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The Deep Soil Organic Carbon Response to Global Change

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deep soil organic carbon, global change, climate change, elevated CO_2, land use and land cover change

Abstract

Over 70% of soil organic carbon (SOC) is stored at a depth greater than 20 cm belowground. A portion of this deep SOC actively cycles on annual to decadal timescales and is sensitive to global change. However, deep SOC responses to global change likely differ from surface SOC responses because biotic controls on SOC cycling become weaker as mineral controls predominate with depth. Here, we synthesize the current information on deep SOC responses to the global change drivers of warming, shifting precipitation, elevated CO_2, and land use and land cover change. Most deep SOC responses can only be hypothesized because few global change studies measure deep soils, and even fewer global change experiments manipulate deep soils. We call on scientists to incorporate deep soils into their manipulations, measurements, and models so that the response of deep SOC can be accounted for in projections of nature-based climate solutions and terrestrial feedbacks to climate change.

1. INTRODUCTION

With the now decades-old realization that most of the world's soil organic carbon (SOC) is stored below 30 cm (Jobbágy & Jackson 2000) and evidence that deeper SOC is neither inert nor unreactive (Berhe et al. 2008), studying only topsoil is no longer sufficient to understand soil responses to global change. Deeper soils have the potential to be our ally or foe when it comes to mitigating climate change, depending on whether they can be managed to actively sequester SOC (Button et al. 2022) or whether global changes increase the decomposition of deep SOC, causing it to be respired to the atmosphere as CO_2 (Hicks Pries et al. 2017, Soong et al. 2021). The response of SOC to global change is currently one of the largest sources of uncertainty in Earth system models (Todd-Brown et al. 2013, Ito et al. 2020). To reduce this uncertainty and to inform the next generation of Earth system models, many of which explicitly include soil carbon and nutrient cycling with depth (Lawrence et al. 2019, Zhu et al. 2019), the response of deeper soils to changes must become a research priority. Neglecting to sample and study deep soils can lead to erroneous conclusions about the effect of global changes on soil carbon sequestration (Harrison et al. 2011).

Deep soil is a relative term. The thickness of soil is determined by soil age and its degree of weathering, which depends on climate and parent material (Hugelius et al. 2014). Generally, the warmer and wetter a climate, the deeper a soil has developed (Jenny 1994), with highly weathered Oxisols reaching depths of over 4 m (e.g., Mancini et al. 2021). However, a review of over 1,000 studies from four soil science journals found that the average depth of soil studied was only 27 cm across all studies and 23 cm for soil carbon studies (Yost & Hartemink 2020). Soil biology studies, a critical domain for understanding global change responses, are even more biased toward shallow horizons, with an average depth of 18 cm (Yost & Hartemink 2020). This lack of deeper soil biology investigations likely reflects the legacy of agricultural research—the highest concentrations of roots and nutrients are found in the A horizon or plow layer (Richter & Markewitz 1995)—and the increased difficulty and cost of sampling deep soils. In contrast, many soil geochemists would not consider 20 cm to be very deep; soil mineralogy and weathering studies regularly measure >100 cm of the soil profile (Yost & Hartemink 2020). At the same time, some shallow soils, like those in mountainous or recently glaciated regions, have high proximity to saprolite or regolith, which can have substantial SOC storage (Moreland et al. 2021) (see the sidebar titled The Importance of Weathered Bedrock) and biological activity (Richter & Markewitz 1995). In addition, deep soil can include buried surface horizons (Marin-Spiotta et al. 2014). In this review, we consider soil below the top 20 cm as deep, corresponding with the average depth of biological studies. However, because soils differ and not all studies define deep soil similarly, we specify the depth studied where possible.

Deep soils contain 68% of global SOC from 30 to 200 cm (Jackson et al. 2017). In mineral soils specifically, 1,263 Pg SOC is stored in the top two meters, with 59% found below 30 cm (Jackson et al. 2017). In permafrost and peatlands, deep soils store an even larger proportion of SOC, and significant SOC stores can extend many meters deep (Hugelius et al. 2014). Permafrost and peatlands store 466 and 427 Pg SOC in the top 200 cm, with 70% and 84% of that storage held beneath 30 cm, respectively (Jackson et al. 2017). Deeper still, another 201 Pg C may be stored in weathered bedrock globally (see the sidebar titled The Importance of Weathered Bedrock). Deep SOC cycles significantly more slowly than surface SOC—radiocarbon ages increase with depth, and ages of 1,000 to >10,000 years are common (Shi et al. 2020). Despite these typically long

THE IMPORTANCE OF WEATHERED BEDROCK

Whole-profile soil C stock accounting along a Sierra Nevada climosequence showed that warm and moist ecosystems that do not experience extreme drying or cold tend to have the deepest soil layers and store the largest amount of C in soil (O, A, and B horizons) and weathered bedrock (C and even Cr horizons) (Moreland et al. 2021). In some cases, the depth of the weathered bedrock beneath the soil can be up to 8 m, for a total soil depth of more than 10 m. However, in most soil C accounting, C stored in weathered bedrock is missing. Including weathered bedrock in C stock accounting could increase C stocks by 23–29%. Based on general assumptions about the distribution of bedrock globally, and the distribution of climates that are conducive for the weathering of deep soils, inclusion of C stored in weathered bedrock could increase the estimate of global soil C by approximately 201 Pg C (Moreland et al. 2021).

turnover times, deep SOC plays an active role in global carbon cycling (Berhe et al. 2008, Hicks Pries et al. 2017, Rumpel & Kögel-Knabner 2011).

Deep soils are affected by global change. Because temporal variability is often reduced in deep soils relative to surface soils, it is a common misconception that deep soils lag behind surface soils when it comes to experiencing the full magnitude of global change drivers, such as warming. However, Coupled Model Intercomparison Project Phase 5 (CMIP5) ensemble projections show that near-surface and deep (100 cm) soils will warm at nearly the same rate throughout the next century, with deep soils predicted to warm 4.5°C by 2100 under representative concentration pathway (RCP) 8.5 (Soong et al. 2020). Drought decreases water storage in both deep soils and regolith (2 m deep), as tap roots mine water stored in deeper soils (Bales et al. 2018). Shifts to more variable precipitation regimes dominated by extreme rainfall events are expected to increase deep soil water storage in xeric systems and increase percolation of water through deep soils in mesic systems (Knapp et al. 2008). Shifting organic matter inputs due to land use and land cover change (LULCC) also affect deep soils. In forests, deeper mineral horizons can continue to lose SOC for decades after intensive biomass harvesting (Dean et al. 2017). In cropland, switching from plowing to no-till practices can reduce deep SOC storage (Olson 2010, Cai et al. 2022).

Given the vast amount of C stored in deep soils and deep soils' sensitivity to global change drivers, deep soil C responses to global change must be taken into account as we project future terrestrial C storage and evaluate the potential to manage soils for climate change mitigation. Here, we synthesize current information on deep SOC responses to global change. We focus on potential shifts in C balance reflected in changing C inputs (root growth, root exudation, and leaching of dissolved organic carbon from above), C outputs (gaseous CO_2 flux and leaching losses of dissolved carbon), and SOC pools below 20 cm deep.

2. THE WEDGE CONCEPT: HOW CARBON CYCLING CONTROLS CHANGE WITH DEPTH

We cannot assume that deep SOC will respond to global change in a similar manner as shallow SOC. The soil depth profile is a gradient of many biotic and abiotic factors with different dominant mechanisms that control SOC input, loss, transformation, and stabilization at the soil surface versus at depth (Rumpel & Kögel-Knabner 2011). Soil C persistence (indicated by more depleted radiocarbon values) increases with depth (Shi et al. 2020, Heckman et al. 2022) (**Figure 1*a***), reflecting these changes in C cycle drivers. The reasons for increased C persistence with depth have been attributed to C limitation of microbes (Fontaine et al. 2007, Hicks Pries et al.

