

# Heterotrophic respiration by soil microbes in a changing climate

Janet K. Jansson <sup>1</sup>✉, Avi I. Flamholz <sup>2</sup>, Raquel Peixoto<sup>1,3</sup>, Joana Falcao Salles <sup>1,4</sup>, Jay T. Lennon <sup>1,5</sup>, Alexandre Soares Rosado <sup>1,3</sup>, Ian R. Sanders <sup>1,6</sup>, Carsten S. Jacobsen<sup>1,7</sup>, Thulani Makhalanyane <sup>1,8</sup>, Christopher W. Schadt <sup>1,9</sup> & Jack A. Gilbert<sup>1,10</sup>✉

## Abstract

Soil microbes strongly influence the soil organic carbon (SOC) pool, which globally stores ~2,000 PgC. Specifically, the balance between microbial heterotrophic respiration ( $R_H$ ), which degrades SOC, and plant–microbe interactions that stabilize SOC determines whether terrestrial ecosystems are a net source or sink of CO<sub>2</sub> to the atmosphere. In this Review, we evaluate how climate change alters these competing processes.  $R_H$  is approximately half of total soil respiration, at ~50 PgC yr<sup>-1</sup>, with 70% occurring in topsoils. Warming accelerates microbial metabolism, with a 10 °C temperature increase estimated to raise  $R_H$  by ~50%, an effect that is particularly strong in Arctic soils. Warming also reduces soil moisture, further modulating  $R_H$ , which responds nonlinearly to soil moisture, being limited by saturation and desiccation and meeting a maximum at intermediate levels. Consequently,  $R_H$  is highly sensitive to future precipitation changes and drought. However, soil management strategies could enhance SOC stocks and persistence under climate change. Bacterial and fungal inoculants can promote SOC production and stabilization, while deep-rooting plants increase SOC inputs to deeper layers that experience lower  $R_H$ . Agricultural practices and biochar amendments can also enhance SOC and reduce  $R_H$ . Expanding field trials across regions, climates and soil types would improve empirical understanding of these responses and support better representation of  $R_H$  in predictive models, enabling more accurate assessments of climate impacts on SOC storage.

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A full list of affiliations appears at the end of the paper. ✉e-mail: [janetraejansson@gmail.com](mailto:janetraejansson@gmail.com); [gilbertjack@gmail.com](mailto:gilbertjack@gmail.com)

## Introduction

The balance of terrestrial photosynthesis and respiration determines whether the terrestrial environment acts as a source or sink of CO<sub>2</sub> to the atmosphere<sup>1</sup>. Each year, terrestrial plants take up roughly 115–130 petagrams (Pg; 10<sup>18</sup> g) of carbon as CO<sub>2</sub> (refs. 2,3), corresponding to approximately a fifth of the carbon in the atmosphere<sup>3</sup>. Of this, about half is respired by plants back into the atmosphere (autotrophic respiration,  $R_A$ ), and much of the remainder (~50 PgC yr<sup>-1</sup>) is returned to the atmosphere by heterotrophic respiration ( $R_H$ ) by soil microorganisms<sup>4</sup>. Today, the global terrestrial biosphere is a net CO<sub>2</sub> sink that offsets roughly a third of annual anthropogenic emissions, absorbing ~3 PgC yr<sup>-1</sup> compared with ~10 PgC yr<sup>-1</sup> of CO<sub>2</sub>-equivalent emissions<sup>3,5</sup>. Whether this land sink will strengthen or weaken in the future depends, in part, on how soil microorganisms respond to a changing climate.

In soils, microbial heterotrophs perform respiratory metabolism, converting soil organic carbon (SOC), mostly deposited by plants, into atmospheric CO<sub>2</sub>. These organic deposits include leaf litter, woody debris, root exudates, and microbial structures (for example fungal mycelia) fed by interactions with plants. Some of this carbon is quickly degraded, but other fractions persist for thousands of years, especially in cold climates<sup>6</sup>. Like most biological phenomena,  $R_H$  is strongly affected by environmental variables including temperature, water availability and the amount of organic carbon available in the soil<sup>7</sup>. Furthermore, elevated atmospheric CO<sub>2</sub> can fertilize plant growth, potentially resulting in increased photosynthetic output<sup>8–11</sup>. The resulting plant-derived carbon is stored in a variety of living and non-living forms, in plant, animal and microbial biomass, and as plant detritus. SOC is subsequently respired back to CO<sub>2</sub> over timescales ranging from years to millennia<sup>12</sup>.

Atmospheric carbon dioxide (CO<sub>2</sub>) levels have been increasing owing to anthropogenic emissions and other activities, driving a steady rise in mean global temperatures<sup>1</sup>. The planet reached a 1.5 °C increase above pre-industrial average global temperature for the first time in 2024 (ref. 13), with the NOAA Global Monitoring Laboratory recording unprecedented atmospheric CO<sub>2</sub> concentrations exceeding 430 ppm in May 2025. These atmospheric CO<sub>2</sub> levels are equivalent to a stock of ~1,000 Pg of carbon<sup>3</sup> and roughly half the global SOC stock (~2,000 Pg)<sup>3</sup>. The response of soil microbes to this and future global warming will strongly influence the terrestrial biosphere's status as a net CO<sub>2</sub> sink or source. On the one hand, warming tends to accelerate microbial respiration in soils, increasing CO<sub>2</sub> efflux<sup>7</sup>. On the other hand, soil microorganisms might also form symbioses with plants and stabilizing interactions with SOC that enhance the land sink<sup>7</sup>. It is therefore crucial to understand the spatial and temporal heterogeneity of these microbial effects and accurately predict whether they will intensify or attenuate the land sink.

In this Review, we synthesize diverse observational and experimental data on soil  $R_H$  (Fig. 1). First, we discuss the role of  $R_H$  in the global carbon cycle, before exploring how  $R_H$  is influenced by soil carbon chemistry and climate change. Next, we discuss interventions that might help soils lower  $R_H$  and retain soil carbon in the future. Finally, we outline priorities for future work, including expanding observational networks and using artificial intelligence (AI) to support the development of evolving microbial trait evolution in Earth system models (ESMs).

## Role in the global carbon cycle

The amount of SOC contained in Earth's soils is approximately 2,000 PgC (refs. 14,15). Globally, total soil respiration estimates

( $R_S$ ), including autotrophic respiration from plant roots ( $R_A$ ) and  $R_H$ , range from ~90 to 130 PgC yr<sup>-1</sup>, which is roughly tenfold greater than anthropogenic CO<sub>2</sub> emissions<sup>2,4,16</sup>. The highest  $R_S$  values are found in tropical regions<sup>4</sup>. Specifically, the highest predicted annual  $R_S$  is in evergreen broadleaf forests (~1,300 gC m<sup>-2</sup> yr<sup>-1</sup>), followed by savannas (~930 gC m<sup>-2</sup> yr<sup>-1</sup>) and deciduous broadleaf forests (~880 gC m<sup>-2</sup> yr<sup>-1</sup>) (Fig. 2). In addition, machine-learning predictions indicate that  $R_S$  is significantly higher in high-income regions owing to differences in the vegetation index in those regions<sup>17</sup>. Furthermore, simulations suggest that  $R_H$  from the topsoil layer (0–10 cm) represents ~70% of total estimated  $R_H$ , or ~282 gC m<sup>-2</sup> yr<sup>-1</sup> (ref. 18).

Total soil respiration is often not directly measured but estimated by scaling up site-level measurements<sup>4,19</sup> or by carbon balance<sup>20</sup> (Fig. 1). Subtracting respiration and wildfire from total photosynthesis gives the quantity of organic carbon retained by the biological land sink for carbon<sup>7</sup>. Both  $R_S$  and  $R_H$  are typically measured as CO<sub>2</sub> efflux from soil, which results from a composite of several biotic and abiotic processes<sup>7</sup>. Data compilations are then used to estimate global quantities<sup>21</sup> based on the Soil Respiration Database (SRDB)<sup>22</sup>. The mean  $R_H$  value in SRDB is 480 gC m<sup>-2</sup> yr<sup>-1</sup> (ref. 22). There are, however, substantial uncertainties in these global estimates (10–30%; refs. 4,21), and estimated respiration rates are sometimes inconsistent with other measured ecosystem properties<sup>23</sup>. What remains clear is that the  $R_H$  flux is large (tens of PgC yr<sup>-1</sup>) and sensitive to Earth's changing climate, which affects  $R_H$  through changing temperatures<sup>24–26</sup>, water availability<sup>27–30</sup> and organic carbon inputs<sup>29,31,32</sup>, among other factors.

By applying estimates of the  $R_H/R_S$  ratio from sites where both values were measured<sup>33,34</sup>, soil heterotrophic respiration is estimated at  $R_H \approx 50$  PgC yr<sup>-1</sup>, or approximately half of  $R_S$  (refs. 4,35). Although  $R_H$  is uncertain, sensitive to climate and a key source of uncertainty in climate projections<sup>36–39</sup>, most climate model estimates indicate that  $R_H$  has been steadily increasing<sup>18</sup>. Extrapolating available model estimates into the future predicts a 40% global increase in heterotrophic respiration by the end of the century, driven largely by declines in soil moisture in the Arctic<sup>18</sup>.

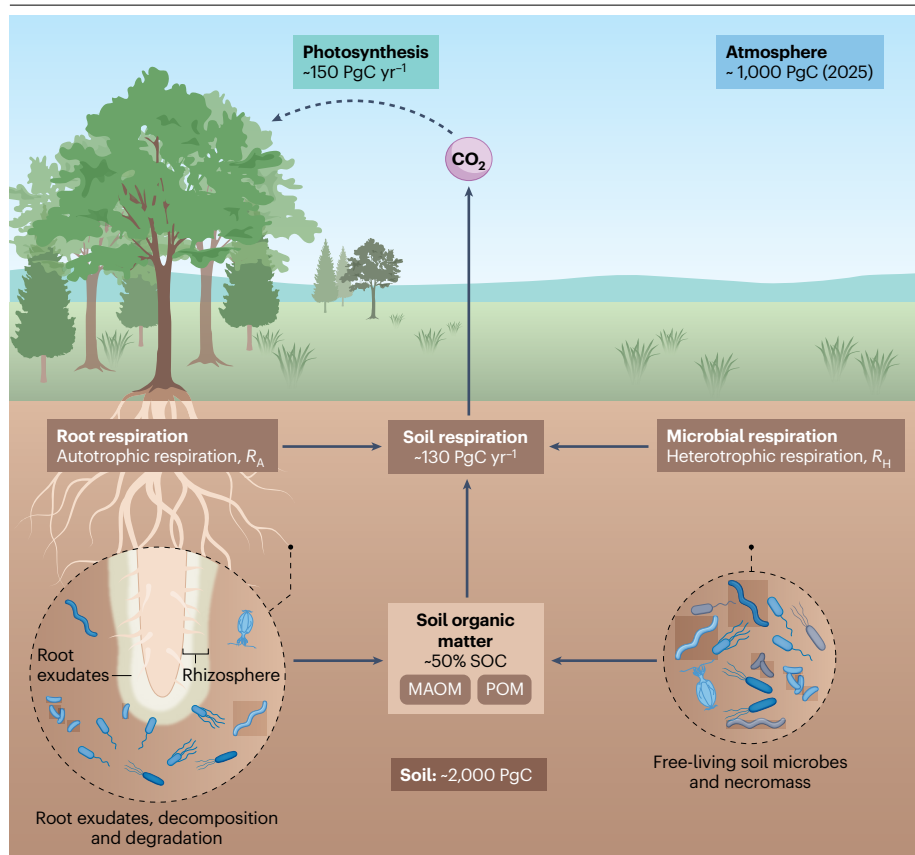
## Soil carbon chemistry and respiration

SOC consists of different types of molecules, including organic and inorganic forms. This section discusses the influence of SOC chemistry on microbial respiration.

### Carbon forms in soil

The inorganic part of soils is formed by chemical and physical weathering of minerals, and so the dry mass of soils is ~90% mineral: rocks, sand, silt and clays<sup>40</sup>. Most of the remainder (~10%) is soil organic matter (SOM), of which approximately 50% is carbon by mass<sup>40</sup>, which includes all organic components of soil, such as decomposing plant and animal residues, exudates from roots and mycorrhizal fungi, living and dead microorganisms, and various substances synthesized by soil organisms<sup>41</sup>.

Soil organics primarily originate from plants<sup>42</sup> and are subsequently transformed and respired by diverse microbes<sup>43,44</sup> yielding microbial biomass, CO<sub>2</sub>, and other terminal products such as methane (CH<sub>4</sub>) (Box 1). Like all organic materials, SOM contains carbon bonded to other elements such as nitrogen (N), phosphorus (P) and oxygen (O<sub>2</sub>). SOC refers specifically to the carbon in SOM and is often measured to assess the amount of carbon stored in soils and to evaluate soil health. Generally, SOM constitutes ~50% carbon by mass, and so SOC  $\approx$  SOM/2 (ref. 40). Globally, SOC stocks are likely to be growing<sup>12</sup>.



**Fig. 1 | Soil carbon cycle.** Plants take up carbon dioxide ( $\text{CO}_2$ ) from the atmosphere by photosynthesis. Some of the plant-incorporated carbon is deposited into the soil through root exudates and decomposing plant material in the rhizosphere (area of soil influenced by the root). Soil carbon is returned as  $\text{CO}_2$  to the atmosphere via soil respiration, including both microbial respiration (heterotrophic respiration,  $R_H$ ) by free-living soil and rhizosphere microorganisms, and root respiration (autotrophic respiration,  $R_A$ ). Soil organic matter contains  $\sim 50\%$  soil organic carbon (SOC) and consists of particulate organic matter (POM) and mineral-associated organic matter (MAOM). Both free-living microbes and necromass can contribute to the soil organic matter pool, with necromass more often stabilized by association to minerals as MAOM. Black arrows represent the flow of carbon from the soil to the atmosphere. Dashed arrow represents flow of carbon from the atmosphere to plants via photosynthesis. In summary, soil respiration processes have an important role in the flow of carbon from the atmosphere to and from the soil.

SOM is traditionally subdivided into operationally defined categories that display characteristic differences in chemistry and stability<sup>41,45</sup>. For example, water-soluble organics are extractable with water and pass a filter. Particulate organic matter (POM), which does not pass the filter, consists mainly of highly structured and chemically complex organics<sup>41,45</sup>. POM is formed from the fragmentation and aggregation of plant and microbially derived materials. The structural complexity of POM means that microbes must secrete enzymes to break it down extracellularly, producing smaller molecules for uptake and intracellular metabolism<sup>41,45</sup>. Mineral-associated organic matter (MAOM) is formed from the sorption of SOC to soil mineral surfaces that act as a barrier to microbial access. Indeed, mean estimates of MAOM turnover times,  $\sim 130$  years in the top metre of soil<sup>46</sup>, are notably longer than the typical mean turnover time of  $\sim 23$  years for POM<sup>41,46–48</sup>. Meta-analyses of soil fractions indicate that MAOM represents  $>50\%$  of SOC in surface and deeper soil layers<sup>49,50</sup>. As such, the prevalence of MAOM in global soils motivates a thoughtful consideration of the factors affecting microbial access to organic substrates.

