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TOPICAL REVIEW

What do we know about soil carbon destabilization?

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Abstract

Most empirical and modeling research on soil carbon (C) dynamics has focused on those processes that control and promote C stabilization. However, we lack a strong, generalizable understanding of the mechanisms through which soil organic carbon (SOC) is destabilized in soils. Yet a clear understanding of C destabilization processes in soil is needed to quantify the feedbacks of the soil C cycle to the Earth system. Destabilization includes processes that occur along a spectrum through which SOC shifts from a 'protected' state to an 'available' state to microbial cells where it can be mineralized to gaseous forms or to soluble forms that are then lost from the soil system. These processes fall into three general categories: (1) release from physical occlusion through processes such as tillage, bioturbation, or freeze-thaw and wetting-drying cycles; (2) C desorption from soil solids and colloids; and (3) increased C metabolism. Many processes that stabilize soil C can also destabilize C, and C gain or loss depends on the balance between competing reactions. For example, earthworms may both destabilize C through aggregate destruction, but may also create new aggregates and redistribute C into mineral horizon. Similarly, mycorrhizae and roots form new soil C but may also destabilize old soil C through priming and promoting microbial mining; labile C inputs cause C stabilization through increased carbon use efficiency or may fuel priming. Changes to the soil environment that affect the solubility of minerals or change the relative surfaces charges of minerals can destabilize SOC, including increased pH or in the reductive dissolution of Fe-bearing minerals. By considering these different physical, chemical, and biological controls as processes that contribute to soil C destabilization, we can develop thoughtful new hypotheses about the persistence and vulnerability of C in soils and make more accurate and robust predictions of soil C cycling in a changing environment.

1. Background

A large literature exists on the mechanisms by which carbon (C) is stabilized in soils. Much of this focuses on processes and practices that increase soil C storage. However, there is less clarity surrounding C persistence in soils. For predictive models, the fates of different C inputs, and the turnover times of different C pools in soil have been inferred using multi-pool curve fitting, isotope dating, and inverse modeling. However, for all this research, we lack a strong, generalizable understanding of the mechanisms through which soil organic carbon (SOC) is destabilized in soils, knowledge that is crucial to improving predictions of C cycle feedbacks to the climate system.

There is observational evidence of destabilization pathways including desorption and priming, and contradictory literature on the response of different soil C pools to warming or changes in detrital inputs or chemistry, but these processes are not yet generalizable across soils and ecosystems and are rarely included in soil C models. Given the urgent need for accurate predictive models of greenhouse gas fluxes out of the soil that can be applied to *never before seen environmental conditions*, we review the current understanding of the mechanisms through which SOC is destabilized to microbially bioavailable or more soluble forms and ultimately mineralized to CO_2 or CH_4.

A useful paradigm for SOC stabilization has been the balance between biochemical alteration and

physicochemical protection [1, 2]. Biochemical alteration is the transformation of SOC to chemical forms that are 'recalcitrant,' or less microbially available, or else more readily sorbed to soil solids. In physicochemical protection, decomposition of SOC is slowed or prevented by organomineral interactions at molecular to millimeter scales; SOC stabilization occurs via sorption to soil binding sites, physical occlusion within aggregates, and isolation in soil pores. Recent evidence suggests that chemical recalcitrance may not be as significant to SOC persistence as previously thought [3, 4], and that overcoming the restrictions posed by spatial isolation results in rapid and extensive microbial decomposition of SOC [3]. Microbial decomposition of SOC is the primary mechanism of C loss from soils, and yet microbes are critical to the formation of aggregates and organomineral associations in soils. Thus, microbial C use efficiency may be a key balance between soil C stabilization and destabilization, but this is not well described in soil models. Destabilization of C is generally defined as a process that leads to C loss from the soil system as gaseous or soluble microbial products. However, we want to consider destabilization as processes that occur along a spectrum through which SOC shifts from a 'protected' state to an 'available' state to microbial cells where it can be mineralized. The terms protected and available are ill-defined; protected C can include C that is nominally stable (either 'slow,' 'passive,' or 'recalcitrant') as well as more labile C forms traditionally considered part of the 'active' or 'fast' pools. Therefore, it is important that researchers be extremely clear in what they are saying when they describe C destabilization and C losses.

Few reviews focus specifically on C destabilization [2, 5], yet, in a modern era of increasing rates of soil C respiration, understanding this part of the terrestrial C cycle is imperative. A review of the literature suggests that the papers that focus specifically on mechanisms of destabilization largely emerge over the past decade (e.g. [6–19]), with a sharp increase in these sample publications in the past 3 years. It has become evident that the processes of C destabilization are not mere reversals of the processes of C stabilization. For example, the positive priming of soil C occurs when new inputs of C stimulate the additional decomposition of existing, older SOC; priming by root exudates is a destabilization process that counteracts C accumulation in soils from root inputs and can cause the destabilization of centuries-old C under the right environmental conditions [20]. The microbial processes that cause priming are quite different from the process that cause the stabilization of root C inputs. Similarly, the Birch Effect, the large pulse of CO_2 that is emitted by soils immediately following the rewetting of a dry soil, does not have a corresponding stabilization process, but rather is a unique process that can significantly decrease soil C stabilization. Sorption and desorption processes of organic molecules on soil

minerals often exhibit hysteresis [21], as can the temperature-respiration relationship [22], and also a range of hydrobiogeochemical processes [23]. Thus, thermodynamics that govern C sorption to mineral surfaces are not reversable on the same time and spatial scales. Changes to local chemical environments cause structural changes to C molecules, which may alter where and how they are bound—and even such simple reaction cascades do not operate in reverse. In practice, the competing factors that promote the stabilization versus the de-stabilization of soil C under different environmental conditions drive changes to soil C pools and yet are not well understood, a knowledge gap that invites this discussion.