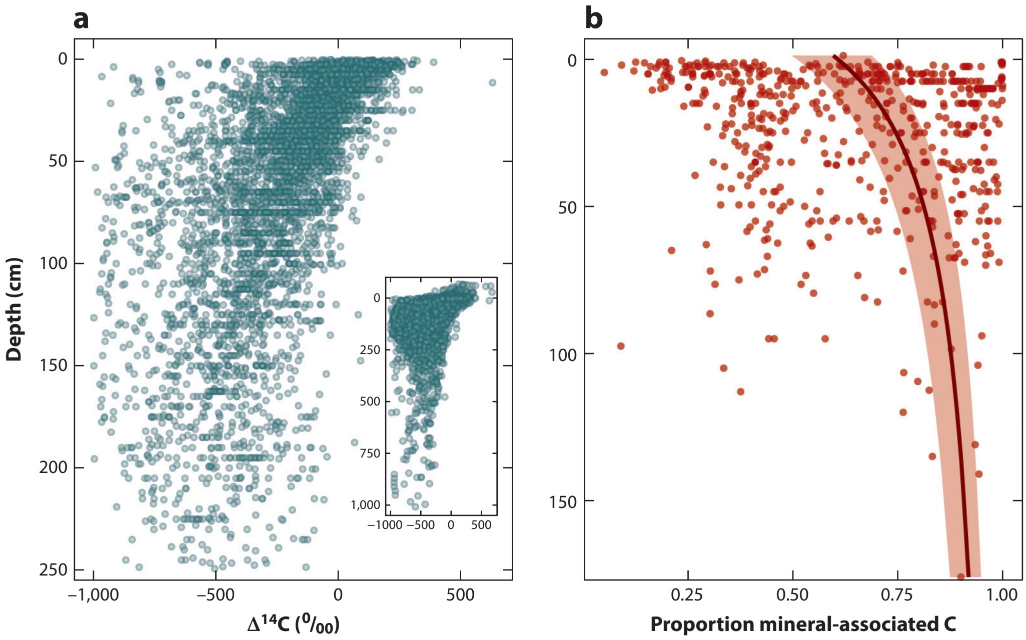

Figure 1

(*a*) Soil organic carbon persistence implied by bulk radiocarbon values increases with depth globally. The inset shows data for depths up to 10 meters. (*b*) The proportion of organic C that is mineral associated significantly increases with depth globally ($p < 0.00001$, $n = 611$). The solid red line shows the predicted relationship between depth and the proportion of mineral-associated organic C, with the 95% confidence interval shaded red. Figure based on data from the International Soil Radiocarbon Database (Lawrence et al. 2020).

2018), lower oxygen availability in wet systems (Silver et al. 1999), physical separation of SOC from microbes (Lützow et al. 2006, Lehmann et al. 2020), aggregate protection, and enhanced potential for organo-mineral interactions at depth (Rumpel & Kögel-Knabner 2011, Schmidt et al. 2011). Another potential cause of older C at depth is simply soil development and transport, as it takes time for soils to weather and for C to be deposited at depth (Heckman et al. 2022).

Reflecting the changing C cycle with depth, the dominant forms in which SOC is stored shift with depth. Bulk SOC is a heterogeneous pool encompassing a continuum of turnover rates, a variety of molecules, and different degrees of accessibility to soil microbes. Bulk SOC is often split into particulate and mineral-associated fractions using physical fractionation methods such as size or density (Lavallee et al. 2020). Globally, the proportion of C associated with soil minerals increases with soil depth (**Figure 1*b***), which can have major implications for how deep SOC will respond to global changes (Lavallee et al. 2020, Heckman et al. 2022). Particulate organic carbon (POC) is less protected from microbial decomposition than C associated with minerals via adsorption, coprecipitation, and microaggregates, leading to longer turnover times of this mineral-associated organic carbon (MAOC) (Lavallee et al. 2020, Heckman et al. 2022). POC is more responsive than MAOC in global change experiments (Rocci et al. 2021). However, even within the more available POC pool, there are significant interactions with depth. Globally, POC decreases with increasing mean annual temperature (MAT) in the top 30 cm, but POC has the opposite response to MAT below 30 cm (Heckman et al. 2022).

While the influence of soil minerals increases with depth, the activity of living organisms decreases. Microbial and root biomass decrease exponentially with depth following a similar relationship to SOC (Jackson et al. 1996, Xu et al. 2013). An asymptotic equation is often used to describe the cumulative vertical distributions of root and microbial biomass pools:

$$Y = 1 - \beta^d,$$

where Y is the proportion of the total profile pool from the surface to a given depth (d, in cm), and β is the extinction coefficient, a numerical index that can be used to compare depth-wise distributions (**Supplemental Figure 1**). A lower β indicates a steeper decline with depth. Root and microbial biomass have statistically similar β coefficients in many ecosystems, ranging from 0.943 (82% of biomass in top 30 cm) in grasslands to 0.975 (53% of biomass in top 30 cm) in deserts (Jackson et al. 1996, Xu et al. 2013). Globally, 72% of microbial biomass ($\beta = 0.959$) (Xu et al. 2013) and 65% of root biomass ($\beta = 0.966$) (Jackson et al. 1996) are found in the top 30 cm of soil. In contrast, only 36% of global SOC is stored in the top 30 cm (Jackson et al. 2017). Thus, β coefficients are usually greater for SOC than for roots or microbial biomass (e.g., Cusack & Turner 2021). As a consequence, not only is there less microbial biomass at depth, there is also less microbial biomass per gram of SOC.

Supplemental Material >

Depth-dependent changes in microbial biomass are accompanied by changes in root and microbial activity with consequences for the amount and form of SOC stored at depth. Fine root turnover times increase with depth (Joslin et al. 2006). Root exudation declines (Peixoto et al. 2020) because there are fewer roots and smaller root-mass specific exudation rates with depth. In one estimate, the root exudation rate at 130 cm was only 2% of the rate in the topsoil (Tückmantel et al. 2017). Slower root turnover and exudation rates reduce plant inputs to the subsoil, affecting SOC formation (Sokol et al. 2019), SOC priming (see the sidebar titled Positive Priming in the Deep Soil), and weathering (Wen et al. 2021). Overall, the majority of plant inputs in the form of dissolved organic matter leached from litter, senescent roots, and exudates are in the surface soil (Schrumpf et al. 2013, Jobbágy & Jackson 2000). Due to decreasing plant inputs, organic carbon (OC) molecules are less complex in subsoils, with greater proportions of smaller, highly oxidized molecules derived from microbial activity (Lützow et al. 2006, Gleixner 2013, Angst et al. 2018). Microbial activity declines with depth, with exponential decreases in soil respiration (e.g., Hicks

POSITIVE PRIMING IN THE DEEP SOIL

New organic matter inputs can promote the decomposition of existing SOC at depth through the priming effect (PE), which has several potential mechanisms (Fontaine et al. 2007, Karhu et al. 2016, Heitkötter et al. 2017). The first two mechanisms alleviate limitations on the activity of deep soil microbes. (*a*) When nitrogen (N) is limiting, new inputs can cause microbes to increase decomposition in order to mine N from organic matter, leading to an increase in deep SOC mineralization and a positive PE (Craine et al. 2007). (*b*) When C is limiting due to low substrate quality or inaccessibility (Fontaine et al. 2007, Dove et al. 2021), new inputs can increase extracellular enzyme production leading to a positive PE. Or (*c*) the enzymes released by microbes during the decomposition of new inputs can coincidentally degrade existing SOC, accelerating its decomposition through a process known as cometabolism (Bernard et al. 2022). Other mechanisms involve roots, which can destabilize SOC through (*d*) aggregate destruction (Cheng et al. 2014) or (*e*) organic acid exudation (Keiluweit et al. 2015). Studies have found that deep SOC is as or even more vulnerable to priming than surface SOC (Tian et al. 2016, Shahzad et al. 2018). Roots and rhizodeposition can reduce the physical separation between microbes and SOC, destabilize MAOC, and alleviate microbial energy limitation at depth, all of which can promote deep SOC mineralization. There is some experimental evidence that in the absence of new root inputs, deep SOC tends to remain only partially decomposed (Hicks Pries et al. 2018). While it may seem that lower root biomass should protect deep SOC from the positive PE, global changes can increase deep root growth (Norby et al. 2004, Leppälammi-Kujansuu et al. 2014), stimulating CO_2 loss from deep soils via the PE.

