregate organic matter pools, based on evidence suggesting that these fractions are physically protected from microbial decomposition through mineral–organic bonds and small pore spaces and correspond well with slow-turnover SOM pools (Baldock & Skjemstad, 2000; Schmidt et al., 2011; Six et al.,

TABLE 1 Commonly used proxies used to inform process understanding in soil carbon research

Key process	Mechanisms	Measurements	Model representations	Potential proxies	Proxy model reps	Uncertainty
Microbial C processing	Microbial physiology, enzyme activity, substrate quality/availability	¹³ C-labeled substrate incorporation into biomass and CO ₂	CUE*biomass_uptake	CUE, microbial allocation and stoichiometry, metabolic quotient/mass-specific respiration	Model depends on proxy; CUE can also refer to transfer rate (as a % of total C) between SOC pools	PP
Soil heterotrophic C flux	Microbial respiration	Change in biomass to CO ₂ flux	dCO ₂ = growth_respiration + basal_respiration	Proportion of total soil flux	dCO ₂ = k*SOC	PP
Microbial SOM access and aggregate formation	Physical protection of SOM	NMR, tomography, aggregate size fractions	dB/dt = S*uptake_rate-biomass_cost dS/dt = -dP/dt-S*uptake_rate dP/dt = SOC_protection_mech	% clay, bulk density, mineral composition	dC/dt = k(perc_clay)*SOC	KU
Direct microbial community interactions	Community dynamics, consortial processes, community shifts in response to perturbations	Omic	Track biomass pool size of various guilds; presence/absence of microbial capacity of soil	Multiple biomass pools (e.g., F:B, r:K); indicator traits; phylogeny	Representation of collective biomass pools; proportional to soil carbon quality pool size or rate kinetics in traditional model (proposed)	UU

Mechanisms, measurements, and models are noted, as well as the type of uncertainty in the measurement. Degrees of uncertainty: PP = poorly constrained parameters (we know these are important and why, but we do not have good measurements), KU = known unknowns (we know these are important and why, but do not the mechanism), UU = unknown unknowns (suspected to be important with hypothesized mechanisms, but we lack data and cannot stay how it works).

2002; Von Lutzow et al., 2006). However, the direct comparison of these correlative proxies with mechanistically defined model pools may be problematic if the methods do not correspond directly with model assumptions. For example, models may assume that mineral-associated organic matter has a single source (e.g., products of microbial turnover), a single turnover rate, and uniform accessibility to microbial decomposition (e.g., Sulman et al., 2014; Wieder et al., 2014), while actual mineral-associated soil fractions can contain a wide range of compounds with different chemical characteristics and levels of binding strength with mineral surfaces (Lehmann, Kinyangi, & Solomon, 2007), as well as variable SOM turnover times among physically defined pools (e.g., aggregate size classes, Baldock & Skjemstad, 2000; Von Lutzow et al., 2006).

In many cases, difficulties in modeling OM decomposition stem from uncertainties in the underlying physical processes. Organic matter sorption and desorption on mineral surfaces are poorly understood, so it can be difficult to relate these fractions to model-defined pools of C. Empirical studies have similarly used aggregate size as a proxy for another type of physical protection in both elevated CO₂ experiments (Jastrow et al., 2005; Lichter et al., 2008) and land use manipulations (Denef, Zotarelli, Boddey, & Six, 2007; McCarthy et al., 2008). Some modeling studies treat these fractions as measurements of protected and unprotected SOM pools that can be directly compared with models (e.g., Sulman et al., 2014), in spite of the clear differences in scale and mechanism. While it is important to remain cognizant of the complex factors underlying these OM protection mechanisms, the physical fractionation approach is a convenient correlative proxy that provides information about the distribution of C between fractions that differ in their accessibility to microbial decomposers. The current need for improved data-model fusion demands greater thought and communication of how properties of C accessibility are defined, measured, and translated into meaningful parameters that represent the persistence and vulnerability of soil organic C.

4 | NEW AND EMERGING PROXIES AND NEXT-GENERATION INSTRUMENTATION

The persistence and vulnerability of OM in soils is the product of both physical accessibility and microbial activities. This has prompted the recent surge in microbially explicit models of soil C dynamics. One of the major drivers of microbially explicit models is the desire to use “omics” data—biochemical datasets based on the nucleic acid, protein, or metabolite profiles associated with microbial communities—to inform soil decomposition models. Incorporating microbial parameters into Earth system models improves projections of global soil C stocks (Allison, Wallenstein, & Bradford, 2010; McGuire & Treseder, 2010; Wieder, Bonan, & Allison, 2013), and omics data are abundant and relatively easy to measure. Soil biogeochemistry models are generally mass balance models, breaking down soil C into discrete pools that exchange C over time via parameterized kinetics. From this standpoint, high-resolution data such as 16S and

metagenome sequences and high-resolution mass spectrometry C/metabolite profiles are only useful to the extent that they can either inform the sizes of these discrete C pools or the parameters of the transfer kinetics. Much of the field of omics is still heavily focused on phylogenetic diversity and has yet to make the nontrivial leap to function that is needed to incorporate these data into models.