We offer this perspective to facilitate understanding the conditions under which C loss as CO_2 or CH_4 is likely to accelerate as climate and land uses change. Anthropogenic activities exert a strong influence on the soil C cycle, and these influences are increasingly identified as gaps in global C models [24]. The consequences of these impacts, particularly those driven by land use [25], soil warming [26], and soil moisture [27, 28] can be framed through fundamental principles of soil science: physics, chemistry, and biology. While future scenarios include local conditions that could increase soil C stocks, these increases are largely due to increased productivity; globally, however, increased C destabilization is likely to offset these limited accruals [29]. By focusing on these processes and mechanisms of C destabilization, we provide a context for empirical and computational scientists to focus on questions that directly inform the potential for soils to affect climate through the carbon cycle.

Soils vary in composition, structure, and origin, and this complexity makes it difficult to extract generalizable principles. It is also not possible to thoroughly review every cause of C destabilization in soils, when one considers the range of different land management decisions, perturbations, and climate zones in which soils occur. However, we can categorize the essential destabilization mechanisms at a biogeochemical scale, and in doing so, provide insights to the conditions under which C is most likely to be lost from soils. We focus here on 3 high-level mechanisms of soil C destabilization which can expose otherwise protected C to microbial transformation; these mechanisms align with physical, chemical, and biological drivers:

1. Release from physical occlusion: Physically protected SOC (e.g. pores, aggregates) can be destabilized by soil mixing (bioturbation, freeze-thaw, wetting-drying), changing hydrologic connections, and aggregate turnover. These processes are part of 'typical' soil dynamics but are exacerbated by disturbance.

2. C desorption: Local chemical conditions (e.g. redox, pH) affect the forms of SOC that desorb

from soil solids and colloids. These desorbed SOC forms have different transport potentials.

3. Increased C metabolism: Fundamentally, soil C desorption and transport renders C bioavailable. Microbial transformations (rates and extent) are a function of overall soil C inputs and are sensitive to changes in temperature and moisture. As we move from a 'pool-based' understanding of soil C to one that is more process-based, phenomena such as soil C priming and microbial mining of soil organic C for N are potentially more predictable.

Challenging the search for a generalized understanding of C destabilization mechanisms is the myriad of ways that we classify soil C. In many ways, these definitions are defined by the observations: density, rate of decomposition, chemical form. Each of these descriptors has value in particular applications; soil C is best defined along a spectrum of forms and chemistry. The forms of C that are destabilized, therefore, may be best understood in the context of the type of C most vulnerable to a destabilization process (figure 1); destabilization processes largely converge to solubilization of SOC, which renders it available for microbial metabolism. For each section, we explicitly identify the form or source of C most vulnerable, and we endeavor to describe that C in the context of other classifications of C, or with its native chemistry. We focus on the climate and environmental drivers that increase C availability to decomposition, and the actual increases in greenhouse gas emissions. In particular, we review the mechanisms (potential and demonstrated) of C loss (e.g. breakdown of pore-scale protection through physical disturbance), not simply system factors that correlate with C loss (e.g. soil moisture). This review is needed to inform the next generation of carbon-land models.

We conclude this perspective with discussions of soil C priming and of the Birch effect, two well-known phenomena through which increased losses of soil organic C may occur, for which the actual mechanisms remain ill-defined. We posit that both phenomena should be evaluated as emerging from the combined influences of the high-level classes of destabilization processes discussed below.

2. Soil C destabilization

2.1. Release from physical occlusion
Physical protection of soil C is well-studied [30, 31], and much of what we know about C destabilization comes from research that studies how different types of soil mixing release SOC from physical occlusion. Notably, soil tillage breaks up soil structures, and this has led to significant losses of SOC as CO_2 from agroecosystems [32]. However, naturally occurring processes can also mix the soil leading to new losses of
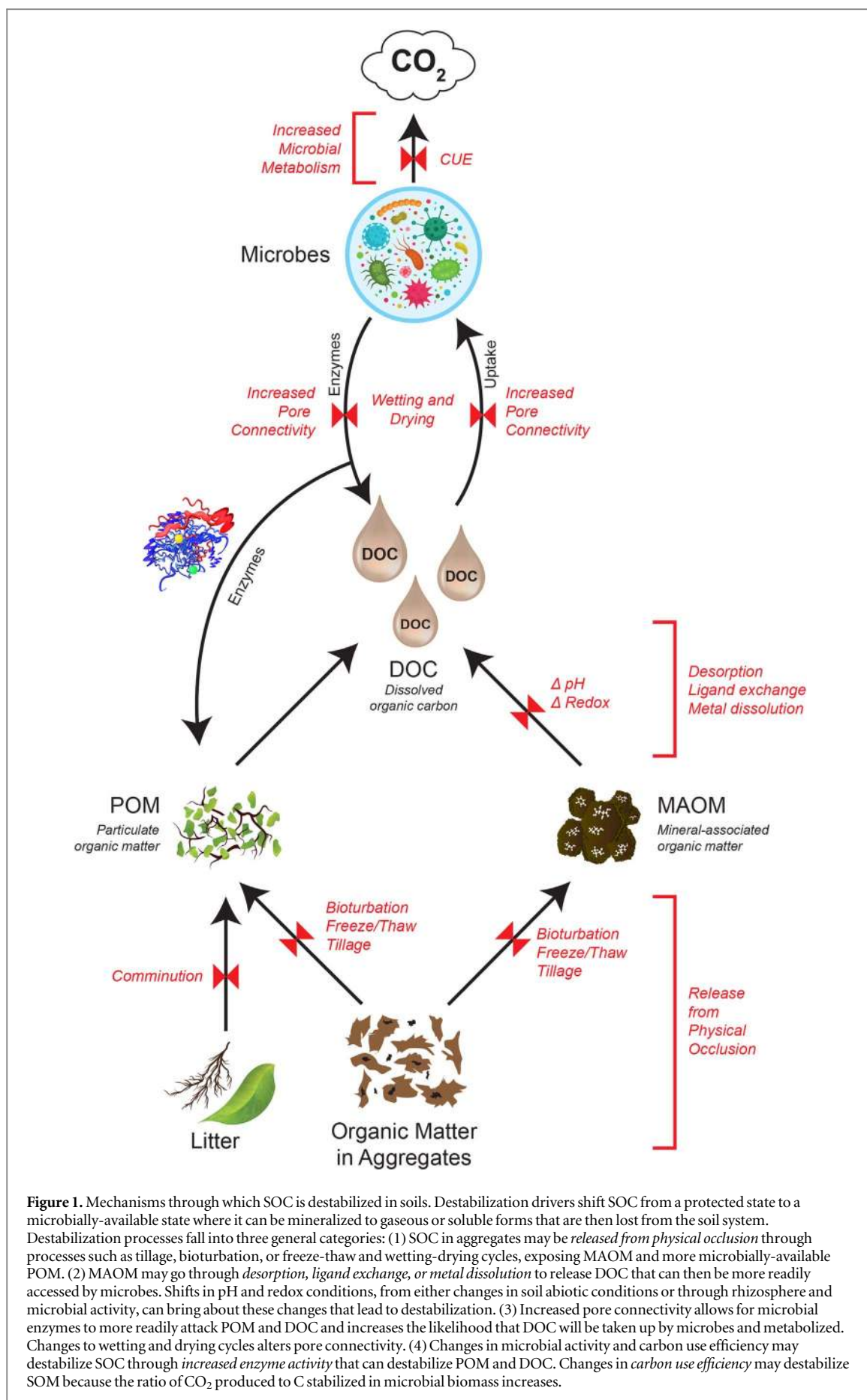
soil C, previously presumed to be stable. This mixing exposes previously occluded soil C, and also brings it into contact with soil microbes that were previously isolated (figure 1).