Pries et al. 2017), declines in specific respiration (normalized to SOC content) (Fang & Moncrieff 2005), slower microbial biomass turnover (Spohn et al. 2016, Li et al. 2021), less active microbial biomass (Min et al. 2021), and lower potential extracellular enzyme activities (Dove et al. 2020). However, the microbial metabolic quotient (respiration normalized to microbial biomass) does not decline with depth, and the amount of exoenzymes per unit microbial biomass may either stay the same or increase with depth (Stone & Plante 2015, Dove et al. 2020). In addition, microbial carbon use efficiency (CUE; a measure of SOC retained in microbial biomass versus respired), which is hypothesized to control the amount of microbial necromass sequestered on mineral surfaces (Cotrufo et al. 2013), has conflicting depth-wise trends across ecosystems (Spohn et al. 2016, Wordell-Dietrich et al. 2017, Li et al. 2021).

Microbial community structure, genomic capacity, and ecophysiology are also strongly depth dependent (Brewer et al. 2019, Dove et al. 2020). The organisms, biosynthetic potential, and metabolic pathways of deep soils differ dramatically from better-studied shallow soils (Butterfield et al. 2016, Diamond et al. 2019, Sharrar et al. 2020). Surface soils contain more eukaryotes like fungi (Fierer et al. 2003) and worms (Jégou et al. 1998) that play an active role in bioturbation and aggregate formation. Fungi to bacteria ratios typically decrease with depth (Kohl et al. 2015), changing the nature of the microbial necromass that contributes to SOC (Ni et al. 2020). Overall, the diversity of bacteria, archaea, and fungi declines with depth, and communities in the subsoil are distinct compared to those in surface soil (Fierer et al. 2003, Eilers et al. 2012, Schlatter et al. 2018, Brewer et al. 2019), likely due to declines in SOC availability and more favorable conditions for oligotrophs (Fierer et al. 2003, Brewer et al. 2019). Autotrophs that do not need organic energy sources may also be favored in deep soils. Deep soils are enriched in autotrophic archaea implicated in ammonia oxidation (Brewer et al. 2019) and genes encoding inorganic N metabolism (Diamond et al. 2019). Further indications of dark autotrophy, such as genes encoding CO_2 fixation pathways or iron and sulfur oxidation, have been uncovered in bacterial genomes at depth (Brewer et al. 2019). Understanding the interaction between microbial traits and soil depth is crucial because microbial products—including extracellular enzymes, extracellular polymeric substances, and cell necromass—contribute to long-lived soil organic matter (SOM) in deeper soil horizons (Dove et al. 2020, Peixoto et al. 2020, Sher et al. 2020). Microbial necromass contributes to 62% of SOC below 50 cm but only 33% of SOC at 0–20 cm (Ni et al. 2020).

The soil profile can be conceptualized as two opposite wedges of influence representing biotic and mineral control of SOC cycling (**Figure 2**). At the surface, the volume of rhizo- and hyphosphere soil and resulting number of hotspots of microbial activity are much greater. With fewer C inputs and less biota, the influence of minerals predominates in subsoils (Heinze et al. 2018). Since microbes compete with mineral sorption sites for SOC and nutrients (Zhu et al. 2016), mineral type, charge, and reactive surface area may be more important controls on SOM stabilization at depth than at the surface. Decomposition is also limited by the spatial disconnect between microbes and SOC in subsoils (Gleixner 2013, Heinze et al. 2018), where microbes' return on exoenzyme investment is less assured (Lehmann et al. 2020) and hotspots of microbial activity are sparse (Heitkötter & Marschner 2018). Mineralization rates in subsoils are often increased by disturbances that make SOC more available to microbes (Xiang et al. 2008, Salomé et al. 2010). Preferential flow paths created by roots, spaces between soil peds, or animals can extend biotic influence into the mineral wedge, bringing microbes into close contact with OC from the surface.

Based on this wedge concept, we predict that the response of deep SOC to global change will depend on (*a*) deep soil mineralogy, specifically the degree of weathering a soil profile has undergone, and (*b*) how global change affects carbon inputs to and microbial activity within the deep soil. Mineral stabilization of SOC peaks in intermediately weathered soils (Torn et al. 1997, Slessarev et al. 2022), so we expect deep SOC in soils that contain high surface area and highly charged

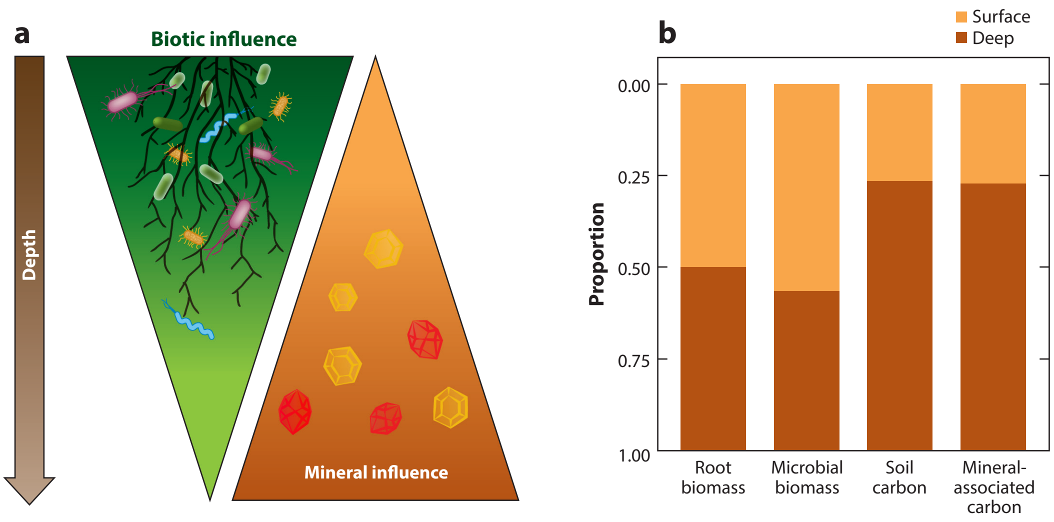

Figure 2

(*a*) The wedge concept. (*b*) Generally, in mineral soils, over 50% of root and microbial biomass is found within the top 20 cm of the soil profile. In contrast, 75% of total soil carbon and mineral-associated carbon is found below 20 cm in the deep soil. Thus, we can envision soil carbon cycling as controlled by two wedges of influence, as shown in panel *a*. The first wedge points down and represents the decrease in biotic influence with depth due to declining plant inputs and microbial activity. The second wedge points up and represents the increasing influence of minerals with depth as a greater proportion of the soil carbon is associated with, and may be protected from decomposition by, minerals.

poorly crystalline minerals will lose less C in response to global change and may be more likely to increase C storage in response to management. Deeper rooting plants and increased dissolved organic carbon transport to depth could increase C storage (see the sidebar titled Mechanisms for Increased Deep Soil Carbon Storage) but could also sustain active microbial communities

MECHANISMS FOR INCREASED DEEP SOIL CARBON STORAGE

Despite the potential for causing positive priming, some studies report that increased C inputs lead to more SOC accumulation in deep relative to surface soils (e.g., Liao et al. 2020). This increase can be attributed to the following mechanisms: (*a*) Increased C inputs may lead to larger deep SOC pools because deep soil microbes have a catabolic preference for labile substrates (Jia et al. 2017) and thus preferentially decompose new inputs rather than the existing SOM, which is a negative PE (de Graaff et al. 2014, Bernard et al. 2022). (*b*) Roots at depth can encourage soil aggregation, thereby making SOC less accessible to microbes (Dijkstra et al. 2021). (*c*) New C inputs can be assimilated by microbes wherein microbial residues and metabolites could be selectively sorbed to soil minerals or incorporated into organo-mineral complexes, increasing MAOC formation through the in vivo pathway (Liang et al. 2017). Up to 68% of litter-derived C was recovered in the mineral-associated clay fraction of soil during the early stage of litter decomposition (Cotrufo et al. 2015). Since deep soils have a higher proportion of clay minerals than surface soils (Liao et al. 2020), deep soils could sequester a larger proportion of microbial-derived C than surface soil. (*d*) Lastly, according to the conceptual model of C saturation, C-poor deep soils might have greater potential and efficiency to retain exogenous C than surface soils (Stewart et al. 2007, Poirier et al. 2013, Angst et al. 2021). Overall, increased C inputs can lead to larger C pools in deep soils compared to surface soils by increasing the formation of new, persistent SOC.

that promote positive priming of deep SOC (see the sidebar titled Positive Priming in the Deep Soil).