Representing microbial species in models is impractical, and the large degree of apparent functional redundancy suggests that it is also not necessary. A key outstanding question is the identification of effective proxies for key functional traits within the wealth of omics-derived data. Higher level taxonomic groups, such as phyla and families, have been somewhat successful when considering certain key traits (Fierer et al., 2012; Placella, Brodie, & Firestone, 2012), with phylogenetic analyses supporting these proxies (Berlemont & Martiny, 2013; Martiny, Treseder, & Pusch, 2013). For example, Amend et al. (2016) recently determined that a phylogenetic trait-based framework could help predict soil microbial functional responses to climate change factors such as drought. Morrissey et al. (2016) found clustering of growth and glucose assimilation across the bacteria phylogeny, with signals similar in strength to those found for ecological traits in plants and animals. However, because many aspects of heterotrophic C physiology are shared across phyla, this simplification is not likely to be broadly successful in soils.

Microbial representation into two or three functional groups based on their ecological or physiological traits is a more common way of integrating molecular data into proxies (Allison, 2012). Fungi and bacteria are a common choice of functional groups, reflecting expected differences in physiology and food webs (De Vries et al., 2013; Rousk, Brookes, & Bååth, 2009). For example, Waring, Averill, and Hawkes (2013) determined that a two-pool representation of fungi and bacteria significantly improved on a single-pool “black-box” microbial model of soil C cycling (Schimel & Weintraub, 2003). However, recent studies have empirically demonstrated that the ratio of fungi to bacteria is not a useful predictor of soil C cycling, quality, or turnover because their C physiologies were more similar than expected (Rousk & Frey, 2015; Throckmorton, Bird, Dane, Firestone, & Horwath, 2012). An improved understanding of microbial functional group roles in C cycling will be needed to advance these approaches.

An alternative proxy relates to the large role that active and dormant functional groups play in community functional responses (Wang, Mayes, Gu, & Schadt, 2014; Wang et al., 2015). Under stressful conditions, many microbes enter a dormant state, increasing survival at the expense of reduced opportunity for resource acquisition and responsiveness to favorable epochs. Dormancy is widespread among microbial taxa, but relatively little is known about its effects on community-wide function and it has not been linked to ecosystem function (Jones & Lennon, 2010). Simple measures of microbial biomass and community structure added little explanatory power when soil respiration was considered in a recent meta-analysis (Graham et al., 2016), supporting the idea that better metrics are needed.

Another possibility is that higher level traits of the collected microbial community may serve as a more direct integrative proxy for soil function, particularly, when metabolic interactions among microbes are more important than individuals (Ponomarova & Patil, 2015). Omics data can generate community-level aggregate traits for both microbial metabolic potential and actual metabolic activity (Fierer, Barberán, & Laughlin, 2014); metagenomics, metatranscriptomics, metaproteomics, and metabolomics are direct measures of genes, expressed genes, and gene products that could reveal soil functions such as respiration, DOC, and microbial C. However, the wealth of high-resolution omics data currently being generated is not being translated into models for several reasons: the depth and quality of annotated genes for identification remains limited and statistical tools and computational capacity for interpreting this enormity of data are only in their infancy.

Ultimately, we are confident that omics data contain useful representations of microbial community function, but urge resolution of a number of issues to facilitate the use of omics data in the next generation of models: (1) The relationship between sequence-relative abundance and function is obscure. The use of internal standards in marine systems (Gifford, Sharma, Rinta-Kanto, & Moran, 2011) and soils (Smets et al., 2015) makes it possible to measure transcripts on a per gram soil or per cell basis, but the relationship between genes or transcripts and proteins can still vary widely (Schimel, 2016). (2) It is estimated that only a small subset of microbes are active at any one time (Jones & Lennon, 2010), and it is not clear whether omics can help us infer which ones. The microbial enzyme-mediated decomposition (MEND) model explicitly accounts for dormancy and better represents long-term trends in microbial biomass in the process (Wang et al., 2014). (3) Kinetic effects like temperature sensitivity are poorly captured by omics, although it is well established that temperature sensitivity of respiration and CUE can change independently of microbial community structure (Bradford et al., 2008; Frey, Drijber, Smith, & Melillo, 2008; Kallenbach, Grandy, Frey, & Diefendorf, 2015). Whether there are accompanying changes in gene content (as seen through metagenomics) or gene expression profiles (metatranscriptomics) remains to be seen.

5 | CONCLUSIONS

In summary, it is not currently tractable to measure, or even identify, all the driving factors of the complex soil C cycle, and how they interact with one another, and the Earth's physical system in the face of global climate change and increasing land use pressures. Our current measurement and predictive successes have been based on the coupling of specific measurements of the soil system with proxies for driving factors or internal dynamics (for example Q_{10}). The weaknesses of this approach are well known, and in some cases proxies have been used with little examination of their implications. We argue, however, that in our push for increasing mechanistic detail, driven by the flood of data from new imaging and genetic techniques, we risk losing sight of the value of correlative and integrative proxies

—variables that yield significant insight while being simpler, easier, or cheaper to measure. We provide specific examples of proxy variables that improve management decisions, adaptation choices, and modeling skill, while noting their mechanistic underpinnings. A closer examination of the current knowledge gaps in soil C cycling, and of the proxies we already use, may allow us to develop new hypotheses, and also specify criteria for new and needed proxies.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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