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Abstract

Soil organic matter (SOM) is an indicator of sustainable land management as stated in the global indicator framework of the United Nations Sustainable Development Goals (SDG Indicator 15.3.1). Improved forecasting of future changes in SOM is needed to support the development of more sustainable land management under a changing climate. Current models fail to reproduce historical trends in SOM both within and during transition between ecosystems. More realistic spatio-temporal SOM dynamics require inclusion of the recent paradigm shift from SOM recalcitrance as an “intrinsic property” to SOM persistence as an “ecosystem interaction”. We present a soil profile, or pedon-explicit, ecosystem-scale framework for data and models of SOM distribution and dynamics which can better represent land use transitions. Ecosystem-scale drivers are integrated with pedon-scale processes in two zones of influence. In the upper vegetation zone SOM is affected primarily by plant inputs (above and belowground), climate, microbial activity and physical aggregation and is prone to destabilization. In the lower mineral-matrix zone SOM inputs from the vegetation zone are controlled primarily by mineral-phase and chemical interactions, resulting in more favourable conditions for SOM persistence. Vegetation zone boundary conditions vary spatially at landscape scales (vegetation cover) and temporally at decadal scales (climate). Mineral-matrix zone boundary conditions vary spatially at landscape scales (geology, topography) but change only slowly. The thicknesses of the two zones and their transport connectivity are dynamic and affected by plant cover, land use practices, climate and feedbacks from current SOM stock in each layer. Using this framework we identify several areas where greater knowledge is needed to advance the emerging paradigm of SOM dynamics - improved representation of plant-derived carbon inputs, contributions of soil biota to SOM

storage and effect of dynamic soil structure on SOM storage – and how this can be combined with robust and efficient soil monitoring.

Introduction

Soils underpin many aspects of a functioning society including agriculture, food security, water security, climate regulation, flood risk management, urban development and human health. Soil organic matter (SOM), of which roughly 55-60 percent is soil organic carbon (SOC), is widely acknowledged as a critical property of healthy soils and necessary for delivery of many soil functions. This is recognised with the inclusion of SOM as one of the indicators of the United Nations Sustainable Development Goals 15 ‘Life on Land’ (UN General Assembly 2017).

On a global level, SOC is the largest terrestrial C pool, with an estimated 1,505 Pg-C in the upper 100 cm of global soils (Batjes, 2014). Deeper soils also contain significant amount of SOC and doubling the soil depth from 150 cm to 300 cm results in a 2/3 increase in estimated global SOC stocks from 1,778 Pg-C to 3,000 Pg-C (Lal, 2018). Even small changes in the global SOC pools can have large consequences for delivery of soil function. For example, the ‘4 per mille Soils for Food Security and Climate’ was launched at COP21 with a target of increasing global SOC stocks by 4‰ per year as a way of offsetting global anthropogenic greenhouse gas emissions (Minasny et al., 2017). While the utility of this target for setting policy is problematic in part because of substantial challenges in accurately quantifying soil C emissions (Paustian et al., 2016), the effect that a 4‰ change (gain or loss) in global SOC stock can have on the global atmospheric CO₂ budget is quite large and increases almost linearly with the depth considered (Figure 1).

Despite this global significance, current scientific understanding of SOM distributions and dynamics is limited (Green et al., 2019; Koven, Hugelius, Lawrence, & Wieder, 2017). Some large monitoring programmes have reported clear signals that topsoil SOM stock is changing in many ecosystems. Management of arable soils is depleting the SOM stocks (Chapman et al., 2013; Reynolds et al., 2013; Sleutel, De Neve, & Hofman, 2003; van Wesemael et al., 2010) and SOM increases have been recorded in woodlands at high northern latitudes in the last few decades (Tipping et al., 2017). Evidence indicates that conifer forest soils, recovering from the acid rain peak of 1950-1970, have been losing topsoil C (Lawrence et al., 2012; Oulehle, Hofmeister, Cudlin, & Hruska, 2006). Land use changes (LUCs) in low- to intensively-managed ecosystems have resulted in important SOM stock changes (Lal, 2018), with the clearest signal being consistent SOM loss on conversion to crop/arable land (Guo & Gifford, 2002; Woodall et al., 2015).