## Plant and microbial inputs to soil carbon

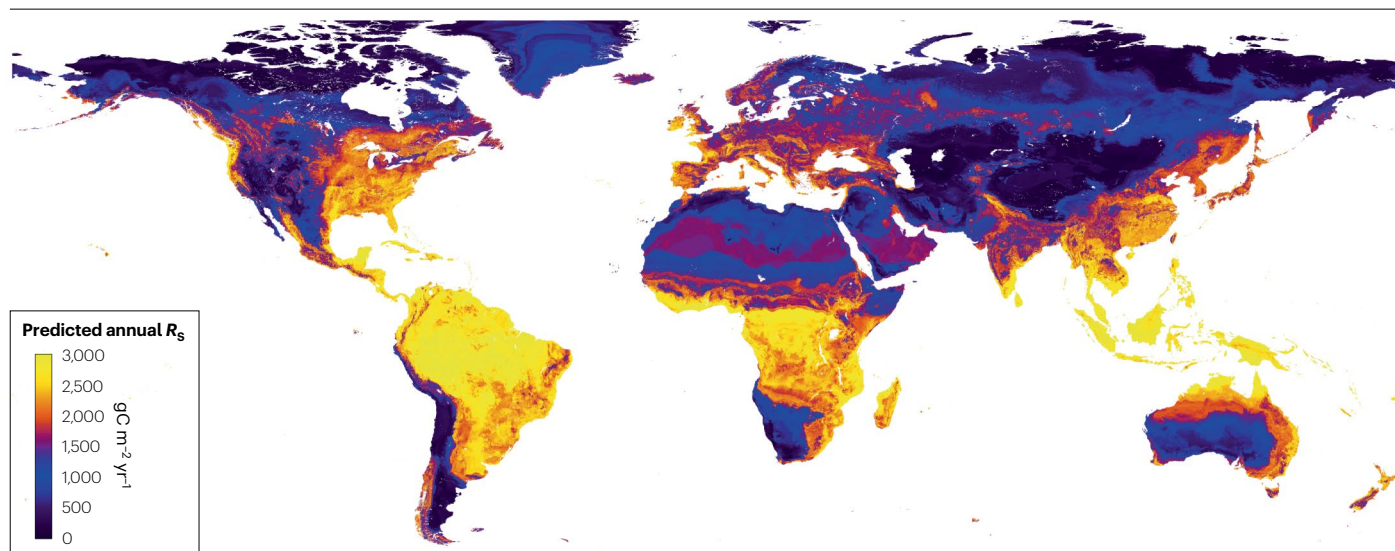
The various plant tissues forming SOC have different physical structures and distinct chemical compositions that affect their ability to be respired by soil microorganisms<sup>51,52</sup>. For example, woody plant tissues are mostly composed of sugar polymers (cellulose, hemicellulose and pectin) and lignin (a cross-linked network of aromatic monolignols)<sup>51</sup>. Microbes secrete enzymes, which use metals (such as Mn, Cu) and

reactive oxygen species (for example  $\text{H}_2\text{O}_2$ ,  $\bullet\text{OH}$ ), to attack these polymer networks and generate monomers suitable for intracellular catabolism<sup>53</sup>. Further, woody tissues contain little protein, nucleic acid or lipids, and, consequently, far less N than leaves, microbial biomass or animal excreta. A resulting elemental imbalance is generated that makes woody tissues poor substrates for microbial growth<sup>54</sup>. By contrast, root exudates from perennial grasses are a mixture of smaller polar and semipolar compounds that are more readily degraded and respired<sup>55</sup>.

In addition to plant inputs, soil microorganisms can contribute directly to the SOC pool. The microbial carbon pump concept suggests that microbial necromass (the biomass of dead microbes) is a relatively stable SOC pool<sup>56</sup>. Indeed, microbial necromass is potentially prone to mineral association, as the small size of microbial cells could promote association with minerals<sup>56,57</sup>. If microbes convert organics into biomass efficiently and then die in close association with minerals, this would form a microbial pump that contributes to MAOM formation and soil carbon stabilization<sup>56,58,59</sup>. Meta-analyses of proxies for microbial biomass estimate that microbial fractions of SOC<sup>60,61</sup> and MAOM<sup>62</sup> are of the order of 10–30%, even exceeding 50% in some cases. These estimates are consistent with the concept of a microbial carbon pump in soils.

Historically, it was presumed that some organic molecules are intrinsically recalcitrant to decomposition. Recalcitrant SOM was thought to be composed of highly cross-linked polymers formed by a humification process<sup>63</sup>. Yet these polymers have proven challenging to identify<sup>64,65</sup>. More broadly, the term ‘recalcitrance’ accommodates a range of definitions, limiting its conceptual usefulness<sup>64,66</sup>. A more





**Fig. 2 | Predicted total soil respiration.** Global annual estimated total soil respiration ( $R_s$ ,  $\text{gC m}^{-2} \text{yr}^{-1}$ ) at 1-km spatial resolution (modified from ref. 4). On a global scale, soil respiration is predicted to be higher in tropical regions.

nuanced contemporary framework posits that the rate of organic carbon degradation is an ecosystem property<sup>65,67</sup>, meaning that SOC decomposition depends on a range of intrinsic and environmental factors. Such factors include molecular structure (for example polymerization), chemistry (for example aromaticity) and the local environment, which is itself characterized by a host of factors such as pH,  $\text{O}_2$  tension, water potential, mineral protection, clay content, porosity and microbial community composition, as discussed in the next section. Anaerobic processes can also decompose SOC into  $\text{CO}_2$ , but aerobic processes are generally faster (Box 1).

## Key factors influencing microbial respiration

Compiled evidence for key chemical features of organic molecules that affect microbial respiration is now discussed, acknowledging the highly complex chemistry of SOC. This synthesis includes organic carbon in sediments in addition to soils, given the large conceptual overlap between soils and sediments. For example, mineral association protects organics in both sediments and soils<sup>68–71</sup>.

Evidence from sediment studies highlights that  $\text{O}_2$  exposure time is a major factor determining microbial respiration capacity<sup>72</sup>. In the presence of  $\text{O}_2$  it is both thermodynamically favourable and biochemically feasible for microbes to attack polymers, and degrade and respire all common soluble organics<sup>53,73–75</sup>. When  $\text{O}_2$  is absent, however, the initial steps of SOC oxidation are less thermodynamically favourable, especially when the carbon is reduced (electron rich), as in lipids and aromatics<sup>74–77</sup>. As a result, lipids and waxes tend to be retained in floodplain sediments as well as wetter and deeper soils<sup>76,78,79</sup>. Similarly, lignified plant tissues degrade much more rapidly in oxic settings<sup>80</sup>, partly owing to the many enzymes involved in microbial lignin degradation that rely on  $\text{O}_2$  and reactive oxygen species<sup>53,81,82</sup>.

## Descriptors of SOC impacts on respiration

Apparent respiration rates, based on measured  $\text{CO}_2$  efflux from the soil surface, are influenced by certain descriptors of soils and SOC. These include the redox state of carbon, its physical accessibility to microbes,

the availability of key nutrients such as N and P, and the presence of high-potential electron acceptors, specifically  $\text{O}_2$  and  $\text{NO}_3^-$  (refs. 71–79). The character of the soil, its texture, lithology, chemistry and resident plants, also determines the nature of organic inputs, the penetrance of  $\text{O}_2$ , the forms of mineral association, and the physicochemical environment that microorganisms encounter<sup>83</sup>.

Together, these descriptors determine both the rate of  $R_H$  and the spectrum of organics that microbes can profitably oxidize. In well-drained, mesic mineral soils – such as temperate agricultural fields, grasslands and tropical upland forests – air-filled pores keep  $\text{O}_2$  replenished<sup>84,85</sup>, aerobic heterotrophs dominate, and  $R_H$  can consume nearly the full range of plant inputs. Such inputs include labile sugars, amino acids and organic acids within hours to days<sup>86,87</sup>; structural polysaccharides such as cellulose and hemicellulose over weeks to months<sup>88</sup>; and even lignin and other aromatic polymers, given the  $\text{O}_2$ -dependent oxidative enzymes (peroxidases, laccases, mono-oxygenases and dioxygenases) needed to attack them<sup>89,90</sup>. Under these conditions,  $R_H$  commonly accounts for 50–70% of total soil respiration and can exceed  $500 \text{ gC m}^{-2} \text{yr}^{-1}$  in productive tropical and temperate systems<sup>91,92</sup>.

By contrast,  $R_H$  is effectively switched off where  $\text{O}_2$  supply collapses, most obviously following inundation or flooding; for example in peatlands, rice paddies, floodplain sediments, the active layer of thawing permafrost, and deep horizons below the water table. Because  $\text{O}_2$  diffuses roughly four orders of magnitude more slowly through water than through air, aerobic demand quickly outstrips supply, and microbes shift down the thermodynamic ladder of alternative electron acceptors ( $\text{NO}_3^- \rightarrow \text{Mn(IV)} \rightarrow \text{Fe(III)} \rightarrow \text{SO}_4^{2-} \rightarrow \text{CO}_2$ ; Box 1), each yielding progressively less energy<sup>93</sup>. The accessible substrate spectrum narrows accordingly, whereby relatively oxidized, low-molecular-weight compounds (sugars, organic acids, some amino acids) continue to be respired or fermented, and reduced or polymeric compounds (such as lipids, waxes, lignin and other aromatics), accumulate because their initial oxidation is no longer thermodynamically or enzymatically feasible. The net effect is that  $R_H$  in waterlogged peats and wetlands is often

one to two orders of magnitude slower than in adjacent aerobic soils, which is a central reason that these ecosystems store a disproportionate share of global SOC despite their limited areal extent<sup>94,95</sup>. Even within a single profile, millimetre-scale anoxic microsites can coexist with oxic pores, sustaining aerobic and anaerobic metabolisms in parallel and producing the heterogeneous  $R_H$  signal observed at the soil surface<sup>84</sup>.

Small monomers that are redox neutral (sugars) or oxidized (organic acids) are more readily degraded than more complex compounds because they can be transported directly into microbial cells without prior extracellular hydrolysis, and their partially oxidized carbon requires few enzymatic steps to reach central metabolism and yield a favourable energy return<sup>86,96</sup>. By contrast, polymeric and reduced molecules are preferentially preserved in wet and deep soils (as outlined above), where the  $O_2$  needed to make their oxidation thermodynamically favourable is scarce<sup>96</sup> (Box 1). Indeed, deeper soil layers (~3 m) are enriched in reduced molecules compared with surface soils<sup>79</sup>. Notably, as fractionation and detailed chemical characterization of SOM are technically challenging, the residence times of different carbon forms in different soil types, depths and climate zones merit further study.

## Carbon-use efficiency and respiration

SOC can be respired by soil microorganisms to  $CO_2$ , excreted in various forms, or converted into biomass<sup>97</sup>. The ratio of respiratory  $CO_2$  production to total carbon uptake ( $R/U$ ) determines the fraction of total microbial carbon uptake (flux  $U$ ) that becomes  $CO_2$  (respiration

flux  $R$ ) and can be estimated from measurements<sup>97</sup>. One way to estimate the respired fraction is through its inverse, the carbon-use efficiency (CUE), which equals  $1 - R/U$ . CUE is a carbon yield whose value reflects the fraction of microbial SOC uptake that is not respired to  $CO_2$  but instead retained in soil<sup>97</sup>.

Given this definition, soils with high CUE might be expected to have high SOC stocks<sup>59,98</sup>. However, CUE values are usually derived from measuring the incorporation of labelled substrates, such as  $^{13}C$  glucose, into microbial biomass over hours or days<sup>98,99</sup>, whereas SOC is often hundreds or thousands of years old and its stocks result from processes occurring over much longer timescales<sup>100</sup>. Thus, to observe a correspondence between CUE and SOC stocks across sites, CUE values would need to be relatively consistent over decades and centuries, which is not at all obvious. Further challenges arise from noting that efficient carbon utilization produces microbial biomass, which can catalyse additional respiration, and microbial anabolism requires many nutrients in addition to carbon, including N and P (refs. 98,101). In addition, although CUE is widely used to understand<sup>98,102,103</sup> and estimate microbial respiration in global soils<sup>36</sup>, a profound disconnect remains between physiological understanding of the CUE of laboratory cultures<sup>104,105</sup> and the carbon utilization that occurs in complex microbial communities in soils<sup>97</sup>. Thus, several confounding variables could influence the relationship between CUE and SOC stocks.

Despite these material caveats, there is a significant and positive correlation between SOC and CUE<sup>98</sup>. A meta-analysis of 132 sites found

## Box 1 | Soil microbial respiration and greenhouse gas production

Soil microorganisms use respiration to generate energy by extracting electrons ( $e^-$ ) from available  $e^-$  donors and donating them to  $e^-$  acceptors.

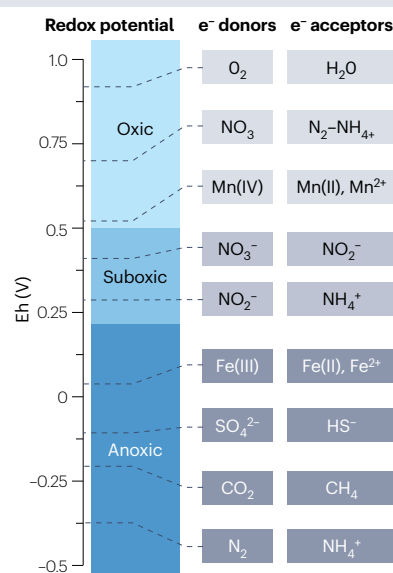
Heterotrophic respiration ( $R_H$ ) generates biological energy by coupling the oxidation of organic matter to the reduction of an  $e^-$  acceptor, such as  $O_2$  or nitrate ( $NO_3^-$ ). Although the most thermodynamically favourable and vigorous process — aerobic respiration — uses  $O_2$ , microbes can use a wide range of  $e^-$  acceptors. The order of preference of  $e^-$  acceptors is  $O_2$ , then  $NO_3^-$  and then  $Fe^{3+}$ .

Denitrification is a respiratory process that uses  $NO_3^-$  as an  $e^-$  acceptor in low  $O_2$  settings. The sequential oxidation of  $NO_3^-$  to  $N_2$  passes through an intermediate, nitrous oxide ( $N_2O$ ), the third most potent greenhouse gas (GHG) after  $CO_2$  and methane ( $CH_4$ ).  $N_2O$  and  $CH_4$  production are strongly associated with low  $O_2$  concentrations typical of waterlogged, suboxic or anoxic soils.

Respiration can draw  $e^-$  from other sources than organics. For example, some methanogens use molecular hydrogen ( $H_2$ ) as an  $e^-$  donor to sequentially reduce  $CO_2$  to  $CH_4$ . As  $CO_2$  is a very poor  $e^-$  acceptor, methanogenesis typically occurs when other  $e^-$  acceptors have been exhausted, such as in anoxic and waterlogged environments.

However, moisture levels and redox conditions can fluctuate. Under these fluctuations, a substantial fraction of soil microbes can enter dormancy, later reactivating. Upon reactivation, short-term pulses of  $R_H$  are generated as intracellular reserves, and labile substrates are rapidly respired.

Therefore, applying thermodynamic concepts to natural environments requires nuance. Heterogeneous  $O_2$  concentrations — driven by spatiotemporal variation in local microbial production and



consumption — permit the coexistence of aerobic and anaerobic metabolisms at sites that seem oxic based on bulk concentrations. Thus, concentrations are imperfect proxies for fluxes. From a climate perspective, a forcing-weighted average of GHG fluxes is most important, focusing attention on rapid aerobic respirations and anaerobic metabolisms producing potent GHGs, such as  $N_2O$  and  $CH_4$ .

that CUE is more informative than other factors in explaining variation in SOC stocks<sup>98</sup>, highlighting the usefulness of CUE in understanding the persistence of SOC.

