Review

# Microbial modulators of soil carbon storage: integrating genomic and metabolic knowledge for global prediction

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**Soil organic carbon performs a number of functions in ecosystems and it is clear that microbial communities play important roles in land–atmosphere carbon (C) exchange and soil C storage. In this review, we discuss microbial modulators of soil C storage, 'omics'-based approaches to characterize microbial system interactions impacting terrestrial C sequestration, and how data related to microbial composition and activities can be incorporated into mechanistic and predictive models. We argue that although making direct linkage of genomes to global phenomena is a significant challenge, many connections at intermediate scales are viable with integrated application of new systems biology approaches and powerful analytical and modelling techniques. This integration could enhance our capability to develop and evaluate microbial strategies for capturing and sequestering atmospheric $CO_2$.**

## Overview of global carbon budget and microbial contribution

One of the major challenges of the 21st century is to mitigate the effects of global environmental changes brought about by increasing emissions of greenhouse gases (GHGs), especially $CO_2$ [1,2]. Over the past 200 years, $405 \pm 30$ Gigatons (Gt; $10^{15}$ g) carbon (C) has been emitted into the atmosphere primarily via anthropogenic activities and as a result the global concentration of $CO_2$ has risen from 280 to 382 ppm in 2007, with a current annual increase of 0.88 ppm [3]. There is thus an imminent need to identify cost-effective strategies for mitigating anthropogenic $CO_2$ emissions if we are to minimize the impact of climate change and ensure global environmental security [4,5]. Important feedback exists between the atmosphere and soil, and a clear understanding of how rising atmospheric $CO_2$ and associated climate change might affect soil C sequestration (see Glossary) and GHG exchange in terrestrial ecosystems is urgently needed [1–5].

Soils represent a massive stock of potentially volatile C and act both as a buffer against atmospheric $CO_2$ increase and as a potential sink for additional C depending on the balance between photosynthesis, the respiration of decomposer organisms, and stabilization of C in soils [4,5] (Figure 1). Soil biospheric C sequestration can meaningfully

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## Glossary

**Carbon sequestration:** reduction of $CO_2$ emissions to the atmosphere through abiological and biological processes. There are three main methods in various stages of discovery and development: (i) near-term storage in the terrestrial biosphere where vegetation would soak up the $CO_2$ and store it in biomass and soil; (ii) long-term storage in the earth's soil by pumping $CO_2$ into existing or drilled/excavated sub-surface reservoirs; and (iii) long-term storage in the earth's oceans where $CO_2$ would be injected thousands of feet deep and trapped by the water.

**Copiotrophs:** copiotrophs (*r*-strategists) are defined as microbes having high growth rates under nutrient-rich conditions and mainly target labile C pools.

**Ecological models:** the conceptualization and implementation of computer simulations of the behaviour of living systems. Ecological models have two major aims: (i) provide general insight into how ecological systems or ecological interactions work; and (ii) provide specific predictions about the likely futures of particular populations, communities, or ecosystems.

**Metagenomics:** the application of modern genomics techniques to the study of communities of microbial organisms directly in their natural environments, bypassing the need for isolation and lab cultivation of individual species. Metagenomics is presently divided into two research areas driven by technological applications, (i) environmental single gene surveys, and (ii) random shotgun studies of all environmental genes.

**Microaggregate:** organo-mineral complexes operationally defined as 53–212 μm in size consisting of primary particles, plant roots, and simple biomolecules stabilized together by bacterial and fungal proteins. They contain pore space for air and water and harbour a range of microbes, but organic matter turnover occurs slower than in macroaggregates (>212 μm).

**Oligotrophs:** oligotrophs (*k*-strategists) are slow growing microbes that are dominant in nutrient-poor environments, and mainly target recalcitrant C pools.

**Soil organic matter (SOM):** traditionally classified into two major groups comprising humic and nonhumic substances. SOM is thermodynamically unstable and is part of the natural balance between production, decomposition, transformation, and resynthesis of various organic substances. The humified fraction is composed of humic, fulvic, and humin and is very stable. The nonhumic portion is the relatively unstable, most labile fraction and is easily decomposed. However, recent analytical and experimental advances have demonstrated that humic substances represent only a small fraction of total organic matter and persistence of SOM is primarily not a molecular, but an ecosystem property [1]. SOM is made up of 50–58% soil organic carbon (SOC).