In contrast, systematic surveys tracking subsoil C stock changes are scarce (Chapman et al., 2013). It has been hypothesized that climate can destabilize (prime) older C in the subsoil (Bernal, Megonigal, & Mozdzer, 2017; Fontaine et al., 2007; Wordell-Dietrich, Don, & Helfrich, 2017). Comparison across land uses reveal that LUCs have the potential to affect both the top and subsoil SOM stocks (Guo & Gifford, 2002; Keith et al., 2015). In particular, plant rooting is considered a major driver of SOM distribution to depth: vertical redistribution of SOM stock to upper layers has been recorded in the conversion from grassland to woodland (Jobbagy & Jackson, 2000; Sheng et al., 2015; Woodall et al., 2015).

SOM models in current use, such as RothC and CENTURY (Jenkinson, 1990; Parton, Stewart, & Cole, 1988; J. Smith et al., 2010), focus on the chemical quality control of SOM turnover and assume that soil matrix, structure and biology don't change, while they are dynamic and

constantly evolving. As a result, there are critical limitations and uncertainties in our ability to project the likely rate, location and extent of SOM change in response to the complex interacting set of global drivers (Todd-Brown et al., 2013). Given the relative lack of SOM data in the subsoil, models might be useful tools for investigating and predicting SOM stock and change at depth. Widely used SOM models have been applied to the subsoil (Jenkinson & Coleman, 2008), but have mostly been calibrated and evaluated with topsoil data (Guenet et al., 2013; J. Smith et al., 2010; M. D. Smith, Knapp, & Collins, 2009). Recently, there has been a renewed interest for subsoil SOM and a few mechanistic models have attempted the simulation of its distribution at depth at quasi-steady state conditions (Ahrens, Braakhekke, Guggenberger, Schrumpf, & Reichstein, 2015; Braakhekke et al., 2011; Riley et al., 2014); the promising results suggest that more effort is needed to advance these depth-explicit models into dynamic simulations.

Here we consider the changing paradigm of SOM dynamics and suggest a conceptual approach for developing an ecosystem-scale SOM framework that incorporates simultaneously, and with appropriate feedback linkages, all major concepts of the new paradigm and aligns data and models for SOM distribution and dynamics at depth. We examine the opportunities and difficulties of linking data and models across spatial and temporal scales and suggest some starting points for collecting the critical knowledge needed in key areas to further advance understanding and modelling of SOM dynamics. We posit the key hypothesis that landscape-scale drivers determine the spatial locations and distributions of the soil profiles to be simulated and the dominant processes and properties in two zones of influence for each profile. SOM stock distribution at depth is an emergent property of the vertical extent of the two zones at any point in the landscape and their transport connectivity. The thicknesses of the two zones and their

transport connectivity are dynamic (time-variable) and affected by plant cover, land use practices, climate and feedbacks from the SOM stock in each layer.

Changing paradigm of SOM dynamics

The traditional paradigm of SOM dynamics was based originally on the assumption that linear-kinetic decomposition was a function of the chemical quality of the SOM, which was split in pools of different recalcitrance. Decomposition of litter inputs generated more complex polymeric substances or humic substances which were less susceptible to microbial decomposition and thus persisted in soils. While humification was not intrinsically depth-dependent, the lower quality of root litter and hydraulic transport of soluble humified substances from topsoil produced the “stable” SOM and high apparent ^{14}C ages observed at depth. This paradigm has been increasingly challenged in recent years, for example by experimental evidence that many “recalcitrant” compounds are easily degradable (Marschner et al., 2008) and humic substances are operational artefacts of the procedure used for humus extraction (Kleber et al., 2011; Lehmann & Kleber, 2015).