As structural soil units, aggregates promote SOC stability by entrapping particulate organic matter and promoting organo-mineral associations between clays and microbial residues [33], but aggregates are sensitive to physical disruption. Soil aggregates range in size and generally consist of microaggregates (<250 um) that are either free in the soil or conglomerated into macroaggregates (>250 μm; [33]). Microaggregates formed within stable macroaggregates, are thought to protect SOM in the long term [33, 34]. The persistence of C in soils is intrinsically tied to the stability of soil aggregates and processes that disrupt normal aggregate turnover destabilize soil organic C [35].

2.1.1. Tillage
Tillage has been variably reported to increase, decrease, or have no effect on soil C content [36–40] with results dependent on soil mineralogy, climate, and native soil C levels [41, 42]. Although tillage appears to consistently destabilize soil C in surface soil layers, studies that included deeper soil horizons observe greater C content in tilled soils below the average depth of plowing, thus effectively enlarging the storage space for C in horizons where potential C mineralization is low [40, 43, 44]. However, Bossuyt *et al* [45] suggest that because this deep C under conventional tillage is relatively undecomposed plant-derived C, that this C may not be stabilized in the long term if conditions at depth decrease its physical isolation from microbes.

Although increased macroaggregate turnover with tillage is often cited as the mechanism of soil C destabilization under tillage [46], several studies have found that across widely different soil mineralogies, most of the total difference in soil C content between no-till and conventional till soil was explained by the difference in C stored in microaggregates within macroaggregates [47, 48]. Such SOC losses with tillage may be due to changes in soil microbial biomass, taxonomy, and function; Sauvadet *et al* [49] reported that soil microorganisms under conventional tillage had lower C use (CUE) and enzyme efficiencies as well as greater priming of older soil C than under reduced tillage, both leading to greater C loss. Changing microbial physiology also explained enhanced C destabilization from convention till agriculture compared to organic agriculture despite fewer total C inputs and greater soil tillage under organic agriculture, which had 50% higher CUE and 56% higher microbial growth rates relative to conventional tillage [50]. Intense cultivation (i.e. tillage) decreases macroaggregate abundances leading to soil OM loss (e.g. [51]), C-poor microaggregates [31], and shorter SOC residence times [51].

Figure 1. Mechanisms through which SOC is destabilized in soils. Destabilization drivers shift SOC from a protected state to a microbially-available state where it can be mineralized to gaseous or soluble forms that are then lost from the soil system. Destabilization processes fall into three general categories: (1) SOC in aggregates may be *released from physical occlusion* through processes such as tillage, bioturbation, or freeze-thaw and wetting-drying cycles, exposing MAOM and more microbially-available POM. (2) MAOM may go through *desorption, ligand exchange, or metal dissolution* to release DOC that can then be more readily accessed by microbes. Shifts in pH and redox conditions, from either changes in soil abiotic conditions or through rhizosphere and microbial activity, can bring about these changes that lead to destabilization. (3) Increased pore connectivity allows for microbial enzymes to more readily attack POM and DOC and increases the likelihood that DOC will be taken up by microbes and metabolized. Changes to wetting and drying cycles alters pore connectivity. (4) Changes in microbial activity and carbon use efficiency may destabilize SOC through *increased enzyme activity* that can destabilize POM and DOC. Changes in *carbon use efficiency* may destabilize SOM because the ratio of CO_2 produced to C stabilized in microbial biomass increases.

2.1.2. Bioturbation

The redistribution of soil caused by the burrowing and mounding action of biota, is one of the main natural physical disturbances experienced by soils. Bioturbation can be both a destabilizing and stabilizing force depending on which bioturbation agents are active in the soil. Bottinelli *et al* [52] distinguished two main categories of bioturbation agents: Bioturbators (*sensu stricto*), which include any burrowing animal, such as small mammals and social insects like ants and termites, and soil aggregate reorganizers, of which earthworms are the best example. The burrowing bioturbators disturb soils by breaking up macroaggregates and changing the distribution of pores, which can increase aeration and water infiltration [52]. The soil aggregate reorganizers break up aggregates as well but also promote and create new aggregates as a result of their feeding behavior. The agents of bioturbation vary across regions. In mesic, temperate soils, earthworms are the dominant bioturbation agents, while termites dominate in arid tropical systems, and mammals in arid temperate systems like grasslands. Roots and fungal hyphae can also be bioturbation agents. While the effect of earthworm bioturbators on SOC stabilization and destabilization has been well-studied [53]; vertebrates such as pocket gophers (*Thomomys bottae*) have not received significant attention [54].