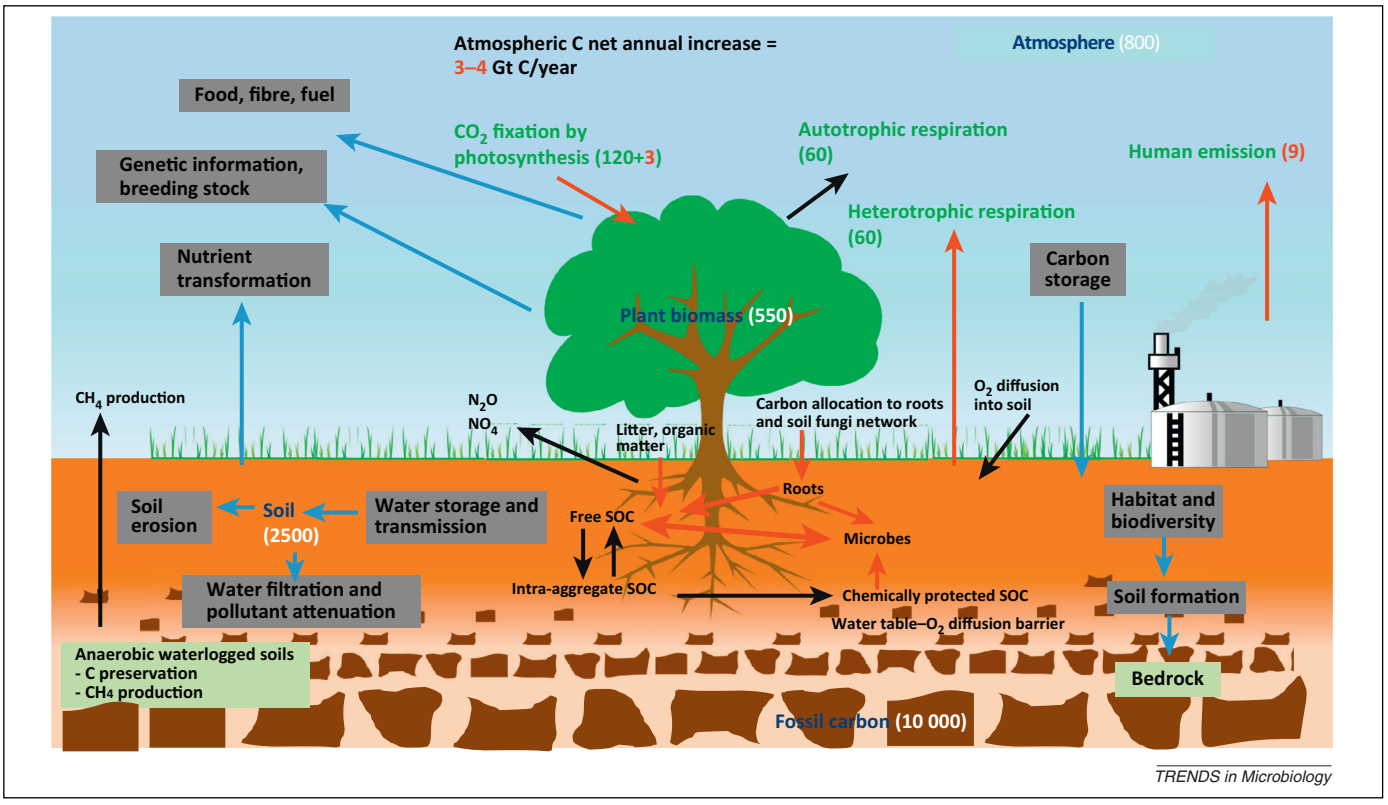


**Figure 1**. Simplified terrestrial carbon cycle. The values in bracket represent the exchange of C between land and atmosphere in Gigatons (Gt) of C per year. Green numbers are natural fluxes; red numbers are human contributions in Gt of C per year. White numbers indicate stored C. Grey-coloured boxes represent the ecosystem services provided by C cycling. Red arrows represent processes that are postulated to increase in future climate scenarios. Modified, with permission, from [2].