## Climate-change impacts on respiration

Climate change is associated with increasing atmospheric CO<sub>2</sub> and soil warming, as well as changes in the frequency and intensity of precipitation, flood and fire<sup>106</sup>. These changes can affect  $R_H$  in myriad ways<sup>106</sup> due to their impacts on microbial activity, community dynamics and substrate availability (Fig. 3). This section focuses primarily on temperature and moisture as key climate variables that influence heterotrophic respiration by soil microorganisms. Although temperature and moisture effects on respiration are linked, these two factors are discussed separately below.

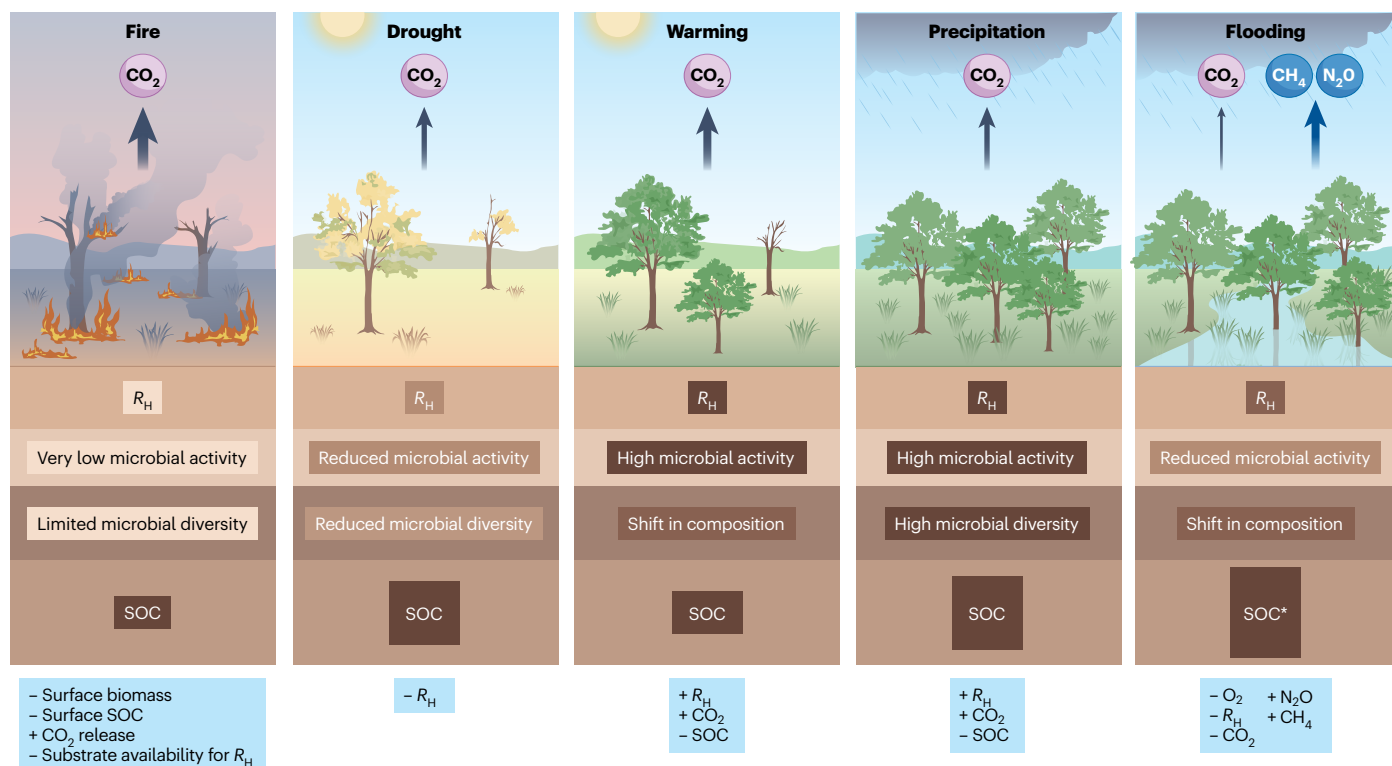
### Impacts on soil microbes

Climate change can affect microbial communities and their ability to respire SOC directly, through effects on microbial growth and survival; and indirectly, through changes in moisture, nutrient availability and vegetation dynamics. One way to predict temperature responses is to experiment with isolated microbes and microbial communities in the laboratory<sup>105,107,108</sup>. Other approaches involve soil incubations<sup>109,110</sup>, field warming experiments<sup>111–113</sup> and meta-analyses of environmental

datasets<sup>114</sup>. Unfortunately, rigorous quantitative connections between laboratory measurements, incubations and field studies remain elusive.

Characterizations of microbial community and functional diversity and composition offer insights into the responses of microbial communities to climate change<sup>114–116</sup>. For instance, sequencing data indicate the abundances of microbial taxa by counting ribosomal marker genes associated with particular lineages<sup>117</sup>. Similarly, chemical analysis of phospholipid fatty acid content reports on the relative abundance of lipids associated with certain taxa<sup>118,119</sup>. Other types of analyses offer insight into the functional response of soil microbes to climate change. Sequencing of total RNA (metatranscriptomics) or quantification of proteins (metaproteomics) can provide detail about how soil microorganisms respond to changes in environmental conditions by making different RNAs and proteins<sup>120</sup>. For example, this combination of approaches was used to document a shift from heterotrophic respiration to methanogenesis in response to permafrost thaw<sup>121</sup>.

These approaches have been used to show that soil warming leads to a simplified microbial community structure, as opportunistic taxa increase in abundance and vulnerable taxa decline<sup>122</sup>. Meta-analyses across warming gradients revealed that increasing temperature reduces the species diversity of soil microbial communities<sup>123</sup>. Across wetland and dryland ecosystems, more than one-third of microbial taxa displayed either opportunistic (increasing) or vulnerable



**Fig. 3 | Influence of climate drivers on soil carbon stocks and heterotrophic respiration.** From left to right: fire, drought, warming, precipitation and flooding are shown on individual panels that represent climate impacts on heterotrophic respiration ( $R_H$ ). Grey-black arrows represent carbon dioxide (CO<sub>2</sub>) efflux, with width proportional to flux; the blue arrow represents methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) effluxes. The beige-to-brown boxes represent heterotrophic microbial respiration ( $R_H$ ), microbial activity, microbial composition and the soil organic carbon (SOC) pool. The relative darkness and/or size of each box reflects

the magnitude of the response. SOC\* indicates that this representation is an estimate, as SOC under prolonged saturation might increase, decrease or remain stable depending on oxygen availability, dissolved organic carbon export, plant inputs, sedimentation and anaerobic mineralization. The blue boxes represent cumulative changes in soil properties as a result of different climate-change scenarios. In summary, different aspects of climate change can have different impacts on soil microorganisms and their activity,  $R_H$  and SOC pools.



(decreasing) responses to elevated temperatures<sup>122</sup>. However, inconsistent responses even within the same phylum highlight the limitations of predicting microbial sensitivity to climate change based solely on taxonomic affiliation. In addition, reductions in photosynthetic cover correlate with declines in vulnerable microbial taxa and increases in opportunistic ones, underscoring strong linkages between aboveground and belowground, and suggesting reduced SOC inputs<sup>122</sup>. Meta-analyses indicate that wetland ecosystems are particularly sensitive to warming and experience the most pronounced microbial shifts towards simplified and thermotolerant communities<sup>123</sup>.

Both fungal and bacterial taxa are affected by climate warming. Laboratory-based incubations revealed measurable shifts in both bacterial and fungal taxa relative abundances over multiyear periods<sup>116</sup>. In another study, fungal taxa that responded opportunistically were positively associated with elevated  $R_s$ , implying that warming could intensify microbial-driven nutrient cycling<sup>122</sup>. In this analysis, drylands exhibited the highest fraction of responsive taxa, particularly among fungi<sup>122</sup>. In soil warming experiments<sup>116</sup>, the ratio of fungi to bacteria<sup>124–126</sup> was correlated to changes in CUE and  $R_H$ , suggesting that this ratio might offer a simple descriptor that could be useful at the regional or global scale.

## Influence on heterotrophic metabolism

Climate change not only influences respiration through altered microbial community composition; it also affects  $R_H$  through changes in temperature, precipitation and/or  $CO_2$  levels<sup>127</sup>. In general, warming tends to accelerate microbial metabolism, whereas changing precipitation and  $CO_2$  levels either slow or accelerate respiration, so that the global impact of climate change is more nuanced and difficult to predict<sup>128</sup> (Fig. 3).

**Influence of  $CO_2$ .** Elevated  $CO_2$  has potential direct effects on  $R_H$ . Several long-term field experiments have used free-air  $CO_2$  enrichment (FACE) to mimic future atmospheric  $CO_2$  levels<sup>129,130</sup>.  $CO_2$  enrichment increases plant productivity, which tends to increase carbon inputs to soil<sup>9–11,130</sup>. Globally, those additional inputs are partially retained as soil carbon, but some soils retain carbon and others do not<sup>12</sup>. In one experiment, soil respiration rates increased ~30% during the first two years of  $CO_2$  enrichment, roughly matching the increase in plant photosynthesis<sup>129</sup>. The stimulatory effect declined over seven years, probably owing to changing nutrient status, in this case the loss of soil nitrogen<sup>129,130</sup>. Although  $CO_2$  has some direct effects on microbial metabolism<sup>131,132</sup>,  $CO_2$  effects on  $R_H$  are generally considered to be the time-integrated result of increased plant productivity and therefore are mostly indirect<sup>130</sup>.

**Temperature impacts on respiration.** Field and laboratory incubations are often used to characterize the temperature and water dependence of  $R_H$ . For example, extended laboratory incubations measuring  $R_H$  at a variety of temperatures<sup>110,133</sup> or with manipulated water content<sup>28,134</sup> enabled mathematical modelling of the isolated effects of temperature and water. Depending on the timescale of interest and the soil in question, manipulating water and temperature can have positive or negative effects on respiration rates. Therefore, more long-term field studies are needed to gain a better understanding of the combined impacts of water and temperature on  $R_H$ .

Generally, elevated temperatures increase respiration rates on relatively short timescales (months to years)<sup>109,110,135</sup>. Warming enhances  $R_H$  across spatial scales from microsites to the global biosphere, by accelerating enzymatic reactions and diffusive transport<sup>136</sup>. In the long

term, increased  $R_H$  will deplete SOC, ultimately reducing observed respiration rates<sup>109,137</sup>. An early meta-analysis of  $R_s$  data in the SRDB indicated that warming does indeed accelerate total soil respiration, with an apparent temperature coefficient  $Q_{10} \approx 1.5$  between 1989 and 2008 (ref. 19). This  $Q_{10}$  value indicates that a 10 °C temperature increase would increase  $R_s$  by 50%. Subsequent analyses updated these estimates and worked to resolve  $Q_{10}$  values for  $R_s$  and  $R_H$  separately, finding global  $Q_{10}$  values ranging from 2 to 3 with substantial geographic and climatological variation<sup>109,138</sup>.

In situ soil warming is another strategy for determining temperature effects on  $R_H$ . A long-term warming experiment in a temperate hardwood forest revealed that there are four phases of respiration: an initial increase, acclimation, a second increase, and acclimation<sup>135</sup>. These different phases might reflect a shifting microbiome, including reductions in total microbial biomass and shifts in the community composition<sup>135</sup>. Therefore, the soil microbial communities adapt to changing temperatures, but their collective respiration is due to multiple complex factors including the metabolic preferences of individual taxa, the nutrient status of the soil and the composition of SOC<sup>122,139–141</sup>.

The ‘quality–availability’ statistical model encapsulates a common understanding of temperature effects on soil heterotrophic respiration<sup>109</sup>. In this model, soil microbes preferentially consume high-quality substrates, so that the average quality and quantity of SOC decrease in time in the absence of new inputs. The model posits that low-quality, recalcitrant SOC has a greater kinetic barrier to respiration (smaller  $Q_{10}$  or larger activation energy), and that temperature increases affect  $R_H$  more when SOC is abundant. As such, it predicts a mixed temperature response in which modest increases in temperature increase  $R_H$  in the short term but the amount and quality of SOC is reduced in the longer term<sup>109</sup>. The quality–availability model accurately captures nearly all the variation in the temperature responses of respiration in a meta-analysis of ~700 soil incubations<sup>109</sup>.

Temperature increases are likely to affect respiration directly and indirectly. For example, increased temperature can also reduce soil water content and provide more direct routes for gaseous  $O_2$  to reach soil microbes. As a result of both direct and indirect effects, substantial increases in soil heterotrophic respiration are predicted in by 2100 (ref. 18). A 40% increase in global  $R_H$  is predicted by the end of the twenty-first century in high-emission scenarios, with particularly pronounced effects in the Arctic<sup>136,142</sup>. Arctic permafrost holds vast amounts of SOC, with estimates that it contains over 50% of the total SOC pool<sup>143</sup>. As global temperatures increase and permafrost thaws, previously frozen SOC can be respired.  $CH_4$  can also be produced at wetter locations<sup>142</sup>. Microbial decomposition of older carbon previously locked in permafrost represents potent feedback of warming on  $CO_2$  and  $CH_4$  release<sup>144,145</sup>. However, the increase in respiration in boreal ecosystems undergoing permafrost transition is partly offset by increased photosynthetic productivity due to greening of the Arctic<sup>146</sup>.

Comparisons of different climate models, such as the Coupled Model Intercomparison Project, show large variations in predictions of  $R_s$  and  $R_H$  with differences spanning hundreds of PgC over 50 years<sup>38,39</sup>. This variation is due to various factors, including limited global data on SOC stocks and changes<sup>147</sup>, limited data on the physical and chemical status of soils<sup>148</sup>, different models for predicting  $R_H$  (ref. 37), and sparse data regarding permafrost carbon dynamics<sup>38</sup>. The application of  $Q_{10}$  and Arrhenius equations to respiration poses yet another challenge. Both are widely used temperature-dependence formulations: that is,  $Q_{10}$  expresses the fold-change in respiration per 10 °C of warming, and the Arrhenius equation describes the same temperature sensitivity

through an activation energy term. This formalism has a fundamental justification rooted in the assumption of a single rate-limiting reaction step<sup>137</sup>. In soils, however, heterogeneous organics are metabolized by a tremendous diversity of soil microbes, suggesting that more than a single barrier is justified<sup>105</sup>. Indeed, the quality–availability model also considers a single time-varying barrier determined via the changing SOC quality<sup>109</sup>. Applying statistical approaches that allow for heterogeneous or disordered kinetic barriers (a distribution of SOC quality) can overcome these single-barrier limitations<sup>149–152</sup>.

**Moisture impacts on respiration.** Soil moisture shifts owing to climate change have strong influences on soil respiration, with complex interactions that amplify or constrain temperature effects<sup>153</sup>. Importantly, the response of  $R_H$  to soil moisture often follows a nonlinear relationship, with maximum  $R_H$  occurring at intermediate moisture levels<sup>27,28</sup>. Measured  $\text{CO}_2$  efflux is generally highest at the soil optimal moisture content and decreases at lower and higher moisture levels<sup>154,155</sup>. One emerging theme is the importance of microscale conditions in determining the observed respiration rate, particularly under varying moisture conditions<sup>30</sup>. The impact of change in soil moisture on  $R_H$  is determined by several factors, including soil porosity, which governs the amount of aeration, and the availability of SOC accessible to microorganisms<sup>156</sup>. Pore-scale models suggest that SOC is metabolized rapidly once it becomes available<sup>30</sup>. However, different variables, including clay content, can restrict SOC availability<sup>29,30</sup>. Thus, it remains challenging to extrapolate from pore-scale models to the field scale. In addition, uncertainties in soil water estimates present a challenge for making accurate predictions of  $R_H$  (ref. 18).