The new emerging view of SOM dynamics is based broadly around two concepts. The first is the concept of SOM persistence as an ecosystem property (Schmidt et al., 2011), which assumes that SOM decomposition occurs when available substrate and active decomposers are brought together under suitable environmental conditions (Dungait, Hopkins, Gregory, & Whitmore, 2012). The biotic and abiotic factors that control SOM decomposition can thus change across ecosystems, over time and between topsoil and subsoil (Rumpel & Kogel-Knabner, 2011). These factors include: a) the state of SOM, i.e. whether it is protected in aggregates, associated with

minerals or is partially decomposed litter (Six, Conant, Paul, & Paustian, 2002; von Luetzow et al., 2008); b) the abundance, diversity and functional traits of decomposer communities (Ekschmitt et al., 2008; Fierer, Bradford, & Jackson, 2007); and c) the availability of oxygen, water and nutrients (Davidson, Samanta, Caramori, & Savage, 2012; Jones et al., 2018).

The second concept concerns the linkages between litter decomposition and the sources of persistent SOM (Cotrufo, Wallenstein, Boot, Deneff, & Paul, 2013). Recent evidence indicates that microbial necromass and microbial metabolites are the primary constituents of stable SOM (Gleixner, 2013). Therefore, how microbes allocate assimilated C (either directly or following enzymatic processing) to growth, respiration and substrate acquisition is important, as this determines the pool of SOC available to be stabilized (Schimel & Schaeffer, 2012). A metric commonly used to measure this partitioning is the microbial carbon use efficiency (CUE) (Manzoni, Taylor, Richter, Porporato, & Agren, 2012). High CUE reflects efficient growth with low losses of CO₂ to the atmosphere and is mainly associated with decomposition of labile plant litter and root exudates. Low CUE, typically associated with less labile litter, indicates less efficient growth, more carbon lost through metabolism, and therefore lower potential for SOC sequestration.

Applying these two concepts to an ecosystem, we argue that two vertically-distinct, but internally aggregated, dynamic zones of influence can be identified and modelled for a soil profile or pedon: an upper zone dominated by the terrestrial plant community, and a lower zone dominated by the soil mineral matrix and geological setting (Figure 2). Zones of influence define spaces where one set of processes dominate relative to another; in ecology the concept has been used to denote when and how trophic interactions are controlled, e.g. predators (top-down) or resources (bottom-up) (Power, 1992). Recent evidence suggests that processes affecting SOM

turnover and persistence differ between the topsoil (O, A and E horizons) and the subsoil (B and C horizons) (L. L. Liu & Greaver, 2010). The proposed framework dynamically re-interprets the traditional concepts of pedogenesis and research on soil formation (Jenny, 1994) and is intended for both mineral and organo-mineral soils with particular reference to freely-draining soils.

Zones of Influence and their Dynamics

SOM dynamics in the upper vegetation zone of influence (VZI) (Figure 2a) are affected primarily by biosphere processes, including plant inputs (above and belowground), climate, microbial activity and physical aggregation. Biotic transformations between states/pools are rapid but prone to surface disturbances increasing risk of SOM loss. SOM dynamics in the VZI are strongly influenced by the plant traits (Jobbagy & Jackson, 2000; Manning et al., 2015) through inputs of root and leaf litter near the surface. The soil in the VZI (topsoil) is engineered by the effects of plant roots and characterized by multiple plant-microbe interactions, such as mycorrhizal symbiosis and microbial adaptation and competition with plants for resources (Morrien et al., 2017; Ramirez et al., 2018; van der Heijden, Martin, Selosse, & Sanders, 2015). These interactions, further influenced by soil type and soil management, generate a unique biophysical soil structure (Young & Crawford, 2004) that provides aeration, moisture, nutrients and energy, all of which enhance biotic activity in the VZI. SOM in the VZI is often found in a hierarchical system of aggregates (Tisdall & Oades, 1982), which determines soil porosity and bulk density. Macro-aggregates, held by temporary binding agents such as extracellular polymeric substances, mucilage and fungal hyphae, dominate the aggregate system and are sites of rapid SOM transformation and metabolization. The relatively small proportion of micro-aggregates (Totsche et al., 2018) preserves SOM in the long term through both physical entrapment (Six, Bossuyt, Degryze, & Denef, 2004) and the formation of mineral associated