The ability of earthworms to destabilize SOC depends on the soil horizon and decomposition stage of the SOC. Some earthworm species directly consume plant litter leading to comminution that increases litter surface area, which can increase C losses via decomposition and leaching. Earthworms accelerate the disappearance of plant litter from the O horizon [55, 56] and in some cases can even cause the disappearance of the forest floor (Oe and Oa; [57]). When earthworms first invade a site, they destabilize soil carbon increasing soil CO_2 efflux by 33% on average [58] and decreasing SOC stock by 28% [59]. However, these carbon losses are transient due to the comminution, assimilation, and decomposition of SOC and litter. In the long term, SOC losses are reduced as more soil carbon becomes physically protected within microaggregates formed within earthworm guts, which are deposited in macroaggregate casts [58]. Thus, while at the soil surface earthworms are a destabilizing force, their feeding can redistribute SOC into mineral horizons and into microaggregates, promoting SOC stabilization [58]. In one temperate forest soil, SOC storage was positively related to earthworm density [60].

The key to whether bioturbation agents are soil aggregate reorganizers versus only a force of physical disturbance comes down to whether the bioturbation agents secrete mucilage or feed on soil [33, 52]. Earthworms do both as they secrete a mucilage that lines their burrows as well as feed on litter and SOC. Some species of termites also feed on SOC creating microaggregates within their digestive system and by secreting saliva into the soil while chewing [33]. In contrast, disturbances by soil movers such as pocket gophers can reduce SOC concentrations by over 50% [61]. However, these disturbances can also cause erosion, which may end up burying SOC, thus increasing its storage in the long term [62].

2.1.3. Freeze thaw cycles

Freezing and thawing is another physical disturbance that can disrupt soil aggregates. *In situ*, freeze thaw cycles can result in a flush of CO_2 [63, 64] and an increase in soil solution dissolved organic carbon (DOC) concentrations [65]. These increases in carbon losses are partially due to the lysing of microbial cells as freeze thaw cycles reduce microbial biomass [63, 66] but may also be due to the destabilization of SOC in aggregates. An isotopic labeling study demonstrated that 65% of the 200%–300% increase in soil carbon fluxes after freeze thaw were derived from the microbial biomass, leaving 35% of the carbon increase unexplained [67]. Freeze thaw cycles can cause aggregates to break apart due to the expansion pressure of water in aggregates expanding as it switches from a liquid to solid phase. Freeze thaw cycles decrease the proportion of soil mass found in large aggregates (>0.25 mm) and can increase the proportion of soil mass found in small aggregates (<0.25 mm; [68]), leading to a decrease in the mean weight diameter of aggregates, a metric of aggregate stability [68, 69]. Freeze thaw cycles also decrease the water stability of aggregates [70]. The initial water content of soil does not change the effect of the freeze thaw cycles on aggregates ([68, 71] but see [72]), while increasing the number of freeze thaw cycles decreases aggregate stability, but only to a point [69, 73]. Soil mineralogy can affect the vulnerability of aggregates to freeze thaw cycles with the macroaggregate proportion decreasing more due to freeze thaw in a fine sandy loam than in a loam with a greater clay and oxide content [74]. In contrast, some studies have shown increases in macroaggregate (1–4 mm) stability with freeze thaw cycles [75]. One explanation for this discrepancy is that freeze thaw cycles disrupt weak macroaggregates, leaving behind macroaggregates that are inherently more stable. By changing aggregate distributions, freeze thaw cycles can also affect the soil hydraulic conductivity: an −18 °C freeze at maximum water holding capacity decreased hydraulic conductivity while freeze-thaw at 0.5 bar of pressure increased hydraulic conductivity [72]. While numerous laboratory studies have shown that freeze thaw cycles disrupt aggregates, we are not aware of any studies that have looked at the effect of freeze thaw cycles on soil aggregates *in situ* or quantified changes in SOC availability. However, we can deduce that the disruption of aggregates will likely make previously physically-protected SOC available.

2.1.4. Wetting and drying

Finally, the most elementary of processes in soil, *wetting and drying*, regulates SOC destabilization in notably complex ways. Physically, wetting and drying cycles reshape aggregates and aggregate size distributions in soils [76] via mechanisms that include shrinking and swelling of some clay types (e.g. smectites) [77]. Hydration of these minerals are crucial mechanisms for aggregate turnover [78] and reformation, and soil clay content is the best predictor of variations in aggregate stability [79]. The outcomes of wetting and drying cycles include increased aggregate stabilities [77], but C persistence and destabilization is variable. Long-held hypotheses suggest that the chemical and physical processes that underpin aggregation are founded in forms of C that do not seem to be readily decomposed [80, 81]; new or soluble C is much more likely to be destabilized [81, 82]. However, the effects of wetting and drying on microbial activities can be significant suggesting that soil moisture, microbial C processing, and access to nutrients should be considered holistically [83–85] to accurately predict C destabilization.