Many areas of the globe are experiencing more frequent and intense precipitation events, owing to climate change<sup>157</sup>. An increase in soil moisture can result in saturation of soil pores, which decreases  $\text{O}_2$  availability because the diffusion constant for  $\text{O}_2$  is several orders of magnitude smaller in water than in air<sup>18,134,158</sup>. In the absence of  $\text{O}_2$  (Box 1), anaerobic microbial processes can dominate, producing other greenhouse gases such as nitrous oxide ( $\text{N}_2\text{O}$ ) and  $\text{CH}_4$ .

Other areas of the globe are experiencing decreased precipitation and, consequently, soil desiccation<sup>157</sup>. Arid soils limit microbial metabolism via osmotic stress and reduced mobility of organic substrates<sup>159</sup>. Satellite gravity observations indicate that climate warming is shifting the balance of Earth's hydrological cycle, with a loss of approximately 1.6 Gt of available soil water between 2000 and 2002 (ref. 160). Soil desiccation is further accelerated by poor landscape management and increased frequencies of fire (itself a source of  $\text{CO}_2$ )<sup>161</sup>. Fire alters soil structure, microbial communities and SOC reserves<sup>162</sup> with short and long-term impacts on  $R_H$ . Fire can also result in permafrost thaw with an immediate release of  $\text{CO}_2$  from surface soils, although the long-term impacts of fire on permafrost are uncertain<sup>162</sup>.

Sensitivity to drought is particularly acute in semiarid ecosystems where reduced precipitation lowers SOM content and constrains  $R_H$ , thereby reducing microbial carbon cycling capacity<sup>163</sup>. By contrast, the thawing of the Arctic permafrost is resulting in an increase in SOC availability for microbial respiration<sup>164</sup>. Higher, drier Arctic locations are more aerobic and therefore prone to respiration, whereas lower, wetter regions are prime locations for methanogenesis<sup>164</sup> (Box 1). Although the amount of SOC becoming available is a concern, SOC composition can also influence  $R_H$  in thawing permafrost, and SOC speciation varies substantially between different sites and with depth and is determined by the prevailing organic or mineral nature of the local soil<sup>165</sup>.

The Birch effect is a phenomenon where apparent respiration rates increase following wetting of dry soils<sup>166–169</sup>. Real-time monitoring of

dry soils incubated with  $^{13}\text{C}$ -labelled glucose showed immediate  $\text{CO}_2$  production following rewetting that was mostly derived from the native  $^{12}\text{C}$ , with the  $^{13}\text{C}$  label only after 15 min (ref. 170). These results suggest that rewetting promotes the consumption of intracellular  $^{12}\text{C}$  before extracellular  $^{13}\text{C}$  glucose, consistent with the notion that SOC pools differ in their accessibility to microbes<sup>170</sup>. The resident  $\text{CO}_2$  might also be inorganic because hydration of minerals releases  $\text{CO}_2$  (ref. 170).

## Mitigating respiration and SOC loss

Climate-smart soil management practices are proposed to reduce  $R_H$  and loss of SOC stocks by promoting accumulation of stable forms of SOC, depressing  $R_H$  directly, or both<sup>171</sup>. These strategies must be evaluated for their ability to increase SOC stocks, as well as their performance under projected climate stressors that can accelerate  $R_H$  and SOC loss. Therefore, understanding how mitigation approaches interact with stressors, such as warming, altered precipitation, drought and extreme weather events, is essential for developing resilient, climate-smart management.

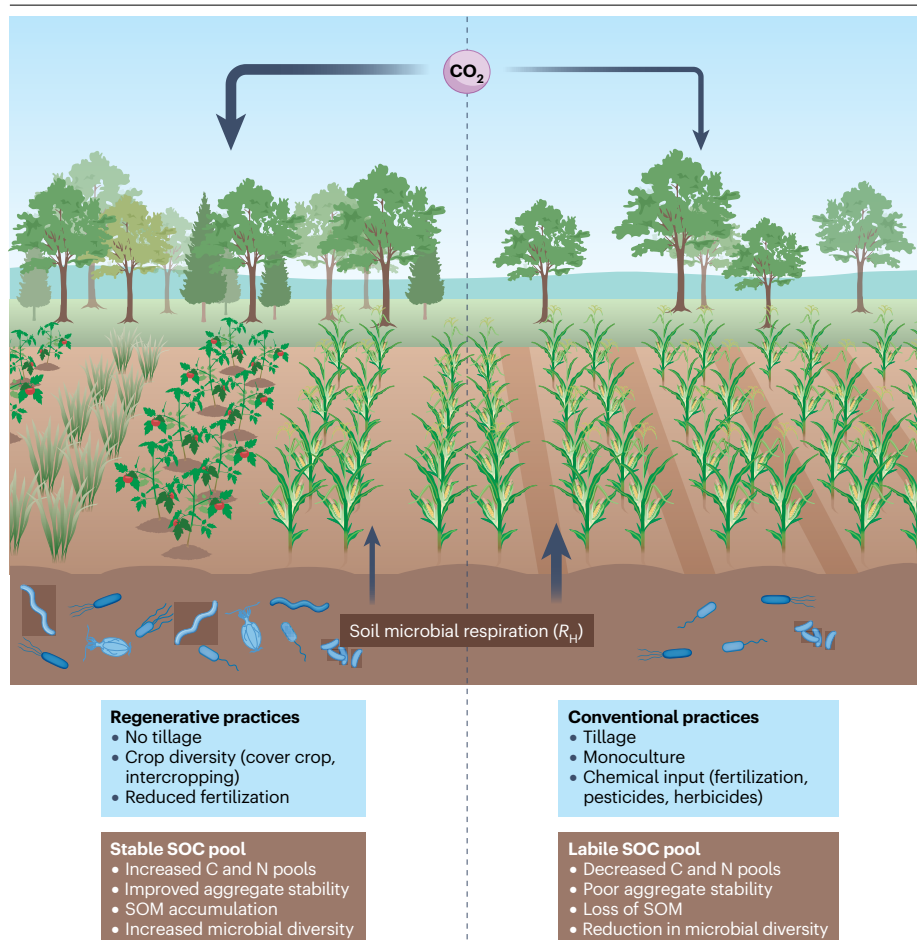
## Microbiome-based interventions

As microbial metabolism is the direct catalyst of most SOC cycling, some proposed manipulations target the microbial community directly<sup>172</sup>. Other agricultural management practices target the broader soil environment in which microbes live and respire<sup>172</sup>. Microbiome stewardship is the science-based management, conservation and manipulation of microbial communities to maintain or restore the health of organisms and ecosystems<sup>173</sup>. Microbial interventions, whether direct, through microbial inoculants<sup>174</sup>, or indirect, through the use of organic amendments or environmental manipulation<sup>172</sup>, are emerging as potential tools for regenerative agricultural practices (Fig. 4). Although not directly related to soil respiration, N-fixing microbial inoculants are already widely deployed, showing the potential for harnessing microbial metabolism to support agricultural productivity and sustainability<sup>175</sup>. For example, N-fixing inoculants applied to Brazilian soybeans generated US\$15 billion in savings and avoided 183 Mg of  $\text{CO}_2$ -equivalent emissions from 2019 to 2020, demonstrating both economic and climate benefits<sup>176</sup>.

One microbial inoculation strategy involves the application of plant-growth-promoting bacteria<sup>177</sup>. These have been used in agriculture (single species and consortia) as alternatives to chemical fertilizers and pesticides<sup>177</sup>. Some of these inocula seem to increase SOC over the short term, potentially by accumulating microbial necromass or by supporting plant growth<sup>178</sup>. For example, Actinomycetes are often used as plant-growth-promoting microbes and might stabilize SOC via formation of filamentous structures<sup>178</sup>.

The tendency of microbial necromass to mineral association and aggregate formation offers a potential mechanism of SOC stabilization<sup>56</sup>. If specific taxa preferentially form stabilized forms of SOC, like MAOM, one management strategy could be to add microbial inoculants that capture plant-derived SOC, die, and form necromass that becomes associated with MAOM. Although the idea of promoting the formation of MAOM-associated necromass has received substantial attention<sup>56–58</sup>, there is still a need to better understand microbial necromass contributions to SOC and MAOM. Studies indicate that microbial residues make up a large fraction of SOC, even exceeding 50% in some cases<sup>60,61,179</sup>, yet these measurements rely on many untested assumptions. Better characterization of necromass content and stability, especially in fluctuating conditions, is sorely needed to support the microbial carbon pump concept that underlies some inoculants<sup>44,56,57,59,60</sup>.





**Fig. 4 | Influence of agricultural practices on soil microbial respiration.** Carbon dioxide ( $\text{CO}_2$ ) fluxes are represented by arrows: downward arrows represent uptake and upward arrows represent efflux. In summary, regenerative practices are better than conventional agriculture at reducing soil carbon loss through soil microbial respiration ( $R_m$ ). SOC, soil organic carbon; SOM, soil organic matter.

There are several uncertainties for deployment of microbial inoculants and other strategies to reduce  $R_m$ . Despite their widespread use, microbial inoculants – whether as single species or communities – face competition from the native soil microbiome<sup>180</sup>. Inoculants with higher diversity tend to be less successful at establishing themselves<sup>180–182</sup>. Additionally, even if these introductions fail initially, they can trigger strong secondary successions, potentially shifting communities to alternative, stable functional states<sup>183,184</sup>. The variability in performance across field conditions, along with the ecological risks linked to the legacy of microbial inoculants, must be carefully considered when implementing these approaches.

Many uncertainties also stem from shifting climatic conditions. For example, temperature-driven metabolic acceleration, altered moisture, and nutrient availability can all change the function and persistence of inocula<sup>177</sup>. A key underlying assumption is that microbes have defined, manipulable roles in stabilizing or destabilizing soil carbon. However, microbes are often facultative (perform different roles in different settings), the environment is variable, and SOC is heterogeneous<sup>185</sup>. A gram of soil typically contains  $10^7$ – $10^9$  individual bacteria representing  $10^3$ – $10^4$  bacterial taxa, suggesting that the specific habits of individual species can average out even at small scales<sup>186,187</sup>.

There are also uncertainties surrounding the extent to which microbial groups perform concrete functions owing to limitations in culturing

or characterizing the full diversity of soil microbes. So, despite promising laboratory and field studies, deployment of microbial inocula is stymied by competition with native microbial populations, environmental variability, and challenges in predicting microbial persistence and function under field conditions<sup>172,188</sup>. Addressing these uncertainties requires a deeper understanding of the genetic or ecological mechanisms by which interventions influence communal respiration, and how these changes translate into long-term carbon stabilization<sup>172,189</sup>.

## Plant-based strategies to increase SOC

Plant-based strategies that promote root development offer a promising indirect route to enhance SOC sequestration and reduce  $R_m$ . For example, larger and deeper root systems can deposit more durable SOC into deep soil layers where it is less accessible to microbial respiration<sup>190</sup>. Importantly, root biomass contributes disproportionately to SOC formation relative to aboveground litter, and deeper root inputs can persist for centuries owing to mineral protection and reduced disturbance<sup>191–193</sup>. Deploying soil-carbon-enhanced cultivars with deeper and more massive root systems could therefore increase SOC at scale without expanding agricultural land. For example, deployment of such cultivars across ~190 Mha (~13% of global agricultural land), focused on the four major commodity crops (soybean, maize, cotton and canola) in the five countries that lead today's genetically modified

crop market, could lead to a rapid ramp-up of carbon removal that peaks at  $-1 \text{ GtCO}_2 \text{ yr}^{-1}$  within  $\sim 13$  years of first deployment, subsequently stabilizing as soils approach saturation<sup>190</sup>. This strategy could optimistically amount to  $\sim 7$  times more  $\text{CO}_2$  removal than all existing offsets supplied today to the global voluntary offsets market. Models of the depth-dependent age of SOC indicate that subsoil carbon can exhibit turnover times that are orders of magnitude slower than topsoil, consistent with carbon inputs below the active rhizosphere contributing disproportionately to long-term SOC persistence<sup>194</sup>.

Enhanced crops also present a complementary approach to microbial inoculants. Instead of altering the microbial community directly, plant inputs alter the structure of the microbial environment<sup>190</sup>. These plant inputs provide substrates for microbial growth and necromass production, thereby driving stable SOC accumulation belowground<sup>190–192</sup>. However, responses of carbon-enhanced cultivars to combined warming,  $\text{CO}_2$  enrichment, and variable precipitation regimes remains unclear.

## Fungal strategies to increase SOC

Fungi are also promising inoculants for enhancing SOC storage. Fungal endophytes form different types of associations with plant roots, exchange nutrients with plants<sup>195,196</sup>, and could increase plant carbon assimilation<sup>197</sup>. Fungi can also enhance plant water uptake and protect roots against thermal and osmotic stress<sup>198,199</sup>. Therefore, fungal symbioses could be especially important as droughts intensify and soils experience more frequent wet–dry cycles. For example, addition of endophytic fungi increased SOC by 17% over 14 weeks in a greenhouse experiment<sup>200</sup>. In addition, some mycorrhizal fungi produce a compound, glomalin, that is promising as a resilient carbon reservoir<sup>200</sup>. Certain fungi also release plant-derived carbon as exudates, with a distinct chemical profile from those released by plants<sup>201</sup>.

The presence of fungi can alter microbial food webs, resulting in interactions with bacteria that positively affect plant growth<sup>202</sup>. As plants produce SOC, positive fungal interactions could potentially boost SOC as well. Indeed, certain fungi seem to transfer exudates to deeper soil horizons<sup>203</sup>, which could result in longer-term carbon storage. In addition, some fungi produce sclerotia – resting structures containing lipids and glycogen – and hold promise for long-term retention of SOC<sup>204</sup>. Soil aggregation by fungi is another mechanism to stabilize SOC<sup>205,206</sup>. Hyphal density is an important contributor to soil aggregation, with Ascomycota fungi being the most efficient soil aggregators<sup>206</sup>. Although mycorrhizal fungi stabilize SOC, how they respond to warming, elevated  $\text{CO}_2$  and moisture regimes remains unstudied. These knowledge gaps limit understanding of the potential of mycorrhizal fungi to mitigate increased  $R_{\text{H}}$  under climate change.

## Indirect strategies for SOC storage

Manipulations of the soil environment can also influence microbial metabolism<sup>171,189,207</sup>. Soil management practices that reduce disturbance and increase cover can buffer  $R_{\text{H}}$  increases caused by warming and erratic rainfall, while enhancing water retention and thermal stability. For example, practices such as no-till agriculture, cover cropping, crop rotation and biochar amendment, especially when combined, have demonstrated the capacity to enhance carbon storage and reduce  $R_{\text{H}}$  (ref. 208) (Fig. 4). Meta-analyses of cover-cropping experiments indicated increased SOC content of surface soils (top 30 cm SOC increased by  $\sim 15\%$ ) and an increased rate of SOC accumulation in surface soils of  $30\text{--}60 \text{ gC m}^{-2} \text{ yr}^{-1}$  (refs. 209,210). Estimated cover-cropping-associated SOC accruals therefore amount to a substantial fraction (5–15%) of the

typical  $R_{\text{H}}$  values ( $\sim 420 \text{ gC m}^{-2}$ ). However, SOC increases are only evident in surface soils (depth  $< 30 \text{ cm}$ ) and diminish with time<sup>209,210</sup>. Moreover, the methods of these analyses have been called into question, producing more conservative revised estimates that are 10–20-fold smaller ( $\sim 3 \text{ gC m}^{-2} \text{ yr}^{-1}$ )<sup>211</sup>. Solving this disagreement is critical because the larger values focus attention on cover cropping as a key tool for carbon sequestration, whereas the smaller values do not<sup>211,212</sup>.