3. CLIMATE AND ATMOSPHERIC CHANGE

3.1. Warming

Earth's temperature is projected to increase 4.4°C by 2100 under the shared socioeconomic pathway (SSP) 5–8.5 emissions scenario (Portner et al. 2022), affecting soil C storage (Ito et al. 2020). Warming's main effect is on the activity of soil biota because warming can increase microbial activity (Conant et al. 2011), increase extracellular enzyme kinetics (German et al. 2012) and activities (Meng et al. 2020), and decrease CUE (Li et al. 2019). Together, these changes can cause soils to become a C source to the atmosphere. However, microbial communities can acclimate to warming, as reduced CUE decreases microbial biomass (Bradford et al. 2008) and enzyme production (Allison et al. 2010). Warming also affects C inputs such as litterfall, root turnover, and exudation (Melillo et al. 2011, Yin et al. 2013). If warming increases productivity without causing positive priming (see the sidebar titled Positive Priming in the Deep Soil), then the additional soil C inputs may offset losses due to increased mineralization. Warming also affects the kinetics and equilibria of abiotic reactions like organic matter sorption to minerals. An increase in temperature decreases the equilibrium constant in sorptive bonding (Stumm & Morgan 2012), favoring desorption of organic molecules relative to adsorption. Based on the Van't Hoff equation, oxides, hydroxides, and phyllosilicate clays will be more soluble with warming (Stumm & Morgan 2012), potentially increasing weathering, which would decrease the surface area of minerals available for sorptive organic matter protection. Together, these responses would increase the susceptibility of MAOC to microbial decomposition with warming.

The strength of temperature responses likely differs with depth. Deeper soils may be less temperature sensitive than surface soils according to kinetic theory because a greater proportion of deep SOC is made up of less complex, necromass-derived SOC compared to surface soils (Davidson & Janssens 2006). Similarly, deep soils may be less affected by warming-induced CUE declines, which are strongest for more complex substrates (Frey et al. 2013). The temperature sensitivity of extracellular enzyme activity is either similar (Zuo et al. 2021) or declines (Steinweg et al. 2018) with depth. Because protected SOC is less temperature sensitive than free POC (Benbi et al. 2014), the increased proportion of mineral-associated and physically protected SOC at depth can also decrease its temperature sensitivity (Gillabel et al. 2010, Qin et al. 2019). Lastly, temperature effects on abiotic reactions may be more important in deep soils where MAOC dominates, but abiotic temperature responses are little studied in situ and likely occur on a longer timescale than microbial responses.

While the temperature sensitivity of CO_2 fluxes from surface soils has been well established through decades of experiments, the temperature sensitivity of deeper soil has been investigated only relatively recently. Soil temperature sensitivity is often quantified using Q_{10}, the factor by which a rate increases in response to a 10°C rise in temperature, and the rate most often measured is that of soil respiration. The temperature sensitivity of deep soils is commonly tested using laboratory incubations. The results of individual lab incubations are equivocal with the temperature sensitivity of subsoil reported as being lower than (MacDonald et al. 1999, Gillabel et al. 2010), greater than (Fierer et al. 2003), and equal to (Gabriel & Kellman 2014) surface soils. A recent meta-analysis of 52 short-term (<2 weeks long), lab-based incubation studies found that Q_{10} values increased with depth in permafrost soils (Ren et al. 2020). Overall, the Q_{10} of subsoil (<30 cm) increased as soil C:N increased. Given that mineral-associated organic matter has a low C:N ratio compared with particulate organic matter (Heckman et al. 2022), this result indicates subsoils with high temperature sensitivity may have a greater proportion of their C stored in particulate forms.

Supplemental Material >

For this review, we performed our own meta-analysis (**Supplemental Material**) that expanded upon the aforementioned meta-analysis (Ren et al. 2020) in several key ways: We included papers with any duration of incubation, we did not include data from permafrost soils, and we included data from Li and colleagues' (Li et al. 2020) extensive analysis of Q_{10} in forested soils across 90 sites in China. Overall, we had 986 data points representing soil depths from 2.5 to 200 cm. We ran three multiple regressions to test the effects of experimental conditions (minimum temperature and incubation duration; $n = 986$), environmental conditions (MAT, MAP, land cover; $n = 831$), and soil conditions (soil carbon, C:N, and pH; $n = 674$) and their interactions with depth on Q_{10}. There was a significant interaction between soil depth and the duration of the study ($p < 0.0001$) (**Supplemental Figure 2**). In deeper soils, the Q_{10} decreased as the study duration increased but remained the same in surface soils. Because the more-available fast carbon pool is accessed and respired by the microbial community first, this implies that the slow carbon pool was less available at depth. We found a strong interaction between soil depth and land cover wherein the Q_{10} of forested sites increased with depth, but the Q_{10} of cultivated, wetland, and rangeland/grassland sites did not (**Figure 3**). Lastly, Q_{10} increased with increasing C:N across all depths ($p = 0.05$) (**Supplemental Figure 3**), and Q_{10} decreased with decreasing pH ($p < 0.0001$) (**Supplemental Figure 4**), an effect that was strongest in deeper soils, likely reflecting increased deep soil mineral protections where soils are more weathered.

Less common tests of deep soil temperature sensitivity are experiments that not only warm whole soil profiles in situ but also make depth-explicit measurements of C pools and fluxes (e.g., Hanson et al. 2017, Hicks Pries et al. 2017). While deeper soil may be warmed in conventional warming experiments with aboveground heaters or buried heating cables (**Supplemental Figure 2**), the depth of warming is often unknown. Only a third of soil warming studies monitor temperatures below 20 cm (Hicks Pries et al. 2017). Responses of deep soil to in situ warming vary by ecosystem and soil type. In a temperate forest, warming the whole soil profile led to a 30% increase in soil respiration that was sustained over 5 years and led to a 33% loss of subsoil (>20 cm) C (Hicks Pries et al. 2017, Soong et al. 2021). Supporting the prediction that unprotected C in the subsoil would be the most sensitive to warming, the largest C losses at depth were in the particulate organic matter fraction (Soong et al. 2021). In contrast, in a tropical Andisol, deep soil (>40 cm) was not responsive to in situ warming where poorly crystalline and noncrystalline minerals likely protected deep soil C from microbial degradation (McGrath et al. 2022). The availability of deep soil C, and thus its temperature sensitivity, can also be affected by environmental factors. In the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment, heating 2 m of peat increased surface methane emissions. This methane originated in the top 30 cm and not the deeper soil, where anoxia limited microbial activity (Wilson et al. 2016). Similarly, the loss of old, deep C from thawing permafrost soils is constrained under saturated conditions (Pegoraro et al. 2021).

Overall, the response of deep soils to warming is likely to be more context dependent than the response of surface soils, where the large microbial biomass pool controls decomposition. Deep-rooted ecosystems that have a large supply of particulate organic matter and exudates at depth, like forests, and soils with a low reactive mineral content, like those derived from granitic parent materials (Rasmussen et al. 2005), will be susceptible to temperature-induced deep SOC losses. In contrast, deep SOC in ecosystems with shallow rooting plants that limit POC at depth, in soils dominated by highly reactive minerals that can strongly sorb SOC, or in soils with shallow water tables that slow decomposition will be more resilient to temperature increases at depth.