organic matter (Cotrufo et al., 2015). Mineral surfaces are also ideal habitats for bacterial colonies (Or, Smets, Wraith, Dechesne, & Friedman, 2007), which poses an open question on the conditions for the long-term stability of mineral associated organic matter in the topsoil (Dungait et al., 2012). The VZI is highly responsive to climatic and land use drivers that enhance or diminish this self-organized, yet fragile, structure.

SOM dynamics in the lower mineral-matrix zone of influence (MMZI) are controlled primarily by geosphere processes, mineral-phase and chemical interactions with SOM inputs derived from the VZI (Figure 2a). Biotic transformations are fewer and disturbances less likely, thus producing more favourable conditions for SOM persistence. SOM protection by the mineral matrix becomes more important with increasing depth (Sollins, Homann, & Caldwell, 1996). The soils of the MMZI affect SOM dynamics through a variety of abiotic reactions. Soil texture, mineralogy, pH, cation exchange capacity and base cation concentrations affect the interactions of SOM with minerals (Angst et al., 2018; Rasmussen et al., 2018; Rumpel & Kogel-Knabner, 2011). SOM associated with secondary minerals and oxyhydroxides (Heinze et al., 2018) have relatively high physical stability, favourable conditions to preserve SOM. SOM in the MMZI is found primarily as LMW substrates, though charcoal, kerogen components, etc. can also be present. The microbial communities are fundamentally different from those in the surface layers within the same soil profile (Blume et al., 2002; Fierer, Schimel, & Holden, 2003; Fritze, Pietikainen, & Pennanen, 2000), which may be indicative of the different conditions encountered in subsoils (Salome, Nunan, Pouteau, Lerch, & Chenu, 2010). Nutrients are in shorter supply than in the topsoil, energy inputs in the form of radiation and accumulated heat are also greatly diminished, and mineral-induced inhibition can affect bacterial growth (Williams, 2017). In parts of the subsoil (cold spots) SOM substrates are too dilute to sustain significant microbial

metabolism (Heitkotter & Marschner, 2018), as in the deep ocean (Arrieta et al., 2015). SOC in the MMZI is usually more persistent than in topsoil, as reflected in higher apparent ^{14}C ages.

The establishment of the two zones of influence under undisturbed conditions is a long-term process of pedogenesis and ecosystem evolution involving drivers such as vegetation development and succession, community assembly processes for soil biota, bed rock weathering, climate and hydrology. All these dynamic processes result in unique combinations across the landscape of upper and lower boundary conditions and soil profiles (Peltzer et al., 2010). However, anthropogenic changes to the upper and/or lower boundary conditions can produce local or landscape re-distributions of the two zones of influence on decadal or shorter time-scales (Figure 3). LUC and land management drivers affect upper boundary conditions from field to regional spatial scales and from essentially instantaneous (e.g. soil ploughing) to decadal (e.g. tree planting and forest maturation) temporal scales. Climate affects upper boundary conditions through relatively fast local and regional events like floods, drought and rewetting, to decadal scale events such as global warming. Lower boundary conditions typically vary spatially at landscape scales (e.g. geologic parent material) and change more slowly over time (e.g. changes in groundwater composition). The vertical position of the VZI and MZI follows these changes in the upper/lower boundary conditions: the VZI depth can be shifted by sowing of novel crops or new grass varieties and planting of trees instead of herbaceous species (Chauvel et al., 1999); by plant acclimation and adaptation under climate change resulting in modifications of root structure and plant strategy (H. Y. Liu et al., 2018); and by extreme events that remove vegetation completely, such as land-slip, fire, flood or drought, and result in species compositional turnover and/or invasion of non-native species (Tamura & Tharayil, 2014).