Nutrient amendments offer another indirect approach to manipulating  $R_{\text{H}}$ . For example, in temperate forests, N addition reduced  $R_{\text{H}}$  by  $\sim 15\%$  on average<sup>213,214</sup>, suggesting that restoring C:N balance increased microbial carbon use efficiency. However, individual sites varied from  $\sim 60\%$  reduction to  $\sim 60\%$  stimulation of  $R_{\text{H}}$  (ref. 214), emphasizing the complexity and context dependence of collective microbial respiration. Results from P addition are similarly variable, indicating that the scientific community lacks the predictive understanding of  $R_{\text{H}}$  that is needed to apply nutrient amendments reliably<sup>215</sup>. Moreover, nutrients can interact strongly with temperature and moisture<sup>216</sup>, highlighting the need for climate-conditioned field trials.

Application of pyrolysed organic material, called biochar, has received particular attention for its potential to stabilize SOC, alter microbial metabolism, and reduce  $\text{CO}_2$  efflux from soils<sup>217</sup>. Biochar is rich in carbon but relatively slow to decay<sup>218</sup>. Meta-analyses found increases in SOC following biochar amendments, particularly in soils with a fine texture and alkaline pH (ref. 219). However, the success and longevity of these effects are highly site specific, with environmental variables modulating microbiomes and, in turn, being modulated by microbial dynamics<sup>220</sup>.

Emission of other microbially produced greenhouse gases, including  $\text{N}_2\text{O}$  produced via denitrification (Box 1), can also be mitigated via management strategies. Co-application of synthetic nitrification inhibitors with N-bearing nutrients can reduce  $\text{N}_2\text{O}$  emissions from agricultural soils<sup>221,222</sup>. Inhibition of biological nitrification limits the production of soil-borne nitrate ( $\text{NO}_3^-$ ), which is a substrate of respiratory denitrification<sup>223,224</sup>. The reduction of  $\text{N}_2\text{O}$  emissions varies with fertilizer and soil types, as well as soil water content<sup>225</sup>. Meta-analyses found a consistent 30–60% reduction in  $\text{N}_2\text{O}$  efflux<sup>223,226,227</sup>, indicating that soil microbial processes can be influenced by chemical treatment. Although nitrification inhibitors have existed since the 1960s, their deployment has been limited because cheap nitrogen fertilizers reduced the economic incentive to conserve N (refs. 228,229). As major dairy supply chains now seek lower climate footprints, inhibitors might see broader adoption owing to their ability to curb  $\text{N}_2\text{O}$  emissions<sup>230,231</sup>. However, their broader biogeochemical effects, including impacts on soil respiration and  $\text{CO}_2$  fluxes, remain poorly quantified<sup>232,233</sup>.

Although the practices reviewed offer some short-term benefits, their long-term ( $> 10$ -year) effects are generally unknown. In cases in which longitudinal observations are available, they are often variable and context dependent, highlighting the need for site-specific assessments and long-term monitoring of SOC. For example, for experiments studying the effects of tillage, multidecade time series are available<sup>234,235</sup>. Yet these experiments can only interrogate specific sites, leaving substantial uncertainty regarding the scalability of interventions across climate zones and soil types. Analysis of long-term field data from the Rothamsted research site in England suggested that conversion of agricultural land to forest or grassland had the greatest benefit with respect to increase in SOC<sup>236</sup>. For example, from 1880 to 2000 there were measurable increases in SOC in soils that transitioned from agriculture to forests. However, the 4 per 1,000 initiative that aims to increase SOC by 0.4% per year was considered unrealistic, owing

to insufficient resources and economic incentives for farmers<sup>237</sup>. As climate change takes place over decades and centuries, it is important to determine the long-term effects of intervention. Yet, for most proposed interventions, there are quite limited long-term data.

Decision-making should consider microbiome-based and plant-based mitigation approaches, accounting for their mechanisms, climate relevance, scalability and uncertainties (Table 1). Although microbial inoculants can rapidly modify SOC dynamics, plant-based strategies provide longer-term, climate-resilient carbon inputs. Co-deployment, which optimizes microbial consortia for specific plant genotypes and climate regimes, represents a promising frontier for reduction of  $R_H$  and increasing C storage in a changing climate.

## Summary and future perspectives

Soil  $R_H$  represents one of the largest and most temperature-sensitive carbon fluxes in the Earth system. It is shaped by nonlinear and synergistic interactions between temperature, moisture, substrate quality and microbial physiology. For instance, SOC persistence reflects chemical recalcitrance, mineral association and spatial protection, whilst microbial traits such as CUE, enzyme kinetics and thermal adaptation can modulate these fluxes<sup>27,65,67,97,98,137</sup>. Field experiments show that management interventions, such as microbial inoculants, biochar and crop diversification, can modify SOC stocks and  $R_H$  (refs. 98,172,177,209,219,238).

Microbially explicit models help to constrain uncertainty in SOC projections<sup>238</sup>. However, incorporating microbial traits into Earth system models (ESMs) is a major challenge as microbial responses to temperature, moisture and substrate quality are context dependent and exhibit pronounced spatial heterogeneity, sometimes shifting within centimetres and diverging further across ecosystems<sup>239,240</sup>. Learning how to properly average this fine-scale variability across space and time to produce responsible and generalizable models applicable at regional or global scales is a priority<sup>238,241</sup>.

A core challenge is that microbial trait measurements do not directly map onto  $R_H$  even at the local scales. CUE, growth rates and enzyme activities are only indirect indicators of microbial processes, whereas  $R_H$  emerges from complex interactions between microbes, minerals, soil physics and hydrology. As a result, trait data often provide only partial observability of the underlying drivers of CO<sub>2</sub> release. This limitation is compounded because measurements of common microbial traits are typically derived from laboratory or small-plot experiments, which do not capture all of the processes at play and do not directly scale to the spatial extent of ecosystems or ESMs<sup>242</sup>. Moreover, microbial traits vary dynamically with environmental conditions, such as local resource supply, redox conditions and disturbance history<sup>243,244</sup>. Consequently, different combinations of microbial traits and soil properties can yield similar CO<sub>2</sub> fluxes, leading to persistent issues with parameter identifiability and equifinality<sup>245,246</sup>.

**Table 1 | Strategies to mitigate soil heterotrophic respiration and soil organic carbon loss**

|                                      | Microbiome-based interventions                                                                                                                                                     | Plant-based interventions                                                                                                                                                | Co-deployment potential                                                                                                                                      |
|--------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Mechanism                            | Directly manipulate microbial communities to alter SOC turnover, enhance necromass formation and shift CUE under changing temperature and moisture                                 | Enhance plant root inputs (carbon quantity and depth) to increase SOC stabilization and reduce labile substrate exposure to $R_H$                                        | Combined strategies couple root-driven carbon inputs with microbially mediated stabilization (for example deep-rooted plants+carbon-sequestering inoculants) |
| Climate-change relevance             | Target microbial responses to warming, drought and redox fluctuations — drivers of accelerated $R_H$ . Effective under scenarios in which microbial respiration dominates SOC loss | Build resilience to elevated CO <sub>2</sub> , temperature and drought by promoting deep rooting, improved water-use efficiency and persistent subsoil carbon deposition | Integration enhances resilience of both biological components — root inputs sustain microbial communities that stabilize C under stress                      |
| Interventions                        | Deploy microbial inoculants, microbial necromass builders and/or engineered consortia (SynComs)                                                                                    | Breed or engineer carbon-enhanced crops (for example deep-rooted perennials); use crop rotations and cover crops                                                         | Bioengineer co-optimized plant–microbe pairs (for example plant genotypes matched with drought-resilient microbes)                                           |
| SOC effects                          | Moderate short-term SOC gains through necromass accumulation and reduced $R_H$ rates; highly context dependent                                                                     | Larger, longer-term SOC gains via increased carbon inputs and protection in deeper, cooler and moister soil layers                                                       | Potential for synergistic SOC stabilization when necromass formation complements deep carbon input                                                           |
| Timescale of impact                  | Months to years (rapid microbial turnover; short feedback cycles)                                                                                                                  | Years to decades (root system development and deep C accrual)                                                                                                            | Multidecadal persistence if co-adapted plant–microbe systems are maintained                                                                                  |
| Feasibility                          | Moderate: requires site-specific microbial selection, containment protocols, and long-term persistence testing                                                                     | High for existing crops; moderate for engineered varieties (regulatory and adoption hurdles)                                                                             | Moderate–high if co-development pipelines (breeding+inoculant) are aligned                                                                                   |
| Scalability and deployment potential | High near-term scalability in managed systems (for example continental-scale deployment of inoculants in Brazil and China), but limited predictability in the field                | Very high scalability through seed-based deployment, but slower owing to breeding cycles and regional adaptation                                                         | High if integrated into regenerative agriculture frameworks or carbon-credit MRV systems                                                                     |
| Data and monitoring needs            | Requires molecular tracking and necromass quantification                                                                                                                           | Requires plant trait phenotyping, root biomass/depth mapping, and belowground SOC tracking                                                                               | Joint monitoring networks combining omics, isotopic tracing, and remote sensing                                                                              |
| Main uncertainties                   | Longevity, ecological displacement and functional persistence of introduced microbes under future climate extremes                                                                 | Trade-offs between productivity, stress tolerance and carbon allocation; uncertain deep-root growth under different scenarios                                            | Interaction stability: will plant–microbe mutualisms persist under long-term warming, CO <sub>2</sub> enrichment and altered hydrology?                      |

CUE, carbon-use efficiency; MRV, measurement, reporting and verification;  $R_H$ , heterotrophic respiration; SOC, soil organic carbon.



Progress therefore requires more than simply expanding parameter sets, but depends on upscaling strategies that treat traits as distributions rather than single values. It also relies on observations jointly constraining traits and fluxes, and model–data integration frameworks that assess when trait-based formulations increase predictive skill relative to simpler empirical or pool-based models<sup>36,238,242,245</sup>. Four detailed recommendations for action to help guide future research and a microbiome-informed soil management strategy over the next 10–15 years are now outlined (Fig. 5).

First, more globally distributed and comparable field trials are needed to assess the efficacy of direct and indirect microbial interventions to increase SOC and reduce  $R_H$ , focusing on degraded or climate-sensitive soils<sup>173</sup>. Microbial inoculants to promote soil health and fertility are a growing global agribusiness, with >800 patents for microbial inoculants in China and >200 million doses applied in Brazil<sup>177</sup>. Priority biomes should include tundra and boreal zones (permafrost thaw gradients), tropical oxisols and ultisols (Amazonia, Cerrado), semiarid rangelands (Sahel, US Southwest) and temperate croplands (mollisols, alfisols). Each site should use standardized measurement, reporting and verification (MRV) protocols. Standardized approaches should include using soil CO<sub>2</sub> flux chambers and eddy covariance partitioning for  $R_H$  and  $R_A$ ; isotopic labelling (<sup>13</sup>C/<sup>14</sup>C) for turnover constraints; metagenomic, metatranscriptomic and metabolomic profiling for microbial trait dynamics; and inoculant tracking via strain-specific quantitative PCR or barcodes. Safety, durability and function persistence should also be evaluated over multiyear intervals under realistic management and climate scenarios. Pre-registration of trial protocols and open-access data sharing will enhance comparability and replication.

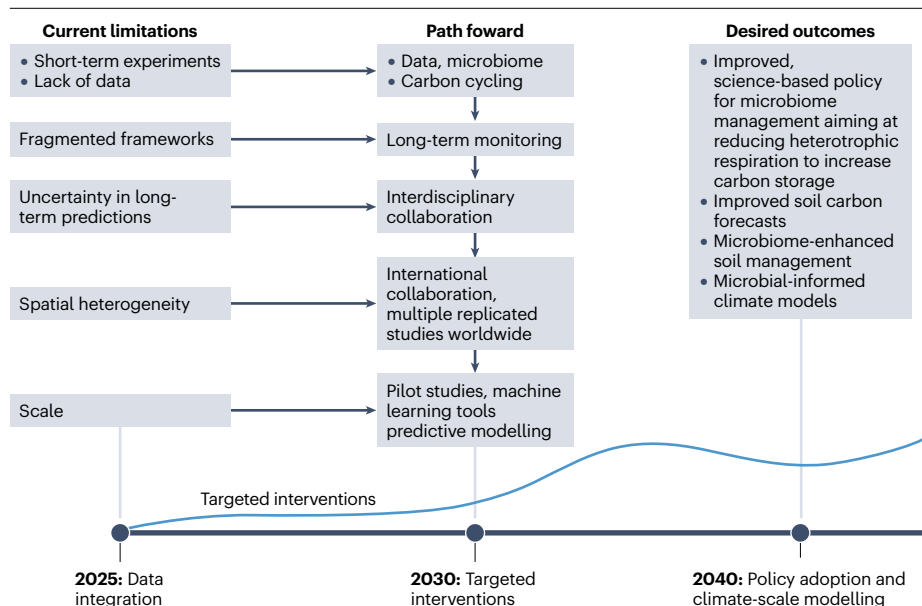
Second, long-term, moisture-explicit observing systems and harmonized datasets for model calibration and validation should be developed. Most existing  $R_H$  estimates rely on short-term data, yet soil processes unfold over decades<sup>4,7,19,34</sup>. A network of long-term field sites co-located with infrastructures, such as NEON<sup>247</sup>, ICOS<sup>248</sup>, FLUXNET<sup>249</sup> and LTER<sup>250</sup>, spanning diverse ecozones should be established. These sites should integrate automated soil temperature and moisture

sensors, oxygen microelectrodes and repeated SOC coring at depth intervals (0–100 cm) for MAOM and POM fractions. Standardized metadata and harmonized protocols should feed into global repositories such as SoilGrids 2.0 (ref. 192), WoSIS<sup>251</sup> and SRDB<sup>252</sup>. Annual resampling and radiocarbon dating will reduce geographic bias and enable recalibration of statistical and process-based models<sup>147</sup>. The goal is to produce benchmark datasets that constrain and validate machine-learning and process-based models predicting  $R_H$  responses to moisture, temperature and management.

Third, microbial metabolic traits should be linked to carbon fluxes through laboratory-to-model pipelines. Controlled laboratory experiments quantifying microbial physiological traits and processes across soil types and climate treatments could help reduce uncertainty in  $R_H$ -related CO<sub>2</sub> fluxes. Upscaling these insights to scale could be supported by AI platforms that leverage genomics, soil chemistry and environmental metadata<sup>253</sup>. Large AI models can summarize omics data into useful trait inputs for ESMs by estimating likely ranges of microbial physiological parameters. Instead of assuming fixed values, these traits (such as CUE, enzyme kinetics, biomass turnover) are quantitatively represented as probability distributions learned from many different data sources<sup>253</sup>. AI models can also mine and combine data from scientific literature, genomic databases and environmental measurements to estimate likely trait ranges across different soil types and climates.

These trait range estimates can then be used as flexible starting assumptions in Bayesian data-assimilation pipelines, allowing traits in microbially explicit submodules (such as MESDM<sup>242</sup>, MEND<sup>254</sup>, CORPSE<sup>255</sup>) in ESMs to be continuously updated as more field observations become available. In the long term, global experimental networks could maintain priors that evolve as soils, climates and management regimes change, analogous to seasonal reanalysis frameworks used in numerical weather prediction. To improve predictive performance, improving transparency and reproducibility, standardized models should report identifiable parameters and trait uncertainty.