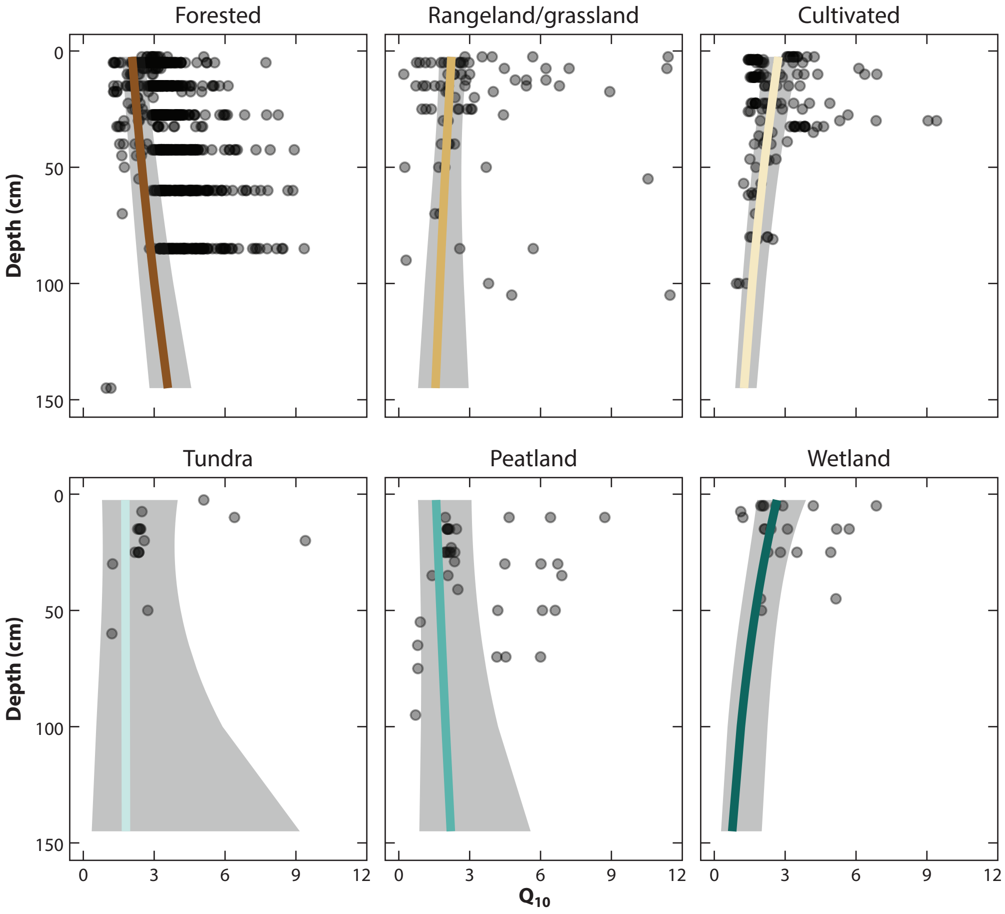

Figure 3

A meta-analysis of lab incubation studies found a significant depth-by-land cover interaction ($p < 0.0001$, $n = 831$) in a linear mixed model that included depth interactions with land cover, mean annual precipitation, and mean annual temperature, along with the random effect of site nested in study. Q_{10} values, measures of temperature sensitivity, increased with depth in forested ecosystems and declined with depth in croplands. Under other land covers, there was no depth effect on Q_{10}. Gray circles represent data points; colored lines are the predictions of the linear regression with the other model effects held at their means; and gray shaded areas represent 95% confidence intervals. For details of the methods, see the **Supplemental Materials**.

3.2. Changing Precipitation Regimes

Supplemental Material >

With climate change, precipitation is projected to increase, decrease, or change its timing and intensity depending on location (Portner et al. 2022). Water is essential for both biotic and abiotic soil processes. Soil water potential and pore connectivity regulate the diffusion and mass flow of dissolved organic carbon (DOC), nutrients, extracellular enzymes, and dissolved minerals. Soil water content and O_2 concentrations affect the availability of electron acceptors, which can affect mineral stability and the amount of energy that can be released from decomposition. Water can indirectly impact soil biogeochemical processes via changes in primary productivity. Vegetation changes can alter the quantity and quality of litter inputs in soil, rooting depth, and preferential flow pathways. Overall, changes in the precipitation regime have the potential to modify deep SOC inputs and decomposition as well as the transport and fate of DOC and reactive minerals along the soil profile.

The total amount of precipitation is projected to increase over high latitudes, the equatorial Pacific, and parts of the monsoon regions (Portner et al. 2022). A recent meta-analysis revealed that the effects of increased precipitation on SOC dynamics vary with region, with arid ecosystems more affected than humid ecosystems (Wang et al. 2021). Experimentally elevated precipitation has increased surface SOC storage in a temperate grassland (He et al. 2012) and semiarid temperate steppe (Song et al. 2012), but deep SOC responses were not measured. Along natural rainfall gradients, more SOC is distributed in the deep soil as precipitation increases, likely due to soil development over longer timescales than global change experiments (Klopfenstein et al. 2015, Raheb et al. 2017). Overall, deep soils in wetter climates have similar amounts of SOC as deep soils in drier climates, but deep SOC in wetter climates is older (Heckman et al. 2022). Thus, where water availability is high, greater C inputs to deep soils may be canceled out by faster decomposition, but more weathered minerals may be better able to stabilize the C that remains.

Precipitation can elevate DOC concentrations (Ma et al. 2014) and total DOC export (Austnes et al. 2008) if sorbed SOC is scoured by percolating water or aggregates are broken due to slaking. The increasing delivery of DOC to depth may prime microbial breakdown of deep SOC (Min et al. 2021) when deep soil microbes are energy limited. In support of a positive priming effect (PE) at depth, the metabolic capabilities of deep soil microbes (30–40 cm) became more similar to those of surface soils (10–20 cm) with amended rainfall (Diamond et al. 2019). Precipitation may also increase plant C inputs such as litterfall (Shen et al. 2019). However, given that most SOC is root derived (Jackson et al. 2017), increasing root inputs may cause more of an effect. Precipitation increases the transport of inorganic C (Schindlbacher et al. 2019). Soil CO_2 concentrations along depths of 0–100 cm can increase with precipitation as water displaces air in soil pores (Min et al. 2021). The increased transport of inorganic C with precipitation can lead to mineral weathering (Kim et al. 2020) and may generate a C sink by transporting dissolved inorganic C to aquifers (Li et al. 2015). Intense precipitation can also lead to the redistribution of SOC into deep soils through erosion and burial (Doetterl et al. 2016).

Wetter conditions also affect oxygen availability, redox potential, and iron solubility, with mixed consequences for SOC. In general, decomposition is slow in waterlogged soils because low O_2 availability leads to thermodynamically less favorable decomposition processes (Schlesinger & Bernhardt 2020). Even in a well-aerated upland soil, SOC decomposition can be slowed within anaerobic microsites. However, C losses can be stimulated in mineral soils under reducing conditions because iron reduction liberates MAOC (Huang & Hall 2017). In Hawaiian rainforests, high rainfall increased the concentrations of dissolved Fe and Al in mineral horizons (40–100 cm) (Marin-Spiotta et al. 2011). Given that Fenton reactions [generation of hydroxyl radicals by iron(II)] can contribute to the mineralization of SOC in anoxic conditions (Merino et al. 2020, 2021), some deep SOC may destabilize if more precipitation promotes anoxic conditions.

In some areas like the Mediterranean, Central Asia, Australia, and much of Africa, the intensity of drought will increase (Portner et al. 2022). Drought can increase the size of soil macropores, enhancing preferential flow, water hydraulic conductivity, and C transport along soil profiles (Hirmas et al. 2018). Dry conditions decrease microbial activity (Stark & Firestone 1995). Model simulations demonstrate that dry conditions limit SOC decomposition despite increases in O_2 availability by reducing substrate availability and matric potential (Ghezzehei et al. 2019). Microbial enzyme activities exhibit varying responses to drying—in some cases decreasing in the soil surface and at 30–40 cm under drought treatments (Zhu et al. 2021) and in others increasing with drier conditions in the surface soil despite reductions in respiration (Geisseler et al. 2011). This limit on decomposition may have caused surface SOC pools (0–30 cm) to be larger in dry sites along an agricultural land rainfall gradient (Alberti et al. 2011).