Hence inclusion in data and model frameworks of a dynamic boundary (more or less diffuse) between the two zones of influence has the potential to integrate processes taking place at different spatial and temporal scales (O'Rourke, Angers, Holden, & McBratney, 2015) and to predict the time-frame of the SOM distribution changes in a given ecosystem (Figure 3). Indeed, the decadal-scale shift (up/down) of the boundary between the zones of influence is likely to affect the SOM distribution (destabilization/accumulation) at depth. Furthermore, the dynamics of the zone boundary can affect the biological, physical and chemical processes taking place at the microscale within each zone of influence over much shorter time scales: these microscale processes, which are usually considered as constant in most mechanistic SOM models, have in turn a feedback control on the SOM distribution at depth. Frameworks that link these multiple scales and feedbacks through a dynamic zone boundary, if properly constructed and queried, can offer the possibilities of estimating potential temporal and spatial scales of SOM behaviour not yet observed and of identifying data not yet collected that could provide reliable monitoring evidence for future soil security.

Zones of Influence Connectivity

The conceptual differentiation of biotic controls and rapid SOM turnover in the VZI versus abiotic controls and longer-term SOM stability in the MMZI suggests an interesting parallel with the 'zero-flux plane' concept of soil hydrology (Richards, 1954) (Figure 4b). In hydrology soil moisture content (SMC) is seen as controlled in two zones of influence. Evapotranspiration in the rooting zone above the zero-flux plane draws water upwards, defining the biologically active pool of soil moisture. Below the zero-flux plane water percolates downward into storage in groundwater. The zero-flux plane position varies in time and space not only as external drivers

vary (land use and climate), but also as the SMC itself varies in the upper and lower zones. This combination of external forcing and internal feedbacks produces a dynamic ‘SMC process boundary’ that is related to, but not defined by, soil taxonomic or pedological layers. Similarly, the boundary between the VZI and the MMZI can be seen as a dynamic ‘SOM process boundary’ separating zones of turnover and persistence of SOM (Figure 4a). Above the boundary in the biologically active zone, SOM turnover is rapid, mineralized CO₂ is lost upwards to the atmosphere, SOM persistence is low, and SOM stocks are maintained by continual SOM inputs from plants. Below the boundary in the MMZI, SOM turnover is low, SOM is lost primarily through downward leaching of DOM and SOM is persistent. The vertical position of the “SOM process boundary” is a function of external drivers (both vegetation above and geology below) and feedback from the dynamic SOM contents in each zone. The two zones of influence (VZI and MMZI) do not necessarily correspond to traditional organic and mineral soil horizons, rather they identify functional zones of predominantly biotic versus abiotic controls on the lability or persistence of SOM. Therefore, the distribution of SOM stock at depth is an emergent property of the relative extents of the two zones at any point in the landscape and the vertical position of the SOM process boundary.

Evidence of these two functional zones and their emergent effects can be found by looking at the typical vertical distribution of SOC for different global soil types (IUSS, 2006). Considering datasets from Batjes (1996) as independent, mean SOC stock data can be calculated incrementally from the reported depth intervals (Figure 4a). In general, SOC accumulates in topsoil, declines at intermediate depths, then increases again in subsoil. Histosols increase SOC through burial, while Podzols have abiotic mechanisms that enable SOC accumulation at depth without apparent constraint. Other predominantly mineral soils have a limited storage capacity

for SOC at depth. Xeresols and Gleysols represent end members for dry and wet mineral soils, respectively. Wet mineral soils subject to anoxia accumulate the most SOC at depth. Arenosols, Luvisols and Vertisols represent a gradient of soil texture from sand through loam to clay, with accumulated SOC increasing along that gradient. Solonchaks (poorly drained, saline, sodic soils) tend to show SOC decline with depth, likely due to the dominance of sodium in the lower soil profile. The SOC stock trends in Figure 4a emphasize the potential for physio-chemical conditions in the MMZI, such as soil texture and anoxia, in maintaining large SOC stocks with depth. Furthermore, these data suggest that SOM storage capacity in the MMZI depends also on the effectiveness of (macroscale) transfer of SOM between VZI and MMZI.