Finally, water-oxygen controls of  $R_H$  need to be quantified across scales. Moisture and oxygen availability are first-order regulators of  $R_H$  (refs. 27,76), yet are underrepresented in most ESMs<sup>27</sup>. Future



**Fig. 5 | A roadmap towards microbiome-informed soil respiration management.** Existing limitations in microbiome-informed soil respiration management can be overcome by specific steps towards a path forward (horizontal arrows). Vertical arrows represent successive steps under the path forward to achieve targeted interventions by the year 2030. Desired outcomes by 2040 are shown at the right. The blue line illustrates the relative increase over time in targeted interventions. To achieve desired outcomes at the policy level and for climate-scale modelling by the year 2040, it is necessary to perform specific steps via targeted interventions by the year 2030.

research should couple microscale (micro-computed tomography ( $\mu$ CT)-derived pore structure, diffusion modelling) and macroscale (distributed soil moisture and temperature sensing) approaches to map oxygen limitation thresholds and anaerobic transitions. Field programmes should set up instruments in thawing permafrost, post-fire boreal soils and drought-prone rangelands to capture  $R_H$ ,  $CH_4$  and  $N_2O$  fluxes alongside microbial trait adaptation. Radiocarbon and stable isotope tracing can partition fast versus slow carbon pools, and metatranscriptomics and metabolomics reveal microbial acclimation. Policy-relevant frameworks should integrate these data into MRV protocols for soil carbon markets, ensuring durability and additionality through moisture-explicit and oxygen-explicit verification<sup>76,171</sup>.

Although not exhaustive, these coordinated empirical and modelling efforts would transform soil respiration from one of the least well-constrained to one of the best-constrained biospheric fluxes. These advances would enable mechanistically grounded and practically verifiable climate projections and mitigation strategies.

## Data availability

The data supporting Fig. 2 are available from the cited primary research article<sup>4</sup>.

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## References

- Keeling, C. D. Atmospheric carbon dioxide in the 19th century. *Science* **202**, 1109 (1978).
- Friedlingstein, P. et al. Global carbon budget 2024. *Earth Syst. Sci. Data* **17**, 965–1039 (2025).
- Keenan, T. F. & Williams, C. A. The terrestrial carbon sink. *Annu. Rev. Environ. Resour.* **43**, 219–243 (2018).
- Warner, D. L., Bond-Lamberty, B., Jian, J., Stell, E. & Vargas, R. Spatial predictions and associated uncertainty of annual soil respiration at the global scale. *Glob. Biogeochem. Cycles* **33**, 1733–1745 (2019).
- Canadell, J. G. et al. in *Climate Change 2021: The Physical Science Basis* (eds. Masson-Delmotte, V. et al.) 673–816 (IPCC, Cambridge Univ. Press, 2023).
- Soil carbon unearthed. *Nat. Geosci.* **13**, 523–523 (2020).
- Bond-Lamberty, B. et al. Twenty years of progress, challenges, and opportunities in measuring and understanding soil respiration. *J. Geophys. Res. Biogeosci.* **129**, e2023JG007637 (2024).
- Burney, J. A., Davis, S. J. & Lobell, D. B. Greenhouse gas mitigation by agricultural intensification. *Proc. Natl Acad. Sci. USA* **107**, 12052–12057 (2010).
- Lobell, D. B. & Field, C. B. Estimation of the carbon dioxide ( $CO_2$ ) fertilization effect using growth rate anomalies of  $CO_2$  and crop yields since 1961. *Glob. Change Biol.* **14**, 39–45 (2008).
- Wang, S. et al. Recent global decline of  $CO_2$  fertilization effects on vegetation photosynthesis. *Science* **370**, 1295–1300 (2020).
- Ainsworth, E. A. & Long, S. P. 30 years of free-air carbon dioxide enrichment (FACE): what have we learned about future crop productivity and its potential for adaptation? *Glob. Change Biol.* **27**, 27–49 (2021).
- Bar-On, Y. M. et al. Recent gains in global terrestrial carbon stocks are mostly stored in nonliving pools. *Science* **387**, 1291–1295 (2025).
- Bevacqua, E., Schleussner, C.-F. & Zscheischler, J. A year above 1.5 °C signals that Earth is most probably within the 20-year period that will reach the Paris Agreement limit. *Nat. Clim. Change* **15**, 262–265 (2025).
- Batjes, N. H. Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* **269**, 61–68 (2016).
- Scharlemann, J. P. W., Tanner, E. V. J., Hiederer, R. & Kapos, V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* **5**, 81–91 (2014).
- Luo, Y. & Zhou, X. in *Soil Respiration and the Environment*, 17–32 (Elsevier, 2006).
- Liu, J., Hu, J., Liu, H. & Han, K. Global soil respiration estimation based on ecological big data and machine learning model. *Sci. Rep.* **14**, 13231 (2024).
- Nissan, A. et al. Global warming accelerates soil heterotrophic respiration. *Nat. Commun.* **14**, 3452 (2023).
- Bond-Lamberty, B. & Thomson, A. Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582 (2010).
- Schlesinger, W. H. Carbon balance in terrestrial detritus. *Annu. Rev. Ecol. Syst.* **8**, 51–81 (1977).
- Hashimoto, S., Ito, A. & Nishina, K. Divergent data-driven estimates of global soil respiration. *Commun. Earth Environ.* **4**, 460 (2023).
- Bond-Lamberty, B. & Thomson, A. A global database of soil respiration data. *Biogeosciences* **7**, 1915–1926 (2010).
- Jian, J. et al. Historically inconsistent productivity and respiration fluxes in the global terrestrial carbon cycle. *Nat. Commun.* **13**, 1733 (2022).
- Sáez-Sandino, T. et al. The soil microbiome governs the response of microbial respiration to warming across the globe. *Nat. Clim. Change* **13**, 1382–1387 (2023).
- Huang, H., Calabrese, S. & Rodríguez-Iturbe, I. Variability of ecosystem carbon source from microbial respiration is controlled by rainfall dynamics. *Proc. Natl Acad. Sci. USA* **118**, e2115283118 (2021).
- Wang, C. et al. The temperature sensitivity of soil: microbial biodiversity, growth, and carbon mineralization. *ISME J.* **15**, 2738–2747 (2021).
- Moyano, F. E., Manzoni, S. & Chenu, C. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. *Soil. Biol. Biochem.* **59**, 72–85 (2013).
- Moyano, F. E. et al. The moisture response of soil heterotrophic respiration: interaction with soil properties. *Biogeosciences* **9**, 1173–1182 (2012).
- Moinet, G. Y. K. et al. Soil heterotrophic respiration is insensitive to changes in soil water content but related to microbial access to organic matter. *Geoderma* **274**, 68–78 (2016).
- Yan, Z. et al. A moisture function of soil heterotrophic respiration that incorporates microscale processes. *Nat. Commun.* **9**, 2562 (2018).
- Herbst, M. et al. Multiyear heterotrophic soil respiration: evaluation of a coupled  $CO_2$  transport and carbon turnover model. *Ecol. Modell.* **214**, 271–283 (2008).
- Li, Y. et al. Biochar reduces soil heterotrophic respiration in a subtropical plantation through increasing soil organic carbon recalcitrancy and decreasing carbon-degrading microbial activity. *Soil Biol. Biochem.* **122**, 173–185 (2018).
- Bond-Lamberty, B., Wang, C. & Gower, S. T. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob. Change Biol.* **10**, 1756–1766 (2004).
- Subke, J.-A., Inglima, I. & Francesca Cotrufo, M. Trends and methodological impacts in soil  $CO_2$  efflux partitioning: a metaanalytical review. *Glob. Change Biol.* **12**, 921–943 (2006).
- Hashimoto, S. et al. Global spatiotemporal distribution of soil respiration modeled using a global database. *Biogeosciences* **12**, 4121–4132 (2015).
- Wieder, W. R., Cleveland, C. C., Smith, W. K. & Todd-Brown, K. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.* **8**, 441–444 (2015).
- Shi, Z., Crowell, S., Luo, Y. & Moore, B. III Model structures amplify uncertainty in predicted soil carbon responses to climate change. *Nat. Commun.* **9**, 2171 (2018).
- Varney, R. M. et al. A spatial emergent constraint on the sensitivity of soil carbon turnover to global warming. *Nat. Commun.* **11**, 5544 (2020).
- O'Sullivan, M. et al. Process-oriented analysis of dominant sources of uncertainty in the land carbon sink. *Nat. Commun.* **13**, 4781 (2022).
- Brady, N. C. & Weil, R. R. *The Nature and Properties of Soils* (Pearson Prentice Hall, 2008).
- Cotrufo, M. F. & Lavalley, J. M. in *Advances in Agronomy* Vol. 172, 1–66 (Elsevier, 2022).
- Hall, S. J., Ye, C., Weintraub, S. R. & Hockaday, W. C. Molecular trade-offs in soil organic carbon composition at continental scale. *Nat. Geosci.* **13**, 687–692 (2020).
- Ma, T. et al. Divergent accumulation of microbial necromass and plant lignin components in grassland soils. *Nat. Commun.* **9**, 3480 (2018).
- Liang, M. et al. Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nat. Commun.* **11**, 2636 (2020).
- Lavalley, J. M., Soong, J. L. & Cotrufo, M. F. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Glob. Change Biol.* **26**, 261–273 (2020).
- Zhou, Z. et al. Global turnover of soil mineral-associated and particulate organic carbon. *Nat. Commun.* **15**, 5329 (2024).
- Yu, W., Huang, W., Weintraub-Leff, S. R. & Hall, S. J. Where and why do particulate organic matter (POM) and mineral-associated organic matter (MAOM) differ among diverse soils? *Soil Biol. Biochem.* **172**, 108756 (2022).
- Heckman, K., Throckmorton, H., Horwath, W. R., Swanston, C. W. & Rasmussen, C. Variation in the molecular structure and radiocarbon abundance of mineral-associated organic matter across a lithosequence of forest soils. *Soil Syst.* **2**, 36 (2018).
- Georgiou, K. et al. Global stocks and capacity of mineral-associated soil organic carbon. *Nat. Commun.* **13**, 3797 (2022).
- Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J. & Lugato, E. Soil carbon storage informed by particulate and mineral-associated organic matter. *Nat. Geosci.* **12**, 989–994 (2019).
- Kögel-Knabner, I. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: fourteen years on. *Soil Biol. Biochem.* **105**, A3–A8 (2017).
- Kögel-Knabner, I. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol. Biochem.* **34**, 139–162 (2002).
- Bugg, T. D. H., Ahmad, M., Hardiman, E. M. & Rahmanpour, R. Pathways for degradation of lignin in bacteria and fungi. *Nat. Prod. Rep.* **28**, 1883–1896 (2011).
- Vitousek, P. M. & Matson, P. A. Nitrogen transformations in a range of tropical forest soils. *Soil Biol. Biochem.* **20**, 361–367 (1988).
- Dietz, S. et al. Root exudate composition of grass and forb species in natural grasslands. *Sci. Rep.* **10**, 10691 (2020).
- Liang, C., Schimel, J. P. & Jastrow, J. D. The importance of anabolism in microbial control over soil carbon storage. *Nat. Microbiol.* **2**, 17105 (2017).