Moisture content is a powerful predictor of soil C mineralization [86, 87] and this may be due to the degree of hydrologic connectivity throughout the soil pore network. Under dry conditions, microsites of potential microbial decomposition are isolated from one another with little potential for organic C and other resources such as enzymes and nutrients to diffuse to potential decomposition hot spots. Few studies have specifically addressed these hydrologic connections through the soil pore network [88–90], though the transport of soluble C via diffusion and mass transport can expose previously occluded soil C [91] (figure 1).
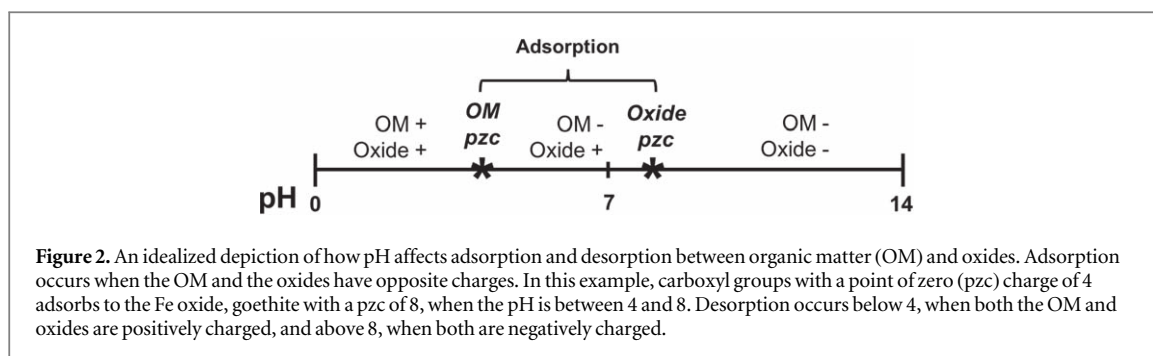
Water availability affects the pore- and mineral-scale chemical environments, changing soil C chemistry, altering the kinetics of C desorption from mineral surfaces. As soils dry, the shrinking water films that result increasingly concentrate soil solutes, and these microsites become locations of osmotic stress [92]. Such high ionic strengths can stress the microbial community and force them to produce osmolytes [92], however, these conditions also influence the forms and availability of organic carbon. During droughts the associated increase in ionic strength decreases the overall dissolved C concentrations in soils [93], however, wetting events that follow a severe drought result in increased C soluble transport via both overland flow and soil water [94]. This transport relocates C to new locations within the soil pore network, and within the landscape, leading to changes in the bioavailability of that C, and its potential decomposition.

2.2. C desorption

Recently, researchers have been able to directly observe the location, distribution, and forms of C stabilized in soil pores and on mineral surfaces [95, 96]. This has contributed to new conceptual models of C association with mineral surfaces. The zonal structure of organo-mineral associations posits that different functional groups of SOC arrange themselves in a particular way when interacting with minerals [97]. In this model, polar groups of amphiphilic molecules are attracted to charged mineral surfaces with hydrophobic groups facing outward creating a zone of hydrophobic interactions to which the hydrophobic groups of other molecules are attracted. Beyond lies the kinetic zone wherein organic molecules interact with multivalent cations. This model has implications for SOC stability because organic molecules within the kinetic zone likely experience higher rates of exchange with the soil solution [97]. Recent research has shown preferential adsorption of different organic compound classes by different phases of Fe-bearing minerals and a wide variety of organic compound classes partially sorbed to minerals, supporting the zonal model [98]. However, destabilization is not merely 'stabilization processes in reverse.' The persistence and vulnerability of the mineral-stabilized C is a product of C chemistry, soil environments, and time.

SOC can be protected by sorption to soil minerals, in particular metal oxides, and by incorporation into organo-metal complexes [99, 100]. SOC concentration is positively correlated with the amount of oxalate extractable Fe and Al in soils from wet or humid climates [101]. The age of SOC, a proxy for soil carbon stability, also positively correlates to the amount of noncrystalline Fe and Al minerals [102, 103]. Thus, changes to the soil environment that affect the solubility of minerals or organo-mineral complexes or change the relative surfaces charges of minerals and organic matter can destabilize SOC. Once no longer associated with minerals, SOC may become vulnerable to enzymatic attack or diffusion into microbial cells (figure 1).

The strength and sign (positive or negative) of surface charges change depending on the pH and ionic strength of the soil solution. Whether SOC becomes sorbed to soil minerals depends on the relative points of zero charge (PZC) of the organic matter and the minerals, which determine whether they have opposite charges in a given soil solution and are thus likely to sorb (figure 2). For a simple example, FeOOH has a PZC at about a pH of 9 below which the acidic solution donates protons to it resulting in a positive charge and above which it is negatively charged. Carboxyl groups on organic matter have a PZC at about a pH of 4. Thus, negatively-charged carboxyl groups on organic matter will sorb to positively-charged FeOOH between a pH of 4 and 9. In reality, soil minerals are a mixture of many types of clays and oxides of varying crystallinity

Figure 2. An idealized depiction of how pH affects adsorption and desorption between organic matter (OM) and oxides. Adsorption occurs when the OM and the oxides have opposite charges. In this example, carboxyl groups with a point of zero (pzc) charge of 4 adsorbs to the Fe oxide, goethite with a pzc of 8, when the pH is between 4 and 8. Desorption occurs below 4, when both the OM and oxides are positively charged, and above 8, when both are negatively charged.

and capacity for surface charge and many types of organic matter, so whether sorption happens or not at any given pH is a balance of many factors, but the principle is the same.

Across laboratory studies, whether pH changes destabilize SOC depends on the soil type and dominant stabilization mechanisms. DOC released from organic soil horizons increases with pH as the adsorption capacity of the soils is lowered [104, 105]. In a year-long planted mesocosm experiment of an acid-affected soil, a pH increase of 0.76 significantly increased the amount of water extractable carbon and microbial respiration [106]. However, in the mineral horizons of already-acidic spodosols, DOC release increased with decreasing pH due to the solubilization of organo-metal complexes by proton competition [105].

As with other test of soil carbon destabilization, the majority of these studies occurred in controlled laboratory incubations of soil or soil slurries. However, there are large scale patterns that indicate increased pH is an important control on SOC stability. In the past few decades, concentrations of DOC have been increasing in freshwater lakes and streams, particularly in the northeast of the United States and northern Europe [107], including a 91% increase in the United Kingdom [108]. One cause is likely that increasing soil pH as these regions recover from decades of acid rain (atmospheric sulfur deposition) is causing increased soil DOC losses [107, 109]. At a global scale, pH has been shown to be a master variable controlling the retention of SOC on various minerals [101], and pH is ultimately controlled by soil moisture [110]. An overall pattern partly resulting from the influence of pH on organo-mineral associations is that a higher proportion of SOC is associated with Fe and Al bearing minerals as soil moisture increases (measured as the mean annual precipitation minus the potential evapotranspiration: MAP-PET; [111]). There is an abrupt, steep increase in the amount of organo-mineral associations from −300 to 800 mm MAP-PET, implying that mineral-associated SOC destabilization across this range of moisture may be highly susceptible to small shifts in rainfall and evapotranspiration.