The concept of (microscale) connectivity is rapidly emerging and evolving in hydrology (van der Ploeg, Baartman, & Robinson, 2018) to explain soil moisture patterns and surface water flows (Western, Blöschl, & Grayson, 2001). In the context of SOM transport between zones of influence, (macroscale) connectivity expresses the likelihood that different SOM substrates released at various depths in the VZI will reach the MMZI. We consider the advective transport of dissolved organic matter (DOM) and soil mixing, i.e. through bioturbation, as the key mechanisms of SOM input to the MMZI (Campbell & Paustian, 2015; Keyvanshokouhi et al., 2019). While root inputs to soil, such as exudates and root litter, are a dominant source of the OM being found at depth (Angst et al., 2018), we limit direct plant inputs, by definition, to the VZI. The greatest activity of earthworms, which are prevalent in many soils, takes place in the topsoil where soil-feeding species are most abundant, and Muller-Landau & van Dorp (1996) suggested an entire topsoil profile would be homogenised in 5-20 years by bioturbation. Anecic earthworm species form deep burrows (often >1 m depth) thus likely acting as a link between the zones of influence. Lateral flows in soils, colluvial flows on hillslopes and soil erosion events

can lead to substantial SOM loss or burial over time in the subsoil (Borrelli et al., 2018). It has been suggested (Wang et al., 2017) that anthropogenic acceleration of soil erosion over the last 8,000 years has had the potential to offset up to half of previously recognized C emissions resulting from anthropogenic land cover change. However, though often overlooked, due to their long time-scales the processes of SOM physical removal from the landscape (i.e., erosion) are beyond the scope of this framework but would constitute the next step forward of it.

The potential of managing the upper zone to promote the SOM accumulation in the lower zone of influence has yet to be explored in its multiple implications. The (macroscale) connectivity between the two zones of influence is a feedback effect of the vertical distribution and SOM content of the VZI and MMZI. The SOM (macroscale) connectivity likely depends on the sources of SOM inputs to the VZI (leaves versus roots), SOM quality, climatic conditions and soil structure. For example, it is claimed that leaf-derived substrates are less likely to be metabolized at their source on the topsoil than root inputs (Churchland & Grayston, 2014; Sokol, Sanderman, & Bradford, 2018). However, leachates produced from the leaf litter must travel longer distances to reach the MMZI, which enhances likelihood of microbial encounters and mineralization during the transport to the MMZI, unless the microbial products get stabilized on the mineral surfaces or entrapped in the micro-aggregates eventually present in the VZI (K. Kaiser & Kalbitz, 2012). Also, plant litter has a more unfavourable stoichiometric ratio than microbially-processed SOM (Manzoni et al., 2012), which might alter or prevent its utilization by local microbial communities at depth (C. Kaiser, Franklin, Dieckmann, & Richter, 2014) and lower its affinity for most of the reactive mineral surfaces (Churchland & Grayston, 2014; Sokol et al., 2018). Therefore, inclusion of SOM input sources and SOM quality in models equipped with dynamic zones of influence might help to answer the question if root-derived SOM

dominates over leaf-derived SOM in the subsoil. These new models need also to include the effects of climate change on time and patterns of rainfall events and the effects of land management and climate change on soil structure, both of which having the potential to alter the hydraulic transport (infiltration and conductivity) of DOM to the subsoil.

Critical knowledge gaps

The conceptual framework presented here highlights areas of knowledge critical to further understanding and modelling of SOM dynamics. These areas could potentially be addressed by re-visiting existing long-term experimental and monitoring sites or by initiating new experimental and/or observational networks harnessing the latest technology (Hill, Chocholek, & Clement, 2017). Here we suggest three crucial areas of investigation.