Thus far, knowledge about the effects of drought on deep soil is limited. Inputs leached from the surface will likely decrease. However, changes in precipitation may alter biome types (Salazar et al. 2007, Chakraborty et al. 2013), with a potential to impact deep SOC by changing rooting depths. In general, rooting depth tends to increase with evaporative demand (Fan et al. 2017, Tumber-Dávila et al. 2022). Thus, it is plausible that drought and decreased precipitation will favor deeper rooted vegetation, increasing the amount of plant C inputs to the deep soil and changing their composition.

The timing of precipitation also influences deep SOC dynamics. Increased precipitation during the usually dry, late spring season increased SOC concentrations at 5–50 cm in California grassland soils, while rainfall during the rainy, winter season did not affect SOC (Berhe et al. 2012). In a 17-year precipitation manipulation in a cold desert, irrigation during and outside of the growing season increased SOC at 95–100 cm while either not affecting or reducing SOC at 15–20 cm (Sorensen et al. 2013). The Birch effect, a pulse of respiration after rewetting a dry soil, has been widely documented in surface soils (Birch 1958, Unger et al. 2010), and deep SOC may be more vulnerable to changes in dry–wet cycles than surface SOC. Repeated cycles of drying and rewetting stimulated microbial growth and enzyme activity more at 90–100 cm compared to 0–5 cm in a California grassland (Xiang et al. 2008). Deep soil microbes respired older C after drying–wetting cycles, implying that these cycles mobilize previously protected deep SOC (Schimel et al. 2011). In addition, upon wetting, CO_2 concentrations drastically increased at 70 cm in a grassland soil in spite of relatively high gas diffusivity, implying substantial microbial respiration in deeper soil layers (Min et al. 2021). However, incubation of intact forest soils showed no evidence of the Birch effect in shallow mineral horizons (Muhr et al. 2008) or deeper 25–50 cm soil (Gabriel & Kellman 2014), so the effects of drying and wetting on deep SOC may be ecosystem specific.

3.3. Elevated Atmospheric CO_2

Atmospheric CO_2 concentrations have risen from 285 to over 410 ppm since 1850 and are projected to keep rising if we do not act to reduce greenhouse gas emissions (Portner et al. 2022). Evidence from field and laboratory experiments, models, and meta-analyses generally show plant productivity is stimulated by elevated carbon dioxide (eCO_2) (Song et al. 2019, Ainsworth & Long 2021), which should increase C inputs to soils. However, an ultimate gain in soil C storage is not guaranteed because increased productivity can heighten nutrient demand and stimulate SOC decomposition via priming (van Groenigen et al. 2017, Terrer et al. 2021). Furthermore, deep soils may have a different response to priming than surface soils (see the sidebar titled Positive Priming in the Deep Soil).

Many efforts have been devoted to investigating the belowground responses of plants to eCO_2. One common observation from in situ experiments is an increase in fine-root production at deeper soil depths under eCO_2 (Iversen et al. 2008, Arndal et al. 2018). Greater root production and deeper root distributions may increase both POC inputs (through root turnover) and root exudation at depth (Phillips et al. 2011, Nie et al. 2013), but direct evidence of changes in exudation intensity (per gram root or per m^2) is rarely reported. Plant C allocation and root exudation strongly depend on environmental conditions, plant traits (e.g., Terrer et al. 2021), and soil properties (Pausch & Kuzyakov 2018), so the impact of eCO_2-stimulated plant C inputs to deep soils is likely to be ecosystem dependent.

Elevated CO_2 may also change patterns of DOC leaching from surface litters (Hagedorn & Machwitz 2007). Nutrient limitation induced by eCO_2 may cause the quality of litter inputs, and hence litter-derived DOC, to decline (e.g., due to higher litter C:N) (Sardans et al. 2012). Because there is no consensus on how DOC properties change during downward transport in the soil (Roth et al. 2019), it is hard to predict how changes in surface litter chemistry may affect deep DOC. The eCO_2 stimulation of root production would also provide additional plant-derived DOC inputs along the soil profile (Lange et al. 2021). Currently, our understanding of how DOC inputs to deep soils are affected by eCO_2 remains limited.

Elevated CO_2 can stimulate symbiotic mycorrhizal fungal biomass and growth (Antoninka et al. 2011, Dong et al. 2018), with effects on SOC that depend on mycorrhizal type. Mycorrhizal fungi increase under eCO_2 as more root biomass becomes available for colonization (Treseder 2004) and more photosynthate is allocated to mycorrhizal fungi to alleviate increased plant nutrient demand (Mohan et al. 2014). Mycorrhizal fungi affect SOC through direct C inputs of hyphal turnover and hyphal exudates and through their effects on decomposition (e.g., Hicks Pries et al. 2022). In arbuscular mycorrhizal systems, SOC tends to increase under eCO_2 but decrease in ectomycorrhizal systems (Terrer et al. 2021). However, since these SOC responses were measured only in the surface 20 cm, the effect of mycorrhizal type on deep SOC is unknown. Our understanding is further hampered by a lack of data on mycorrhizal abundance with depth.

Whether eCO_2 leads to increased deep SOC pools due to enhanced plant inputs is an open question. In one meta-analysis, POC at depth increased in response to eCO_2, while MAOC did not significantly change (Rocci et al. 2021). In field eCO_2 manipulations, SOC accumulated in some experiments [e.g., soils up to 90 cm depth (Iversen et al. 2008)] but not others [e.g., soils to 100 cm depth (Hungate et al. 2013)]. The stimulation of SOM decomposition induced by plant C inputs may be vital to explaining these disparate results. Elevated CO_2 may stimulate fine-root production and root exudation, which, combined with the deeper distribution of roots, increases the amount of labile C entering deep soils under eCO_2. These new inputs could increase SOC (see the sidebar titled Mechanisms for Increased Deep Soil Carbon Storage) or create rhizosphere hot spots that increase deep SOC decomposition. Furthermore, new root growth could destabilize soil structure and reduce the physical disconnect between substrates and microbes, weakening microbial energy limitations at depth (Shahzad et al. 2018), or produce exudates (e.g., oxalic acid) that can liberate organic compounds from protective mineral associations (Keiluweit et al. 2015). Thus, the response of deep SOC to eCO_2 is likely shaped by the vulnerability of deep SOC to priming, driven by these new inputs. Lab incubations testing the sensitivity of deep SOC to priming have had equivocal results (Salomé et al. 2010, Jia et al. 2017, Liu et al. 2022). This inconsistency is likely due to the variety of potential priming mechanisms that depend on a soil's nutrient status and microbial activity (see the sidebar titled Positive Priming in the Deep Soil). We know of no studies that quantify PEs in deep soils with CO_2 enrichment in situ, so a quantitative assessment of the deep SOC response to eCO_2 is not currently possible.