The solubility of iron minerals and thus their sorption capacity can also be affected by redoximorphic

cycles. Iron is a redox sensitive metal and an important stabilizing mechanism of SOC via both sorption to iron oxides and the formation of organo-metal complexes. The mobilization of Fe(III) when it is reduced to Fe(II) can release organic matter into solution. As with pH, many studies of the effect of Fe reduction on organic matter have examined the behavior of soil slurries. Reduction can mobilize colloid-bound elements (e.g. [112]) including organic carbon [113]. In slurries, the reduction of 12.5%–37.7% of Fe(III) corresponded with the release of 3.8%–9.9% of the SOC into the soil solution [114]. However, it can be difficult to separate the effects of redox and pH changes on soils because Fe reduction generates hydroxide ions (OH^-), which increase pH. In an anaerobic incubation of wetland soils, 2.5% of the total organic carbon was released as DOC as the pH rose from 5.5 to 7.4 as a result of Fe and Mn reduction. When the experiment was repeated under a constant pH, only 0.5% of the total carbon was solubilized, implying the effect was due to the pH increase and not the reduction itself [115]. In contrast, some experiments where pH was controlled showed less carbon solubilization due to the pH increase than due to iron reduction, which reduced the surface area of Fe oxides [113, 116]. Furthermore, since Fe-bearing minerals are important binding agents for soil aggregates, their reductive dissolution can increase the availability of occluded C by weakening aggregates [113].

The other half of the Fe redox cycle, Fe(II) oxidation and the subsequent hydrolysis of Fe(III), decreases pH, which can also release organic carbon in acidic soils due to the solubilization of organo-metal complexes as seen in Spodosols (above). In tropical soils, Fe (II) oxidation stimulated organic carbon decomposition as it decreased pH by two units, which doubled DOC concentrations and increased CO_2 production rates; an effect that occurred even when pH was decreased in the absence of Fe(II) oxidation [117]. Furthermore, Fe(II) oxidation in these tropical soils set off a series of reactions that generate hydroxyl radicals, which oxidize organic matter abiotically [117].

Over multiple redoximorphic cycles, the crystallinity of Fe oxides increases, possibly due to leaching losses of Fe(II), which increases the relative proportion of more crystalline Fe [118]. More crystalline Fe is

associated with faster cycling of organic matter implying increased organic matter instability [119]. Thus, redox fluctuations do not only solubilize organic carbon during the reduction half cycle, they also reduce the reactivity of minerals and thus their capacity to sorb organic carbon.

2.3. Increased C metabolism

Destabilization of SOC by microbes is more than a function of microbial access to SOC or the SOC bioavailability (figure 1). The quality of litter inputs and SOC affect the balance between organic carbon destabilization and stabilization, primarily through interactions with microbial physiology. For example, plant litter with high C:N ratios or high concentrations of complex secondary compounds are slower to decompose (i.e. recalcitrant), leading to thick organic horizons while litter or root exudates with low C:N ratios or high concentrations of simple compounds like sugars are more readily decomposable (i.e. labile). Labile inputs are thought to be more efficiently anabolized by microbes, which can ultimately lead to SOC stabilization [120]. Paradoxically, these same labile inputs may result in the destabilization of existing SOC via the priming effect. While not a focus of this section, the availability of other required resources (moisture, oxygen, other terminal electron acceptors) and temperature also affect microbial activity and thus SOC (de)stabilization.

Microbial carbon use efficiency (CUE), the proportion of consumed soil carbon that is ultimately mineralized to CO_2, is dependent upon the efficiency by which microbes turn the organic carbon they are feeding on into biomass. Microbial CUE is controlled by the microbial functional potential, the chemical form of the C substrate, and nutrient availability. The lower the microbial CUE, the more organic carbon taken up by microbes is respired as CO_2. CUE is affected by substrate quality and temperature [121]. According to the microbial efficiency matrix stabilization theory, recalcitrant substrates are more likely to leave the soil system due to the low CUE of microbes feeding on it, while labile substrates are more likely to be incorporated into microbial biomass due to high CUE and then sorbed to mineral surfaces when the microbes die [120]. Generally, CUE is greatest for the highest quality, easiest-to-decompose substrates such as glucose (CUE = 70%–75%) and is significantly less for lower quality substrates like oxalic acid (CUE = 2.8%–4.5%; [121]). CUE is expected to decrease under nutrient limitation as microbes have to release carbon in order to maintain their homeostatic C:nutrient ratios [122]. CUE is also predicted to decrease with warmer temperatures as the respiration costs associated with maintaining biomass and enzyme production and excretion increase. Some studies have found declining CUE with warmer temperatures [123], while others have found no temperature

effects [124, 125]. Frey [121] found that CUE dropped by 30% and 60% over a 20 °C increase in temperature for glutamic-acid and phenol, respectively, but that the CUE of glucose was unaffected by temperature. These inconsistent temperature effects are likely due to methodological differences in how CUE is measured [126]. Decreased CUE with increasing temperatures, however, may not ultimately lead to increased SOC mineralization because lower CUE leads to decreased microbial biomass and therefore an overall lower capacity for decomposition [127].

CUE has largely focused on bacterial activities, and to a lesser extent, on saprotrophic fungi. However, the diversity of soil microbial communities includes other microbial domains, and the turnover of the mycorrhizal external mycelium has been hypothesized to be a fundamental mechanism for the transfer of root-derived C to SOM, thus contributing to SOM stabilization and sequestration [128]. However, mycorrhizae also may stimulate the decomposition of soil carbon to mine nutrients, paradoxically causing destabilization of soil carbon pools. The effects of mycorrhizae on soil carbon balance are thus complicated by the balance between carbon stabilization effects and soil carbon priming effects [129]. The specific type of mycorrhizae matters as well, as recent research [130, 131] has demonstrated that ecosystems dominated by plants with symbiotic ectomycorrhizal fungi store more carbon in soils than ecosystems dominated by arbuscular mycorrhizae–associated plants.