Improved representation of plant-derived C inputs. The impact of vegetation on SOM inputs, turnover and persistence is not predictable solely from photosynthetic rates (Korner, 2011; Maire et al., 2015). Hence a classification of plant types is required that translates the environmental factors that shape the plant assemblage into impacts on the quantity and quality of the C entering the VZI (Cotrufo et al., 2013). Drivers such as land-use, climate and pollution might operate directly or be mediated by the plant assemblage in affecting the C inputs through, among others, water and nutrient availability, soil pH and toxicity, successional stage (Diaz et al., 2016; H. Y. Liu et al., 2018; Wright et al., 2004). For example, land-use change may destroy pre-existing biomass and introduce new sown species. On the other hand, elevated nitrogen deposition can drive a cascading series of effects through the existing plant community. The ensuing dynamics may be gradual up until the point when invasion or abrupt shift in dominance of *in situ* species

occurs. Modelling the timescales and dynamics of gradual or sudden change in above-ground assemblages is a major challenge but is required if the impacts of drivers on the trait composition of the plant assemblage and therefore on soil C inputs and vertical distribution of the two zones of influence is to be done with adequate realism. The crux is deciding what is adequate given the question and spatial and temporal resolution that is appropriate (M. D. Smith et al., 2009; Suding et al., 2008; Wardle, Bardgett, Callaway, & Van der Putten, 2011). To build the empirical knowledge base relating driver impacts to vegetation change to soil C inputs and zone boundary, a large-scale campaign to (re-)sample long-term surveillance sites and experiments should be undertaken where changes in vegetation have been of sufficient duration to potentially impact SOM formation but where the details of the temporal changes are known. This would alleviate reliance on substituting space for time (Ward et al., 2016). The partitioning of root litter and root exudates relative to leaf litter, which is critical for the estimation of the C inputs and depth of the VZI, should also be assessed in the context of how external drivers can change root architecture and nutrient/water acquisition strategy either directly or mediated by plant assemblage. Breakthrough experiments that couple multiple technologies, for example stable C isotope labelling of plant biomass and ground penetrating radar of root architecture (Molon, Boyce, & Arain, 2017), might shed lights on the controls and dynamics of belowground C inputs.

Contributions of soil biota to SOM storage. Research on soil biota has primarily focused on litter decomposition, particularly on manipulation of macrofauna and quantification of extracellular enzymes (Allison, 2005). Large-scale SOM dynamic models have rarely considered the explicit role of soil biota in mediating decomposition processes, except for the use of fixed values for CUE (Sinsabaugh et al., 2016), though it is known that microbial CUE varies with environmental conditions. Advances in molecular metagenomics techniques permit new understanding of how

soil change will affect both biodiversity and the functional potential of microbial communities (Jansson & Hofmockel, 2018). Whilst application of these technologies to global soils has revealed that different microbial taxa and genetic pathways operate across soil physico-chemical gradients (Fierer et al., 2012; Malik, Thomson, Whiteley, Bailey, & Griffiths, 2017), we still lack a systems level understanding connecting these metrics to soil process rates. While there have been a few studies examining whether altered microbial communities affect CUE (Kallenbach, Frey, & Grandy, 2016), the relationship of microbial community structure and the range of biochemical processes in operation to the quality and nature of the microbially derived SOM is largely unknown. There is also little evidence demonstrating the predictive utility of molecular microbial metrics with respect to SOM processing rates (microbial decomposition or post assimilatory processing). New experimental science is needed to identify the critical functional shifts in the soil biotic community performance across a range of environmental conditions in relation to both the rate and nature of decomposition products. Field experiments with labelled material has the potential to combine the study of plant, microbe and faunal ecophysiology. However, all of these potential field experiments should also include measures of abiotic processes in order to fully evaluate the relative importance of different biotic and abiotic controls leading to SOM stabilization.