4. LAND USE, LAND COVER CHANGE, AND MANAGEMENT

Human land use is extensive, affecting approximately three-quarters of the global ice-free land surface. Major categories of land use include grazing lands (30–47%), managed forests (16–23%), and croplands (12–14%) (Shukla et al. 2019). Management of croplands, rangelands, and forests directly impacts SOC stocks and dynamics by changing the quantity and quality of C inputs, SOC decomposition rates, and conditions that affect SOC persistence (Lal 2018). In the last 200 years, agricultural practices are responsible for an estimated loss of 113 Pg C in the top 2 m of soils (Sanderman et al. 2017). This C debt represents an opportunity to mitigate climate change by improving soil C sequestration through land use conversion or improved land management (Soussana et al. 2019). The effect of management practices on soil physical, chemical, and biological conditions in surface soils is well characterized, but how deep SOC responds to management is less certain, even though deep agricultural soils may have a greater potential to store persistent

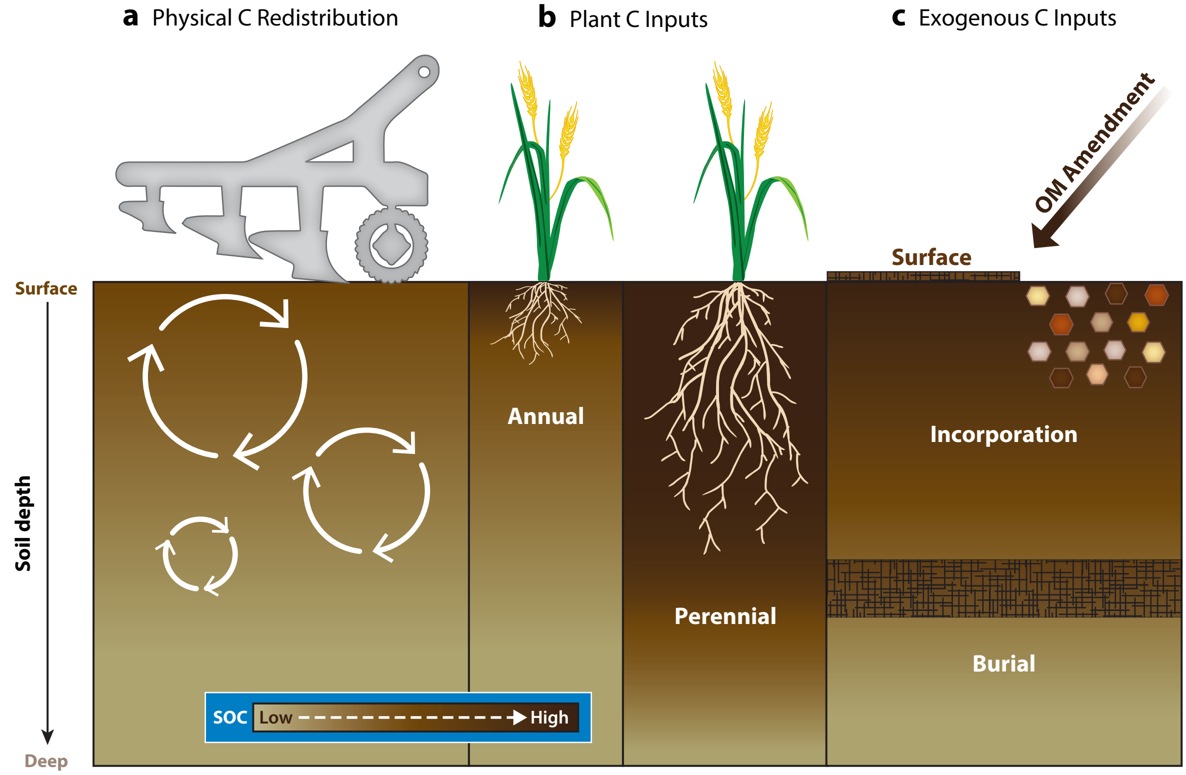

Figure 4

Land management can affect pools of deep soil carbon through (*a*) physical redistribution, (*b*) planting deep rooting perennials, or reforestation/afforestation, as well as through (*c*) exogenous carbon inputs buried at depth or surface applied and subsequently incorporated at depth through biological and physical processes. Abbreviations: OM, organic matter; SOC, soil organic carbon.

SOC than surface soils (Button et al. 2022). Land cover change and management affect SOC dynamics through many mechanisms, three of which we cover here: (*a*) shifting the dominant plant functional type, (*b*) adding exogenous C inputs, and (*c*) disturbing soil's physical structure (**Figure 4**).

4.1. Vegetation Changes

Vegetation type, as dictated by prevalent land cover and use, can have important implications for deep SOC stocks and dynamics. LULCC can occur naturally through succession or as an indirect (e.g., nitrogen deposition) or direct (e.g., food production) result of human activities. Shifts in land cover can alter stocks of deep SOC due to changes in the amount, composition, and distribution of plant inputs, preferential flow paths, and soil microclimate. Belowground plant inputs are preferentially retained in surface soils compared to aboveground plant inputs by an average ratio of 8:1 (Jackson et al. 2017), a ratio that is likely even higher in deep soils. Thus, one of the most important ways LULCC can affect deep SOC is by changing the distribution and biomass of roots.

While deforestation and conversion to croplands typically result in SOC losses throughout the profile (Villarino et al. 2017), reforestation has a high climate mitigation potential (Griscom et al. 2017). Generally, the deep SOC response to the growth of trees or shrubs matches the direction of the surface SOC response, but in deep soil, the magnitude of change and rate of change tend to lag

(Nave et al. 2013, Shi et al. 2013, Hong et al. 2020). In locations where reforestation sequestered SOC, accumulation amounts decreased with depth from a 72% increase within the top 10 cm to a 14% increase at 40–60 cm, at a rate of increase that was only 16% of the surface rate (Shi et al. 2013). Whether the growth of trees or shrubs promote SOC storage is highly dependent on soil conditions (Hong et al. 2020) and land cover prior to reforestation or afforestation (Laganière et al. 2010, Nave et al. 2013, Shi et al. 2013). In one global meta-analysis, reforestation of croplands increased SOC to 60 cm, but afforestation of grasslands reduced or caused no change in SOC down to 80 cm (Shi et al. 2013). This effect of prior land cover might be due to initial SOC storage. Across 619 afforestation plots in China, large SOC decreases occurred in deeper soils (Hong et al. 2020), and responses appeared to depend on initial SOC storage, with low SOC soils (<5 kg m^2) gaining C and high SOC soils (>20 kg m^2) losing C. However, we caution that recent analyses suggest such patterns can be influenced by statistical artifacts (Slessarev et al. 2022). Across the United States, deep (>20 cm) SOC changes were negatively correlated with mean annual precipitation so that deeper soils in the wetter sites had a negative response to afforestation (Nave et al. 2013). While the slower rate of change in deep soils implies an SOC transport limitation that might be overcome by higher precipitation, this negative trend indicates larger initial SOC stocks at depth (Heckman et al. 2022) led to a loss of C with afforestation, as described by Hong et al. (2020). Lastly, tree identity can influence deep soil afforestation responses; broadleaf trees resulted in larger deep SOC increases than coniferous trees because they have larger, deeper root systems (Laganière et al. 2010).

In grass-dominated regions experiencing woody encroachment, a land cover change that is being promoted by rising atmospheric CO_2 (Stevens et al. 2017), rooting depth has deepened by an average of 38 cm due to the shift from grasses to deeper rooted shrubs and trees (Hauser et al. 2022). Deeper rooting woody vegetation may increase SOC accumulation in deep soil layers by supplying C from roots and root exudates into subsoil (Rumpel & Kögel-Knabner 2011), but the introduction of recent photosynthate from deep roots can result in a positive PE and a net loss of SOC (see the sidebar titled Positive Priming in the Deep Soil) or increased SOC storage (see the sidebar titled Mechanisms for Increased Deep Soil Carbon Storage). Significant SOC accumulation following 100 years of woody encroachment in subtropical savanna has been observed; however, the future trajectory of deep soil C sequestration from woody encroachment will be dependent on the balance between gains (e.g., mineral stabilization of new C inputs) and priming losses (Zhou et al. 2017).

Extensive agricultural conversion has reduced C inputs from vegetation, especially at depth. Regions where native perennial vegetation has been converted to shallow-rooting annual crops or managed pasture have experienced dramatic decreases in root C depths and densities (Hauser et al. 2022). Rooting depths are ~60 cm shallower in croplands dominated by annual plants than in natural ecosystems (Hauser et al. 2022). Compared to other land uses, surface and deep soil in croplands have the lowest degree of mineralogical C saturation (Georgiou et al. 2022), likely a direct result of decreased C inputs. Therefore, revegetation of abandoned agricultural lands, cover cropping, and perennialization of agroecosystems are practices likely to increase deep SOC (Mosier et al. 2021).