3. Complex phenomena that result in soil C destabilization

When C destabilization leads to unpredictably high microbial C emissions, it is tempting to overlook the underlying contributions of soil processes that destabilize soil C. For example, both priming and the Birch Effect are often presented as singular processes that result in increased C oxidation to CO_2. However, these are not discrete processes. They are phenomena that result from soil physical, chemical, and biological C destabilization that results in the increased microbial activity. A thoughtful consideration of these phenomena can illustrate their complexity, and perhaps help resolve some of the confusion in these observations.

3.1. Priming

Under many experimental field and lab conditions, the addition of labile C has been shown to cause positive priming. Positive priming occurs when new C inputs lead to an increase in the mineralization of existing, older SOC, and is thus considered here as a destabilizing force. In nature, inputs that lead to priming can occur via the addition of fresh plant litter, the delivery of leached dissolved organic matter through soil pores, or root exudates and rhizodeposits, whose priming effects are known specifically as

rhizosphere priming. Positive priming effects can be significant and have been suggested as the mechanisms behind a lack of increased soil C after long-term CO_2 fertilization [132]. The positive priming effect is thought to be a short-lived, nonequilibrium response to new inputs [133]. Experiments adding either fresh litter [134, 135] or artificial substrates such as glucose [136, 137] have demonstrated an increased decomposition of older, mineral-associated SOM, although several studies, especially those using bare fallow soils or soils that were highly C-poor, have shown either no priming or a negative priming effect [138–140]. The amount of carbon added can affect the magnitude and direction of the priming effect [141], which may explain the lack of positive priming at C-poor sites. The positive priming effect increases linearly when the amount of substrate added is <15% of the microbial biomass C but begins to decrease when the amount of substrate added is >50% of the microbial biomass C. Negative priming can occur when the amount of substrate added exceeds 200% of the microbial biomass C as microbes preferential switch to using the new substrate over existing substrates. The priming effect is also dependent of the native soil C:N ratios and is often stronger in soils with higher C:N ratios than those with lower C:N ratios [142]. Positive priming is not due to any single mechanism and varies with soil type, microbial community, and the composition of the existing SOC and the forms of the new carbon inputs [143].

There are several proposed mechanisms for priming; the first three have to do with microbial responses, while the last mechanism involves disrupting organo-mineral associations. Priming can increase decomposition of existing SOC because the greater availability of energy increases microbial activity. In the short term, this additional energy can awaken microbes from dormancy [141] or can make enzyme production energetically favorable for microbes allowing the microbes to efficiently consume existing SOM. This priming mechanism may be especially important in destabilizing deep soil carbon, which has generally been considered to be stable due in part to low levels of microbial activity [20] and generally lower SOC availability (e.g. [144]). Deeper soils have been shown to be at least as, if not more susceptible to priming-induced losses of SOC than shallower soils [20, 145] because low inputs of fresh substrates have often limited decomposition in deep soils [146, 147]. Thus, changes in land use that increase fresh C inputs through the soil profile, for instance through the introduction of deep-rooted grasses, could stimulate the destabilization of older buried C with root exudates and rhizodeposition [146, 148].

Two other proposed mechanisms for positive priming involve the effects of C inputs on microbial community composition and physiology. When simple sugars or fresh litter are added to soil under N limitation, positive priming appears to be due to a stimulation of slow-growing K-strategists who can decompose older existing organic matter with low C:N ratios for nutrients, resulting in microbial nutrient mining [136]. In contrast, when accompanied by N additions or when N is not limiting, fast-growing r-strategists drive the increase in decomposition of younger existing organic matter with higher C:N ratios, such as plant litter and cellulose, in a process known as stoichiometric decomposition [149]. Thus, in soils where microbial activity is not energy-limited, positive priming is driven by K-strategists when the C:N ratios of substrates do not match microbial needs, while positive priming is driven by r-strategists when the C:N ratio of new inputs is similar to that of existing organic matter and nutrients are not limiting. Blagodatskaya and Kuzyakov [141] suggest that bacteria are the first group to uptake and metabolize most of the easily-available carbon inputs that are deposited into the soil, and it is their necromass that can provide energy to the K-selected fungi that specialize in accessing and degrading the complex substrates of older SOM.

The last priming mechanism does not involve microbial responses directly and instead connects back to mineral dissolution and SOC desorption from minerals. Keiluweit *et al* [150] found that a common root exudate, oxalic acid, released organic compounds from mineral-associations making the compounds bioavailable. In the experiment, adding oxalic acid to soil increased microbial activity more than adding a labile substrate like glucose and increased DOC concentrations by a factor of 8. The magnitude of positive priming has been shown to be dependent on soil mineralogy with the greatest priming responses occurring in soils with a large amount of short-range order minerals [151]. In this study, large priming responses occurred when the C inputs mimicked root exudates (40% organic acids) and when the C inputs were fresh pine needles, which are generally acidic [151].

3.2. Birch effect

Intimately tied to wetting and drying, the Birch effect was first described in 1958 as an initially very rapid phase of respiration occurring immediately after the wetting of dried soil [152]. This phenomenon has been extensively reported across a range of soils, climate zones, and land uses, both in field experiments [153, 154] and laboratory incubations [155, 156], with Birch effect-derived pulses potentially accounting for two-thirds of the soil respiration in a savanna ecosystem [157]. However, only a fraction of the reports of the Birch Effect include experiments and analyses designed to elucidate that underlying controls on this enhanced CO_2 flush (e.g. [158–160]). The controls identified have some common themes that align well with those presented here as controls on soil C destabilization. The Birch effect appears to result from a poorly resolved combination of structural

constraints [159, 161] and chemical changes to microbial habitats and SOC availability [153, 158] to which soil microbes respond [162, 163]. This response can vary depending on drought extent and duration (i.e. antecedent conditions experienced by both the soil matrix and the soil microbes) [156].