57. Zhu, X., Jackson, R. D., DeLucia, E. H., Tiedje, J. M. & Liang, C. The soil microbial carbon pump: from conceptual insights to empirical assessments. *Glob. Change Biol.* **26**, 6032–6039 (2020).
58. Liang, C. Soil microbial carbon pump: mechanism and appraisal. *Soil Ecol. Lett.* **2**, 241–254 (2020).
59. Kallenbach, C. M., Frey, S. D. & Grandy, A. S. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nat. Commun.* **7**, 13630 (2016).
60. Liang, C., Amelung, W., Lehmann, J. & Kästner, M. Quantitative assessment of microbial necromass contribution to soil organic matter. *Glob. Change Biol.* **25**, 3578–3590 (2019).
61. Wang, X., Dai, W., Filley, T. R., Wang, C. & Bai, E. Aboveground litter addition for five years changes the chemical composition of soil organic matter in a temperate deciduous forest. *Soil Biol. Biochem.* **161**, 108381 (2021).
62. Angst, G. et al. Soil texture affects the coupling of litter decomposition and soil organic matter formation. *Soil Biol. Biochem.* **159**, 108302 (2021).
63. Schulten, H.-R. & Schnitzer, M. Chemical model structures for soil organic matter and soils. *Soil Sci.* **162**, 115–130 (1997).
64. Kleber, M. What is recalcitrant soil organic matter? *Environ. Chem.* **7**, 320 (2010).
65. Lehmann, J. & Kleber, M. The contentious nature of soil organic matter. *Nature* **528**, 60–68 (2015).
66. Marin-Spiotta, E. et al. Paradigm shifts in soil organic matter research affect interpretations of aquatic carbon cycling: transcending disciplinary and ecosystem boundaries. *Biogeochemistry* **117**, 279–297 (2014).
67. Schmidt, M. W. I. et al. Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56 (2011).
68. Meyers, P. A. Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chem. Geol.* **114**, 289–302 (1994).
69. Keiluweit, M. et al. Mineral protection of soil carbon counteracted by root exudates. *Nat. Clim. Change* **5**, 588–595 (2015).
70. Hemingway, J. D. et al. Mineral protection regulates long-term global preservation of natural organic carbon. *Nature* **570**, 228–231 (2019).
71. Witzgall, K. et al. Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nat. Commun.* **12**, 4115 (2021).
72. Hartnett, H. E., Keil, R. G., Hedges, J. I. & Devol, A. H. Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. *Nature* **391**, 572–575 (1998).
73. Heider, J. & Fuchs, G. Anaerobic metabolism of aromatic compounds. *Eur. J. Biochem.* **243**, 577–596 (1997).
74. Jin, Q. & Bethke, C. M. The thermodynamics and kinetics of microbial metabolism. *Am. J. Sci.* **307**, 643–677 (2007).
75. LaRowe, D. E. & Van Cappellen, P. Degradation of natural organic matter: a thermodynamic analysis. *Geochim. Cosmochim. Acta* **75**, 2030–2042 (2011).
76. Keiluweit, M., Wanzek, T., Kleber, M., Nico, P. & Fendorf, S. Anaerobic microsites have an unaccounted role in soil carbon stabilization. *Nat. Commun.* **8**, 1771 (2017).
77. Jinich, A. et al. Quantum chemistry reveals thermodynamic principles of redox biochemistry. *PLoS Comput. Biol.* **14**, e1006471 (2018).
78. Boye, K. et al. Thermodynamically controlled preservation of organic carbon in floodplains. *Nat. Geosci.* **10**, 415–419 (2017).
79. Naasko, K. I. et al. Influence of soil depth, irrigation, and plant genotype on the soil microbiome, metaphenome, and carbon chemistry. *MBio* **14**, e0175823 (2023).
80. Zeng, N. et al. 3775-year-old wood burial supports ‘wood vaulting’ as a durable carbon removal method. *Science* **385**, 1454–1459 (2024).
81. Kamimura, N., Sakamoto, S., Mitsuda, N., Masai, E. & Kajita, S. Advances in microbial lignin degradation and its applications. *Curr. Opin. Biotechnol.* **56**, 179–186 (2019).
82. Lankiewicz, T. S. et al. Lignin deconstruction by anaerobic fungi. *Nat. Microbiol.* **8**, 596–610 (2023).
83. Philippot, L., Chenu, C., Kappler, A., Rillig, M. C. & Fierer, N. The interplay between microbial communities and soil properties. *Nat. Rev. Microbiol.* **22**, 226–239 (2024).
84. Fischer, H., Ingwersen, J. & Kuzyakov, Y. Microbial uptake of low-molecular-weight organic substances out-competes sorption in soil. *Eur. J. Soil Sci.* **61**, 504–513 (2010).
85. Gunina, A., Dippold, M., Glaser, B. & Kuzyakov, Y. Turnover of microbial groups and cell components in soil: <sup>13</sup>C analysis of cellular biomarkers. *Biogeosciences* **14**, 271–283 (2017).
86. Snajdr, J. et al. Transformation of *Quercus petraea* litter: successive changes in litter chemistry are reflected in differential enzyme activity and changes in the microbial community composition. *FEMS Microbiol. Ecol.* **75**, 291–303 (2011).
87. Martinez, A. T. et al. Biodegradation of lignocelluloses: microbial, chemical, and enzymatic aspects of the fungal attack of lignin. *Int. Microbiol.* **8**, 195–204 (2005).
88. Jha, H. in *Mycodegradation of Lignocelluloses* (eds Narayan, R.) 35–49 (Springer, 2019); [https://doi.org/10.1007/978-3-030-23834-6\\_3](https://doi.org/10.1007/978-3-030-23834-6_3).
89. Jin, C. et al. Soil autotrophic-to-heterotrophic-respiration ratio and its controlling factors across several terrestrial biomes: a global synthesis. *Catena* **242**, 108118 (2024).
90. Liu, C., Jiang, H. & Guo, X. Converging patterns of heterotrophic respiration between growing and non-growing seasons in northern temperate grasslands. *Plants* **14**, 2590 (2025).
91. Froelich, P. N. et al. Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. *Geochim. Cosmochim. Acta* **43**, 1075–1090 (1979).
92. Dargie, G. C. et al. Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature* **542**, 86–90 (2017).
93. Harris, L. I. et al. The essential carbon service provided by northern peatlands. *Front. Ecol. Environ.* **20**, 222–230 (2022).
94. Gunina, A. & Kuzyakov, Y. From energy to (soil organic) matter. *Glob. Change Biol.* **28**, 2169–2182 (2022).
95. Manzoni, S. et al. Reviews and syntheses: carbon use efficiency from organisms to ecosystems — definitions, theories, and empirical evidence. *Biogeosciences* **15**, 5929–5949 (2018).
96. Tao, F. et al. Microbial carbon use efficiency promotes global soil carbon storage. *Nature* **618**, 981–985 (2023).
97. Geyer, K. M., Dijkstra, P., Sinsabaugh, R. & Frey, S. D. Clarifying the interpretation of carbon use efficiency in soil through methods comparison. *Soil Biol. Biochem.* **128**, 79–88 (2019).
98. Shi, L.-D. et al. Coupled anaerobic methane oxidation and reductive arsenic mobilization in wetland soils. *Nat. Geosci.* **13**, 799–805 (2020).
99. Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L. & Richter, A. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. *Ecol. Lett.* **16**, 930–939 (2013).
100. Wu, W., Dijkstra, P., Hungate, B. A., Shi, L. & Dippold, M. A. In situ diversity of metabolism and carbon use efficiency among soil bacteria. *Sci. Adv.* **8**, eabq3958 (2022).
101. Domeignoz-Horta, L. A. et al. Plant diversity drives positive microbial associations in the rhizosphere enhancing carbon use efficiency in agricultural soils. *Nat. Commun.* **15**, 8065 (2024).
102. Saifuddin, M., Bhatnagar, J. M., Segrè, D. & Finzi, A. C. Microbial carbon use efficiency predicted from genome-scale metabolic models. *Nat. Commun.* **10**, 3568 (2019).
103. Pold, G. et al. Carbon use efficiency and its temperature sensitivity covary in soil bacteria. *MBio* **11**, e02293–19 (2020).
104. Jansson, J. K. & Hofmockel, K. S. Soil microbiomes and climate change. *Nat. Rev. Microbiol.* **18**, 35–46 (2020).
105. Lennon, J. T., Aanderud, Z. T., Lehmkuhl, B. K. & Schoolmaster, D. R. Jr Mapping the niche space of soil microorganisms using taxonomy and traits. *Ecology* **93**, 1867–1879 (2012).
106. Knapp, B. D. et al. Metabolic rearrangement enables adaptation of microbial growth rate to temperature shifts. *Nat. Microbiol.* **10**, 185–201 (2025).
107. Zhang, S. et al. Reconciling carbon quality with availability predicts temperature sensitivity of global soil carbon mineralization. *Proc. Natl Acad. Sci. USA* **121**, e2313842121 (2024).
108. Craine, J. M., Fierer, N. & McLauchlan, K. K. Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat. Geosci.* **3**, 854–857 (2010).
109. Hopkins, F. M., Torn, M. S. & Trumbore, S. E. Warming accelerates decomposition of decades-old carbon in forest soils. *Proc. Natl Acad. Sci. USA* **109**, E1753–E1761 (2012).
110. Karhu, K. et al. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* **513**, 81–84 (2014).
111. Hicks Pries, C. E., Castanha, C., Porras, R. C. & Torn, M. S. The whole-soil carbon flux in response to warming. *Science* **355**, 1420–1423 (2017).
112. Abreu, C. I., Dal Bello, M., Bunse, C., Pinhassi, J. & Gore, J. Warmer temperatures favor slower-growing bacteria in natural marine communities. *Sci. Adv.* **9**, eade8352 (2023).
113. Yue, H. et al. The microbe-mediated mechanisms affecting topsoil carbon stock in Tibetan grasslands. *ISME J.* **9**, 2012–2020 (2015).
114. Yu, K. et al. Nonlinear microbial thermal response and its implications for abrupt soil organic carbon responses to warming. *Nat. Commun.* **16**, 2763 (2025).
115. Thompson, L. R. et al. A communal catalogue reveals Earth’s multiscale microbial diversity. *Nature* **551**, 457–463 (2017).
116. He, L. et al. Global biogeography of fungal and bacterial biomass carbon in topsoil. *Soil Biol. Biochem.* **151**, 108024 (2020).
117. Yu, K. et al. The biogeography of relative abundance of soil fungi versus bacteria in surface topsoil. *Earth Syst. Sci. Data* **14**, 4339–4350 (2022).
118. Jansson, J. K. & Hofmockel, K. S. The soil microbiome — from metagenomics to metaphenomics. *Curr. Opin. Microbiol.* **43**, 162–168 (2018).
119. Hultman, J. et al. Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* **521**, 208–212 (2015).
120. Sáez-Sandino, T. et al. A large fraction of soil microbial taxa is sensitive to experimental warming. *Glob. Change Biol.* **31**, e70231 (2025).
121. Zhou, Z. et al. The biogeography of soil microbiome potential growth rates. *Nat. Commun.* **15**, 9472 (2024).
122. Bailey, V. L. et al. Measurements of microbial community activities in individual soil macroaggregates. *Soil Biol. Biochem.* **48**, 192–195 (2012).
123. Pietikäinen, J., Pettersson, M. & Bååth, E. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiol. Ecol.* **52**, 49–58 (2005).
124. Crowther, T. W. et al. The global soil community and its influence on biogeochemistry. *Science* **365**, eaav0550 (2019).
125. Wan, S., Norby, R. J., Ledford, J. & Weltzin, J. F. Responses of soil respiration to elevated CO<sub>2</sub>, air warming, and changing soil water availability in a model old-field grassland. *Glob. Change Biol.* **13**, 2411–2424 (2007).
126. Zhou, L. et al. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. *Glob. Change Biol.* **22**, 3157–3169 (2016).
127. Bernhardt, E. S. et al. Long-term effects of free air CO<sub>2</sub> enrichment (FACE) on soil respiration. *Biogeochemistry* **77**, 91–116 (2006).
128. Norby, R. J. & Zak, D. R. Ecological lessons from free-air CO<sub>2</sub> enrichment (FACE) experiments. *Annu. Rev. Ecol. Syst.* **42**, 181–203 (2011).



129. Merlin, C., Masters, M., McAteer, S. & Coulson, A. Why is carbonic anhydrase essential to *Escherichia coli*? *J. Bacteriol.* **185**, 6415–6424 (2003).
130. Aguilera, J., Van Dijken, J. P., De Winde, J. H. & Pronk, J. T. Carbonic anhydrase (Nce103p): an essential biosynthetic enzyme for growth of *Saccharomyces cerevisiae* at atmospheric carbon dioxide pressure. *Biochem. J.* **391**, 311–316 (2005).
131. Haddix, M. L. et al. The role of soil characteristics on temperature sensitivity of soil organic matter. *Soil Sci. Soc. Am. J.* **75**, 56–68 (2011).
132. Fairbairn, L. et al. Relationship between soil CO<sub>2</sub> fluxes and soil moisture: anaerobic sources explain fluxes at high water content. *Geoderma* **434**, 116493 (2023).
133. Melillo, J. M. et al. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* **358**, 101–105 (2017).
134. Niu, S. et al. Temperature responses of ecosystem respiration. *Nat. Rev. Earth Environ.* **5**, 559–571 (2024).
135. Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006).
136. Haaf, D., Six, J. & Doetterl, S. Global patterns of geo-ecological controls on the response of soil respiration to warming. *Nat. Clim. Change* **11**, 623–627 (2021).
137. Dacal, M., Bradford, M. A., Plaza, C., Maestre, F. T. & García-Palacios, P. Soil microbial respiration adapts to ambient temperature in global drylands. *Nat. Ecol. Evol.* **3**, 232–238 (2019).
138. Bradford, M. A. et al. Soil carbon science for policy and practice. *Nat. Sustain.* **2**, 1070–1072 (2019).
139. Moinet, G. Y. K. et al. Soil microbial sensitivity to temperature remains unchanged despite community compositional shifts along geothermal gradients. *Glob. Change Biol.* **27**, 6217–6231 (2021).
140. Jansson, J. K. & Taş, N. The microbial ecology of permafrost. *Nat. Rev. Microbiol.* **12**, 414–425 (2014).
141. IPCC *The Ocean and Cryosphere in a Changing Climate* (Cambridge Univ. Press, 2022).
142. Hicks Pries, C. E., Schuur, E. A. G., Vogel, J. G. & Natali, S. M. Moisture drives surface decomposition in thawing tundra. *J. Geophys. Res. Biogeosci.* **118**, 1133–1143 (2013).
143. Torn, M. S. et al. Large emissions of CO<sub>2</sub> and CH<sub>4</sub> due to active-layer warming in Arctic tundra. *Nat. Commun.* **16**, 124 (2025).
144. Watts, M., Maslowski, W., Lee, Y. J., Kinney, J. C. & Osinski, R. A spatial evaluation of Arctic sea ice and regional limitations in CMIP6 historical simulations. *J. Clim.* **34**, 6399–6420 (2021).
145. Le Noé, J. et al. Soil organic carbon models need independent time-series validation for reliable prediction. *Commun. Earth Environ.* **4**, 158 (2023).
146. Batjes, N. H., Calisto, L. & de Sousa, L. M. Providing quality-assessed and standardised soil data to support global mapping and modelling (WoSIS snapshot 2023). *Earth Syst. Sci. Data* **16**, 4735–4765 (2024).
147. Forney, D. C. & Rothman, D. H. Inverse method for estimating respiration rates from decay time series. *Biogeosciences* **9**, 3601–3612 (2012).
148. Forney, D. C. & Rothman, D. H. Common structure in the heterogeneity of plant-matter decay. *J. R. Soc. Interface* **9**, 2255–2267 (2012).
149. Middelburg, J. J. A simple rate model for organic matter decomposition in marine sediments. *Geochim. Cosmochim. Acta* **53**, 1577–1581 (1989).
150. Bosatta, E. & Ågren, G. I. Theoretical analysis of decomposition of heterogeneous substrates. *Soil Biol. Biochem.* **17**, 601–610 (1985).
151. Liang, G. et al. Soil respiration response to decade-long warming modulated by soil moisture in a boreal forest. *Nat. Geosci.* **17**, 905–911 (2024).
152. Bowden, R. D., Newkirk, K. M. & Rullo, G. M. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biol. Biochem.* **30**, 1591–1597 (1998).
153. Xu, Z. et al. Effects of elevated CO<sub>2</sub> and N fertilization on CH<sub>4</sub> emissions from paddy rice fields. *Global Biogeochem. Cycles* <https://doi.org/10.1029/2004GB002233> (2004).
154. Schaefer, K. & Jafarov, E. A parameterization of respiration in frozen soils based on substrate availability. *Biogeosciences* **13**, 1991–2001 (2016).
155. Pfahl, S., O’Gorman, P. A. & Fischer, E. M. Understanding the regional pattern of projected future changes in extreme precipitation. *Nat. Clim. Change* **7**, 423–427 (2017).
156. Davidson, E. A., Samanta, S., Caramori, S. S. & Savage, K. The dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Glob. Change Biol.* **18**, 371–384 (2012).
157. Schimel, J. P. Life in dry soils: effects of drought on soil microbial communities and processes. *Annu. Rev. Ecol. Evol. Syst.* **49**, 409–432 (2018).
158. Seo, K.-W. et al. Abrupt sea level rise and Earth’s gradual pole shift reveal permanent hydrological regime changes in the 21st century. *Science* **387**, 1408–1413 (2025).
159. Pellegrini, A. F. A. et al. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* **553**, 194–198 (2018).
160. Taş, N. et al. Impact of fire on active layer and permafrost microbial communities and metagenomes in an upland Alaskan boreal forest. *ISME J.* **8**, 1904–1919 (2014).
161. Dai, L. et al. Increased asymmetry of ecosystem productivity responses to precipitation in recent two decades. *Geophys. Res. Lett.* **52**, e2024GL113861 (2025).
162. Taş, N. et al. Landscape topography structures the soil microbiome in Arctic polygonal tundra. *Nat. Commun.* **9**, 777 (2018).
163. Pengerud, A. et al. Soil organic matter molecular composition and state of decomposition in three locations of the European Arctic. *Biogeochemistry* **135**, 277–292 (2017).
164. Birch, H. F. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* **10**, 9–31 (1958).
165. Birch, H. F. Mineralisation of plant nitrogen following alternate wet and dry conditions. *Plant Soil* **20**, 43–49 (1964).
166. Griffiths, E. & Birch, H. F. Microbiological changes in freshly moistened soil. *Nature* **189**, 424–424 (1961).
167. Barnard, R. L., Osborne, C. A. & Firestone, M. K. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME J.* **7**, 2229–2241 (2013).
168. Smith, M. L. et al. Real-time and rapid respiratory response of the soil microbiome to moisture shifts. *Microorganisms* **11**, 2630 (2023).
169. Paustian, K. et al. Climate-smart soils. *Nature* **532**, 49–57 (2016).
170. Beattie, G. A. et al. Soil microbiome interventions for carbon sequestration and climate mitigation. *mSystems* <https://doi.org/10.1128/msystems.01129-24> (2024).
171. Peixoto, R. S. et al. Harnessing the microbiome to prevent global biodiversity loss. *Nat. Microbiol.* **7**, 1726–1735 (2022).
172. Ahmad, M. et al. Evaluating biochar-microbe synergies for improved growth, yield of maize, and post-harvest soil characteristics in a semi-arid climate. *Agronomy* **10**, 1055 (2020).
173. Bohlool, B. B., Ladha, J. K., Garrity, D. P. & George, T. Biological nitrogen fixation for sustainable agriculture: a perspective. *Plant Soil* **141**, 1–11 (1992).
174. Telles, T. S., Nogueira, M. A. & Hungria, M. Economic value of biological nitrogen fixation in soybean crops in Brazil. *Environ. Technol. Innov.* **31**, 103158 (2023).
175. O’Callaghan, M., Ballard, R. A. & Wright, D. Soil microbial inoculants for sustainable agriculture: limitations and opportunities. *Soil Use Manag.* **38**, 1340–1369 (2022).
176. Mason, A. R. G., Salomon, M. J., Lowe, A. J. & Cavagnaro, T. R. Microbial solutions to soil carbon sequestration. *J. Clean. Prod.* **417**, 137993 (2023).
177. Joergensen, R. G. & Wichern, F. Alive and kicking: why dormant soil microorganisms matter. *Soil Biol. Biochem.* **116**, 419–430 (2018).
178. Mawarda, P. C., Le Roux, X., Dirk van Elsas, J. & Salles, J. F. Deliberate introduction of invisible invaders: a critical appraisal of the impact of microbial inoculants on soil microbial communities. *Soil Biol. Biochem.* **148**, 107874 (2020).
179. Mallon, C. A., van Elsas, J. D. & Salles, J. F. Microbial invasions: the process, patterns, and mechanisms. *Trends Microbiol.* **23**, 719–729 (2015).
180. Liu, X. & Salles, J. F. Drivers and consequences of microbial community coalescence. *ISME J.* **18**, wrae179 (2024).
181. Mallon, C. A. et al. The impact of failure: unsuccessful bacterial invasions steer the soil microbial community away from the invader’s niche. *ISME J.* **12**, 728–741 (2018).
182. Liu, M. et al. Unprotected carbon dominates decadal soil carbon increase. *Nat. Commun.* **16**, 2008 (2025).
183. Wasner, D. et al. Environment and microbiome drive different microbial traits and functions in the macroscale soil organic carbon cycle. *Glob. Change Biol.* **30**, e17465 (2024).
184. Lee, J., Kim, H.-S., Jo, H. Y. & Kwon, M. J. Revisiting soil bacterial counting methods: optimal soil storage and pretreatment methods and comparison of culture-dependent and -independent methods. *PLoS ONE* **16**, e0246142 (2021).
185. Schloss, P. D. & Handelsman, J. Toward a census of bacteria in soil. *PLoS Comput. Biol.* **2**, e92 (2006).
186. Jansson, J. K. & Wu, R. Soil viral diversity, ecology and climate change. *Nat. Rev. Microbiol.* **21**, 296–311 (2023).
187. McNunn, G. et al. Climate smart agriculture opportunities for mitigating soil greenhouse gas emissions across the U.S. corn-belt. *J. Clean. Prod.* **268**, 122240 (2020).
188. Faggiani Dias, D. et al. Removing atmospheric CO<sub>2</sub> through mass scaleup of crops with enhanced root systems. *Environ. Res. Lett.* **20**, 054004 (2025).
189. Rasse, D. P., Rumpel, C. & Dignac, M.-F. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* **269**, 341–356 (2005).
190. Sokol, N. W. & Bradford, M. A. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nat. Geosci.* **12**, 46–53 (2019).
191. Mathieu, J. A., Hatté, C., Balesdent, J. & Parent, É. Deep soil carbon dynamics are driven more by soil type than by climate: a worldwide meta-analysis of radiocarbon profiles. *Glob. Change Biol.* **21**, 4278–4292 (2015).
192. Balesdent, J. et al. Atmosphere–soil carbon transfer as a function of soil depth. *Nature* **559**, 599–602 (2018).
193. Bennett, A. E. & Groten, K. The costs and benefits of plant-arbuscular mycorrhizal fungal interactions. *Annu. Rev. Plant Biol.* **73**, 649–672 (2022).
194. Duan, S. et al. Cross-kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus–bacterium continuum. *Nat. Rev. Microbiol.* **22**, 773–790 (2024).
195. Suryanarayanan, T. S., Ayesha, M. S. & Shaanker, R. U. Leaf photosynthesis: do endophytes have a say? *Trends Plant Sci.* **27**, 968–970 (2022).
196. Abdalla, M., Bitterlich, M., Jansa, J., Püschel, D. & Ahmed, M. A. The role of arbuscular mycorrhizal symbiosis in improving plant water status under drought. *J. Exp. Bot.* **74**, 4808–4824 (2023).
197. Allen, M. F. in *Progress in Botany* Vol. 70, 257–276 (Springer, 2008).
198. Wang, W. et al. Glomalin contributed more to carbon, nutrients in deeper soils, and differently associated with climates and soil properties in vertical profiles. *Sci. Rep.* **7**, 13003 (2017).
199. Kaiser, C. et al. Exploring the transfer of recent plant photosynthates to soil microbes: mycorrhizal pathway vs direct root exudation. *N. Phytol.* **205**, 1537–1551 (2015).
200. Berrios, L. et al. Ectomycorrhizal fungi alter soil food webs and the functional potential of bacterial communities. *mSystems* **9**, e0036924 (2024).
201. Sosa-Hernández, M. A., Leifheit, E. F., Ingrassia, R. & Rillig, M. C. Subsoil arbuscular mycorrhizal fungi for sustainability and climate-smart agriculture: a solution right under our feet? *Front. Microbiol.* **10**, 744 (2019).