Cover crops are grown for their soil benefits, rather than harvestable grain and biomass. They are typically planted between seasons or intermixed with commercial crops. Cover crops can decrease erosion, and their adoption can build C storage in agricultural systems by increasing plant inputs. Cover crops are well documented in their strong positive effect on surface SOC (Lal 2004, Chahal et al. 2020). In one meta-analysis, cover crops increased SOC in the 0–30 cm depth by 1.11 T C/ha/y on average (McClelland et al. 2021). Globally, cover crops could potentially sequester 0.12 Pg C/ha/y in the top 30 cm of soil (Poeplau & Don 2015), but changes in deeper soil C sequestration are poorly quantified. A key caveat is that cover crops' inputs are typically readily degradable organic matter (Zhou et al. 2012, White et al. 2020). One study found that winter cover crops in annual cropping systems increased SOC stocks by 1.4 T C/ha/y in the top 30 cm but decreased SOC by almost 15 T C/ha/y in deeper (30–200 cm) soil (Tautges et al. 2019). A potential reason for this large subsoil C loss could be priming caused by inputs of easily degradable organic matter and a higher sensitivity to positive PEs in the subsoil (see the sidebar titled Positive Priming in the Deep Soil).

4.2. Exogenous Carbon Inputs

Organic matter amendments, such as compost, biosolids, and biochar, are common sources of exogenous C for agricultural ecosystems. Exogenous C additions to surface soils can increase SOC by providing a slow-release form of nutrients that increase plant production, plant inputs, and SOC protection through improved aggregation (Ryals & Silver 2013, Paustian et al. 2016). Amendments, including straw and biochar, may also be directly buried in subsoils via the process of deep ripping, a technique typically designed to mitigate subsurface compaction. While these amendments necessarily increase the standing C stock, it should be noted that not all the added C will remain (Leskiw et al. 2012), and physical disturbance associated with the amendment process may cause net losses. Shahzad et al. (2019) measured higher soil respiration from maize litter buried in subsoils than in topsoils. The physical and chemical characteristics of organic amendments can influence plant and soil responses, which dictate whether or not the amendment practice leads to net additionality in SOC pools and thus C removal from the atmosphere.

The ability of compost amendments to increase SOC stocks in agricultural soils is well documented (Brown & Cotton 2011, Ryals et al. 2014). What is less understood is how compost and other C amendments affect deeper soil horizons. In a study to assess compost type and application rates, Yang et al. (2014) found significant SOC changes within the top 35 cm across compost types but no significant changes in deeper soil over 10 years. In contrast, a study in rainfed, grazed California grasslands found that long-term (20 years) application of biosolids amendments increased deep SOC storage (30–100 cm) by 50% compared to unamended controls (Villa & Ryals 2021). Results from a long-term (19 years) agricultural experiment in a maize–tomato and wheat–fallow cropping system points to the importance of accounting for changes in deep soil C through time. In this study, the winter cover crop treatment increased SOC to 30 cm by 1.44 Mg C/ha, but SOC decreased by 14.86 Mg C/ha in the 30–200 cm depths, resulting in net SOC loss. In contrast, the addition of poultry manure compost increased SOC by 21.8 Mg C/ha across the 200 cm soil profile (Tautges et al. 2019). These examples show researchers must sample deeper soils to accurately capture the influence of soil amendments on the whole soil profile before making claims as to whether the practice increases SOC storage.

The way in which exogenous C is added to soil can influence deep soil SOC dynamics and stability (Kranz et al. 2020), as exogenous C can be surface applied or buried at depth. Nutrients and organic matter from surface-applied amendments are slowly incorporated into the soil with irrigation/precipitation or bioturbation. Over time, downward vertical transport of C and resulting increases in root biomass can lead to increases in deep soil C pools (Tautges et al. 2019). Biochar, considered a persistent form of C, is more vulnerable to decomposition in surface soils, and therefore may persist longer if buried in deep soil layers (Yin et al. 2022). Recently, the burial of high C content materials has been tested as a way to store larger amounts of SOC by promoting mineral associations and decreasing decomposition. Deeper soils often have a less robust microbial diversity and function, which is often tied to edaphic conditions such as decreased oxygen, pH, or organic matter availability (Hao et al. 2021, Naylor et al. 2022). In agricultural systems with hardpans, subsurface injections of pelletized organic amendments can offset the SOC loss associated with deep tillage (Leskiw et al. 2012). Exogenous C can influence deeper soil C but whether by increasing or decreasing SOC depends upon soil type, climate, microbial communities, and the way in which amendments are applied to soil.

4.3. Physical Disturbance and Redistribution

Soil tillage is often used to reduce bulk density and manage weeds prior to seeding. Tillage reduces SOC by disrupting soil aggregates, which can result in large fluxes of respired CO_2 as microbes decompose newly available C from broken aggregates (Balesdent et al. 2000). However, tillage can also promote deep soil C storage by increasing the rate at which surface SOC is delivered to deep soils (Kirschbaum et al. 2021). Deep tillage can facilitate soil inversion, translocating surface SOC to lower depths (Olson & Al-Kaisi 2015), where it may persist longer, but it also inverts deep SOC to the surface, where it may become more vulnerable to decomposition. Full inversion tillage combined with intensive reseeding of perennial pasture systems or infrequent deep plowing techniques that bury topsoil have been proposed to increase deep SOC stocks (Madigan et al. 2022). This practice is thought to increase deep SOC stocks because buried topsoil OC decomposition slows at depth, while new SOC accumulates in the relative C-poor soil brought to the surface (Alcántara et al. 2016, Schiedung et al. 2019).

Another management option is to implement conservation- or no-till practices, which affect SOC distribution and promote stabilization of SOC within soil aggregates (Balesdent et al. 2000, Olson 2010, López-Garrido et al. 2014). No-tillage management is promoted as reducing soil erosion, increasing water infiltration, and improving biological activity (Nunes et al. 2020); however, the effect of no-till management on soil C sequestration remains debated. While the expectation is that the implementation of no-till practices increases only surface SOC, a study in a prairie ecosystem found 15 years of no-till practices increased SOC across depths of 0–40 cm (Paustian et al. 2019). In contrast, a 20-year-long study comparing no-till practices to chisel plowing found SOC increased in the top 0–5 cm while SOC decreased in the 5–75 cm root zone (Olson 2010). This result prompts us to question whether conservation tillage in any form can promote SOC increases when considering the effects on subsoil C content, as the cessation of tillage cuts off a source of subsoil C inputs. A recent meta-analysis comparing no tillage and conservation tillage highlights the importance of accounting for deep soil C and dynamics through time (Cai et al. 2022). Across 1,061 pairs of experimental data, they found that adoption of no till led to net decreases in C in the soil profile, with SOC increasing in surface soils but decreasing below 10 cm. However, over a longer period (>14 years), net C sequestration of the soil profile approached zero (Cai et al. 2022).

5. CONCLUSION

The fate of deep SOC in the face of global change will be shaped by trade-offs between biotic and mineral influences. If the influence of minerals dominates, deep SOC will likely be less sensitive to global changes like warming that cause losses, and C inputs to deep soil will be more likely to persist. However, if global change deepens the wedge of biological influence (as occurs with eCO_2, woody encroachment, and reforestation) the predicted impact on deep SOC is less clear, due to the priming response. How deep SOC responds to priming is affected by the quality of new inputs, the stoichiometry of new inputs versus existing deep SOC, microbial activity, edaphic conditions, and the potential for mineral stabilization. Over longer time frames, global change may affect mineral sorption of deep SOC via changes to mineral weathering rates caused by altered precipitation regimes or biological activity. The vulnerability of deep SOC to priming by new C inputs and global change effects on mineral SOC protection are both open research questions.

Accounting for deep SOC is critical for evaluating the impact of nature-based climate solutions and for projecting future terrestrial climate change feedbacks. Here, we show that deep soils often diverge from surface soils in their response to global change factors and that there is a severe paucity of data on deep soil responses, particularly in response to climate and atmospheric change. We urge scientists to explicitly manipulate and measure the response of deep soils in their global change experiments and management field trials, and we urge modelers to take the response of deep soils into account when projecting future carbon storage.

DISCLOSURE STATEMENT

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