The underlying cause of the Birch effect is likely no single one of the controls alone; it is more likely the combined effects of physical controls on substrate availability and to the microbial functional state. There is some evidence that changes to the availability of other nutrients may be important; nitrogen, in the form of ammonium has been specifically reported to increase upon rewetting of dry soils [164]. Mineralogical changes to sorption sites during extended drying has also been observed to change the phosphorus sorption capacity, leading to increase phosphorus availability upon rewetting that may be related to the Birch effect [165]. In addition, drying may induce potentially reversable changes to the soil mineralogy by promoting the transformation of amorphous forms of iron oxides to more crystalline structures. This could then reduce the overall phosphorus sorption capacity, as well as the SOC sorption capacity, in the soil, resulting in increased release of P during the rewetting event. The increased nutrient availability is one hypothesis underlying the Birch effect, i.e. soil C is destabilized by the presence of abundant nutrients, provided through drying-induced changes to the mineral fraction.

At a slightly larger scale, physical integrity of soil aggregates controls the extent of the Birch effect as well; at least one report of the Birch effect found that it was only observed in crushed soil aggregates, not in intact aggregates [35]. In the field, higher CO_2 emissions during wet-dry cycles had been attributed to increased supplies of soil C from the acceleration of aggregate degradation due to precipitation events and rewetting [159, 166]. These supplies of resources derive from fresh exposure of occluded C and from alterations to the hydrologic connections through the soil pore network. The hydrologic connectivity within the soil pore network may influence the Birch effect through drying-induced changes to soil C chemical forms [155] coupled with transport (diffusion) processes [167]. The redistribution of previously sorbed or occluded C, or the selective release of certain classes of C, is a destabilization process that can directly result in increased microbial access to substrate and subsequent metabolism.

Finally, microorganisms contribute to the Birch effect in different ways. While drying alone may alter the form of soil C released, some hypotheses about the origin of the Birch effect include that the Birch effect is largely due to extracellular enzymes that are rapidly activated by rewetting, that the Birch effect is due to decomposition of microbial necromass accumulated during the drought phase [168], or that the rapid turnover of the newly stimulated microbial biomass [168]

is the source of the increased CO_2 flush. Stable isotope probing combined with quantitative PCR has shown that cell death during the drought phase, or during rapid wet-up becomes a source of readily available C that contributes in part to the Birch effect [168]. Experiments using sterile soils strongly suggest that microbial metabolism is essential for the increased CO_2 emissions associated with the Birch effect [160], and this is also observed in experiments in which respiration is partitioned; heterotrophic respiration may be driving much of the CO_2 flush [169]. Microbes that are particularly poised to respond to rewetting, can respond within the first hour of wetting, indicating that ecological resuscitation strategies may be factors in this rewetting response [170]. However, other research found that drought-induced increases to the quantities of soluble soil C were not strong influences on the magnitude of the Birch effect [161, 171].

3.3. Impact of global change on C destabilization

Global change will accelerate SOC destabilization processes in several ways. Land use change involving conversion to agriculture can release physically occluded SOC in aggregates through tillage. Historically, soils have lost 133 Pg C due to conversion to agricultural land uses [25]. Freeze thaw cycles, which have been shown to disrupts soil aggregates in the lab, are expected to increase due to climate change in snow-covered regions as the depth and duration of snow cover, which has traditionally insulated soils from freezing temperatures throughout the winter, decreases [172, 173]. Climate change is expected to increase both the intensity and duration of drought in certain regions such as the Western United States, Mediterranean, and Southern Africa [174] which will lead to drier soils. While drier soils are expected to reduce SOC losses, extreme heavy precipitation events are also expected to increase [174, 175]. This increased variability in precipitation will increase the intensity and number of soil drying and rewetting cycles, leading to more SOC destabilized as a result of the many mechanisms contributing to the Birch Effect, such as aggregate disruption. While overall soils are expected to become drier due to climate change as warming temperatures increase evapotranspiration rates [27], some higher latitude regions, such as the Northeastern United States, are becoming wetter [176]. SOC destabilization as a result of soil redox fluctuations will become more likely in these wetter regions. While temperature effects on microbial CUE are equivocal, the fact that rising temperatures will increase microbial metabolism and subsequently destabilize SOC is well known. Countless studies, both incubations and field experiments, have shown increasing CO_2 production from soils as a result of warming (e.g. [177, 178]). Lastly, the antecedent to climate change, rising atmospheric CO_2 concentrations, may increase the destabilization of SOC via

priming. Higher CO_2 concentrations increase root biomass and production throughout the soil profile [179]. The resulting larger volume of rhizosphere soil increases the amount of SOC subjected to root exudates that prime microbial activity and promote desorption or organo-mineral interactions. Overall, the effects of global change will likely increase SOC destabilization ways both large (e.g. the phase change from ice to liquid water in permafrost greatly increasing microbial metabolism) and small (e.g. increased pulses of carbon losses due to the Birch effect). While in some locations increased SOC destabilization may be compensated by increased carbon inputs from faster growing plants, on a global scale this compensation is unlikely as plants are expected to become water-limited [27].

4. Summary

Microbial access to soil carbon is the result of the many different soil physical, chemical, and biological properties, with water dynamics inextricably linked to each of these. Having outlined different properties, and destabilization processes, we explored published reports of both priming and the Birch effect to show that these phenomena are the results of multiple effects of organic matter additions on microbial enzyme production, metabolism, and the disruption of organo-mineral interactions by organic acids, and the Birch effect is governed by the simultaneous effects of some or all of the soil responses to drying and rewetting. In both phenomena, the relative contributions of each factor likely vary for many reasons, including soil type, site, and land use. However, by considering these different physical, chemical, and biological controls as processes that contribute to *soil C destabilization*, we can develop thoughtful new hypotheses about the persistence and vulnerability of C in soils and make more accurate and robust predictions of soil C cycling in a changing environment.

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