202. Smith, M. E., Henkel, T. W. & Rollins, J. A. How many fungi make sclerotia? *Fungal Ecol.* **13**, 211–220 (2015).
203. Wilson, G. W. T., Rice, C. W., Rillig, M. C., Springer, A. & Hartnett, D. C. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecol. Lett.* **12**, 452–461 (2009).
204. Lehmann, A. et al. Fungal traits important for soil aggregation. *Front. Microbiol.* **10**, 2904 (2019).
205. Garcia-Franco, N., Hobbie, E., Hübner, R. & Wiesmeier, M. in *Soil Management and Climate Change* 349–368 (Elsevier, 2018).
206. Huang, W. et al. Comparison of distinctive diversities, co-occurrence patterns and potential ecological functions of microbial communities in heterogeneous soil areas in typical subtropical forests, southeast China. *Catena* **238**, 107838 (2024).
207. Poeplau, C. & Don, A. Carbon sequestration in agricultural soils via cultivation of cover crops — a meta-analysis. *Agric. Ecosyst. Environ.* **200**, 33–41 (2015).
208. Jian, J., Du, X., Reiter, M. S. & Stewart, R. D. A meta-analysis of global cropland soil carbon changes due to cover cropping. *Soil Biol. Biochem.* **143**, 107735 (2020).
209. Chaplot, V. & Smith, P. Cover crops do not increase soil organic carbon stocks as much as has been claimed: what is the way forward? *Glob. Change Biol.* **29**, 6163–6169 (2023).
210. Blanco-Canqui, H. Cover crops and carbon sequestration: lessons from U.S. studies. *Soil Sci. Soc. Am. J.* **86**, 501–519 (2022).
211. Bowden, R. D., Davidson, E., Savage, K., Arabia, C. & Steudler, P. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. *For. Ecol. Manage.* **196**, 43–56 (2004).
212. Janssens, I. A. et al. Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* **3**, 315–322 (2010).
213. Zhu, F., Lu, X., Liu, L. & Mo, J. Phosphate addition enhanced soil inorganic nutrients to a large extent in three tropical forests. *Sci. Rep.* **5**, 7923 (2015).
214. Yang, Y. et al. Global effects on soil respiration and its temperature sensitivity depend on nitrogen addition rate. *Soil Biol. Biochem.* **174**, 108814 (2022).
215. Idbella, M. et al. Long-term effects of biochar on soil chemistry, biochemistry, and microbiota: results from a 10-year field vineyard experiment. *Appl. Soil Ecol.* **195**, 105217 (2024).
216. Lehmann, J. et al. Biochar in climate change mitigation. *Nat. Geosci.* **14**, 883–892 (2021).
217. Gross, A., Bromm, T. & Glaser, B. Soil organic carbon sequestration after biochar application: a global meta-analysis. *Agronomy* **11**, 2474 (2021).
218. Keesstra, S. D. et al. European agricultural soil management: towards climate-smart and sustainability, knowledge needs and research approaches. *Eur. J. Soil Sci.* **75**, e13437 (2024).
219. Soares, J. R. et al. Mitigation of nitrous oxide emissions in grazing systems through nitrification inhibitors: a meta-analysis. *Nutr. Cycl. Agroecosyst.* **125**, 359–377 (2024).
220. Tufail, M. A., Irfan, M., Umar, W., Wakeel, A. & Schmitz, R. A. Mediation of gaseous emissions and improving plant productivity by DCD and DMPP nitrification inhibitors: meta-analysis of last three decades. *Environ. Sci. Pollut. Res. Int.* **30**, 64719–64735 (2023).
221. Qiao, C. et al. How inhibiting nitrification affects nitrogen cycle and reduces environmental impacts of anthropogenic nitrogen input. *Glob. Change Biol.* **21**, 1249–1257 (2015).
222. Subbarao, G. V. et al. Suppression of soil nitrification by plants. *Plant Sci.* **233**, 155–164 (2015).
223. Peixoto, L. & Petersen, S. O. Efficacy of three nitrification inhibitors to reduce nitrous oxide emissions from pig slurry and mineral fertilizers applied to spring barley and winter wheat in Denmark. *Geoderma Reg.* **32**, e00597 (2023).
224. Thapa, R., Chatterjee, A., Awale, R., McGranahan, D. A. & Daigh, A. Effect of enhanced efficiency fertilizers on nitrous oxide emissions and crop yields: a meta-analysis. *Soil Sci. Soc. Am. J.* **80**, 1121–1134 (2016).
225. Yin, J. et al. Nitrogen and carbon addition changed nitrous oxide emissions from soil aggregates in straw-incorporated soil. *J. Soils Sediments* **22**, 617–629 (2022).
226. Norton, J. & Ouyang, Y. Controls and adaptive management of nitrification in agricultural soils. *Front. Microbiol.* **10**, 1931 (2019).
227. Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J. & Garnier, J. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. *Environ. Res. Lett.* **9**, 105011 (2014).
228. Byrne, M. P. et al. Urease and nitrification inhibitors — as mitigation tools for greenhouse gas emissions in sustainable dairy systems: a review. *Sustainability* **12**, 6018 (2020).
229. Uwizeye, A. et al. Nitrogen emissions along global livestock supply chains. *Nat. Food* **1**, 437–446 (2020).
230. Thompson, L. R. et al. Is climate neutral possible for the U.S. beef and dairy sectors? *Front. Sustain. Food Syst.* **9**, (2025).
231. Horstmann, L. et al. Potential risks of the nitrification inhibitors Nitrapyrin and DMPP: a review on non-target effects on microorganisms and environmental fate in agricultural soil. Preprint at *ChemRxiv* <https://doi.org/10.26434/chemrxiv-2025-0tr1r> (2025).
232. Sawinska, Z. et al. How tillage system affects the soil carbon dioxide emission and wheat plants physiological state. *Agronomy* **14**, 2220 (2024).
233. Córdova, S. C., Kravchenko, A. N., Miesel, J. R. & Robertson, G. P. Soil carbon change in intensive agriculture after 25 years of conservation management. *Geoderma* **453**, 117133 (2025).
234. Poulton, P. R., Pye, E., Hargreaves, P. R. & Jenkinson, D. S. Accumulation of carbon and nitrogen by old arable land reverting to woodland. *Glob. Change Biol.* **9**, 942–955 (2003).
235. Poulton, P., Johnston, J., Macdonald, A., White, R. & Powlson, D. Major limitations to achieving '4 per 1000' increases in soil organic carbon stock in temperate regions: evidence from long-term experiments at Rothamsted Research, United Kingdom. *Glob. Change Biol.* **24**, 2563–2584 (2018).
236. Chandel, A. K., Jiang, L. & Luo, Y. Microbial models for simulating soil carbon dynamics: a review. *J. Geophys. Res. Biogeosci.* <https://doi.org/10.1029/2023jg007436> (2023).
237. Becker, J. M., Parkin, T., Nakatsu, C. H., Wilbur, J. D. & Konopka, A. Bacterial activity, community structure, and centimeter-scale spatial heterogeneity in contaminated soil. *Microb. Ecol.* **51**, 220–231 (2006).
238. Cai, Y.-J. et al. Microbial community structure is stratified at the millimeter-scale across the soil–water interface. *ISME Commun.* **2**, 53 (2022).
239. Wieder, W. R. et al. Explicitly representing soil microbial processes in Earth system models. *Glob. Biogeochem. Cycles* **29**, 1782–1800 (2015).
240. Zhang, X. et al. A microbial-explicit soil organic carbon decomposition model (MESDM): development and testing at a semiarid grassland site. *J. Adv. Model. Earth Syst.* **14**, e2021MS002485 (2022).
241. Malik, A. A. et al. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *ISME J.* **14**, 1–9 (2020).
242. Brangari, A. C., Knorr, M. A., Frey, S. D. & Rousk, J. Shifts in microbial thermal traits mitigate heat-induced carbon losses in soils. *Glob. Change Biol.* **31**, e70579 (2025).
243. Van de Broek, M., Govers, G., Schrumpp, M. & Six, J. A microbially driven and depth-explicit soil organic carbon model constrained by carbon isotopes to reduce parameter equifinality. *Biogeosciences* **22**, 1427–1446 (2025).
244. Sircan, A. K. et al. Trait-based modeling of microbial interactions and carbon turnover in the rhizosphere. *Soil Biol. Biochem.* **202**, 109698 (2025).
245. Dalton, R. NEON to shed light on environment research. *Nature* **404**, 216 (2000).
246. Åström, O., Geldhauser, C., Grillitsch, M., Hall, O. & Sopasakis, A. Enhancing carbon emission reduction strategies using OCO and ICOS data. *Sci. Rep.* **15**, 36297 (2025).
247. Baldocchi, D. et al. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* **82**, 2415–2434 (2001).
248. Hobbie, J. E., Carpenter, S. R., Grimm, N. B., Gosz, J. R. & Seastedt, T. R. The US Long Term Ecological Research program. *Bioscience* **53**, 21 (2003).
249. Batjes, N. H. et al. WoSIS: providing standardised soil profile data for the world. *Earth Syst. Sci. Data* **9**, 1–14 (2017).
250. Jian, J. et al. A restructured and updated global soil respiration database (SRDB-V5). *Earth Syst. Sci. Data* **13**, 255–267 (2021).
251. Gilbert, J. A. & Zengler, K. The role of artificial intelligence in microbial sciences to support climate resilience. *Nat. Rev. Microbiol.* **23**, 333–334 (2025).
252. Wang, G., Post, W. M. & Mayes, M. A. Development of microbial-enzyme-mediated decomposition model parameters through steady-state and dynamic analyses. *Ecol. Appl.* **23**, 255–272 (2013).
253. Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E. & Pacala, S. W. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. *Nat. Clim. Change* **4**, 1099–1102 (2014).
254. Tang, J. Y. & Riley, W. J. A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial litter decomposition. *Biogeosciences* **10**, 8329–8351 (2013).
255. Sierra, C. A., Malghani, S. & Loescher, H. W. Interactions among temperature, moisture, and oxygen concentrations in controlling decomposition rates in a boreal forest soil. *Biogeosciences* **14**, 703–710 (2017).

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<sup>1</sup>The Soil Stars, Applied Microbiology International, Cambridge, UK. <sup>2</sup>The Laboratory of Environmental Microbiology, The Rockefeller University, New York, NY, USA. <sup>3</sup>Biological and Environmental Science and Engineering Division (BESE), KAUST — King Abdullah University of Science and Technology, Thuwal, Saudi Arabia. <sup>4</sup>Genomics Research in Ecology and Evolution in Nature (Green), Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands. <sup>5</sup>Department of Biology, Indiana University, Bloomington, IN, USA. <sup>6</sup>Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland. <sup>7</sup>Department of Environmental Science, Aarhus University, Roskilde, Denmark. <sup>8</sup>Microbiology, Faculty of Science, School for Data Science and Computational Thinking, Stellenbosch, South Africa. <sup>9</sup>Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA. <sup>10</sup>Soil Health Center, Scripps Institution of Oceanography, University of California San Diego, La Jolla, USA.