Effect of dynamic soil structure on SOM storage. Soils are usually considered to be structurally static, but are constantly evolving structures that expand, contract, alter pore geometry, change density and modify connectivity, as a result of interacting chemical, physical and biological processes. Neglecting this ‘dynamic soil structure’ in mechanistic models omits important soil responses and feedbacks to climate and land use drivers (Robinson et al., 2019), consequently mis-estimating SOM dynamics as touched upon by Schmidt et al. (2011). Including dynamic

changes in soil structure, as triggered for example by climate change (Hirmas et al., 2018), will provide better representation of soil oxidation status and water holding characteristics, that are primary controls of microbial activity and SOM decomposition (Ghezzehei, Sulman, Arnold, Bogie, & Berhe, 2019). Soil structural dynamics, driven for example by LUC, affect SOM protection, microbial activity and abundance through changes in the number and size of aggregates (Sutton & Sposito, 2005), though important questions remain on the extent to which microbes and geochemical interactions contribute to the stabilization of micro-aggregates (Totsche et al., 2018). As flora and fauna mix and move soil, biopores, that are considered critical in delivering substrates to the subsoil (Athmann et al., 2017; Leinemann, Mikutta, Kalbitz, Schaarschmidt, & Guggenberger, 2016), are created and destroyed. In particular, the impacts of earthworms on soil structure and pore characteristics is likely to alter the transport of DOM (in addition to soil mixing), though these links require further quantification, and experiments, across different land uses (Reck et al., 2018).

Conclusions

- A new generation of ecosystem-scale SOM models and data are needed to improve our understanding of SOM stock changes at depth under land-use and climatic changes.
- We suggest that the soil profile or pedon can be partitioned into two zones of influence: an upper vegetation zone of influence (VZI), mainly controlled by plant traits, and a lower mineral matrix zone of influence (MMZI), mainly controlled by geochemical interactions.

- The vertical location of the SOM process boundary between the VZI and the MMZI is dynamic and responds to landscape-scale drivers and internal SOM feedbacks in each zone.
- In the VZI the SOC flux is mainly upwards to the atmosphere (SOC mineralization to CO₂), while in the MMZI the SOC flux is mainly downwards to deep soil storage (SOC stabilization and persistence), in analogy to the “zero flux plane” concept in hydrology.
- Vertical transport of SOC from the VZI to the MMZI storage depends on the SOC input sources, SOC quality, soil structure and hydraulics and is mainly due to soil mixing and DOC advection.
- Three critical knowledge gaps are identified that need the establishment of new experiments and application of new technology: improving the representation of plant-carbon inputs; contributions of soil biota to SOM storage; and effect of dynamic soil structure on SOM storage.

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Figure captions

Figure 1: Projected C emissions in 2100 (Fuss et al., 2014) compared to $\pm 4\%$ changes of the actual SOC stocks in 0-100 cm, 0-150 cm and 0-300 cm (Lal, 2018) and restoration of managed soils (P. Smith, 2016).

Figure 2: (a) Conceptual framework based on upper vegetation zone of ‘biosphere’ influence and lower mineral matrix zone of ‘geosphere’ influence; (b) Dynamics of the (SOM process) boundary between the two zones: the boundary can move up and down depending on landscape-scale drivers.

Figure 3: Integration of dynamic boundary between zones of influence with multiple-scale processes and feedbacks: changes in boundary conditions determine pedon-scale shift of the zones of influence which triggers microscale dynamic processes; all these effects have feedbacks on the ecosystem-scale distribution of SOM at depth.

Figure 4: Parallel between (a) the SOC distribution for different soil types and C-flux direction in the vegetation and mineral matrix zones of influence and (b) the hydrological concept of “zero-flux plane”; (c) mean and coefficient of variation (in brackets) of the SOC stocks underpinning (a), calculated at various depths considering datasets from Batjes (1996) as independent.