contribute to a portfolio of mitigation approaches and potentially offset a significant fraction of diffuse $CO_2$ sources for which direct capture is not yet feasible [4–6]. In particular it has been estimated that through judicious management, the world agriculture and degraded soils could sequester an additional 0.4–1.2 Gt C/year, which is equivalent to 5–15% of global fossil fuel emissions [5]. Terrestrial C storage not only represents an important option for partially mitigating anthropogenic emissions but also provides a number of other ecosystem services such as soil fertility, water quality, resistance to erosion, and climate mitigation through reduced feedbacks to climate change [5] (Figure 1).

In terrestrial ecosystems, the uptake of $CO_2$ from the atmosphere by net primary production (NPP) is dominated by higher plants, but microorganisms contribute greatly to ecosystem C budgets through their roles as detritivores, plant symbionts, or pathogens, thereby modifying nutrient availability and influencing C turnover and retention in soil [5,6]. It has been proposed that terrestrial ecosystems can potentially be manipulated through land use and land management practices for the build-up of distinct microbial communities that favour C sequestration [4–8]. Additionally, ecological classification of microbial groups (i.e., copiotrophs and oligotrophs) has been proposed based on their ability to utilise soil organic carbon (SOC) [9] but evidence for such life styles under relevant environmental conditions is lacking. Challenges in manipulating microbial community for enhanced C sequestration arise from the enormous diversity and unculturability of soil microbial communities, which has precluded their comprehensive characterization and limited our understanding on their ecological functions [8–10]. The new generation of omics methods (e.g., genomics, transcriptomics, proteomics, metabolomics, metagenomics) are proving instrumental in providing valuable information about the taxonomic, genetic, and functional properties of soil microbial communities (Table 1) [8–16]. These techniques have begun to allow investigation of functional processes of terrestrial microbial communities involved in C cycling that can be incorporated into mechanistic and predictive ecological models [17]. This review will discuss selected examples of genomic and metagenomic studies that have provided a mechanistic understanding of the role microbes play in C storage and suggest pathways to include these data to modify existing ecological models.

## Microbial modulators of soil C storage

Decomposition of biomass by microbes results in C loss from the soil due to microbial respiration (heterotrophic respiration) while a small proportion of the original C is retained in the soil through the formation of stable organic matter (Figure 1) [1,2]. When C inputs from photosynthesis exceed C losses through soil respiration, SOC levels increase over time resulting in net soil C sequestration [1–5]. Based on the C mineralization potential and growth rates, soil-dwelling bacteria can be classified into two ecological functional categories of copiotrophs (*r*-strategists) and oligotrophs (*k*-strategists) [9]. Members of phyla Actinobacteria and Acidobacteria and class Deltaproteobacteria are considered as oligotrophs whereas phylum Bacteroidetes and class α and γ *Proteobacteria* are copiotrophs [9,18]. It has also been postulated that soils dominated by oligotrophs may have

**Table 1. Metagenomic studies of terrestrial ecosystems**[a]

| Geographic location | Habitat | Strategy (metagenome size) | Information on | | Refs |
|---|---|---|---|---|---|
| | | | Community structure | Community function | |
| Cedar Creek Ecosystem Science Reserve (CC) and Kellogg Biological Station (KB), USA | Grassland (CC) and agricultural field (KB) | 454-FLX Titanium (518 Megabase) | N fertilization might induce a shift in the predominant microbial life-history strategies, a pattern that parallels the often observed replacement of *k*-selected with *r*-selected plant species with elevated N | N fertilization increases the relative abundances of genes associated with DNA/RNA replication, electron transport, and protein metabolism | [10] |
| Spruce plantation at Breuil-Chenue, France | Temperate forest | 454-FLX Titanium and Illumina (14 Gigabase) | The organic soil horizon was significantly enriched in sequences related to Bacteria, Chordata, Arthropoda, and Ascomycota whereas the mineral horizon was significantly enriched in sequences related to Archaea | Significant increase in the relative abundance of sequences related to glycoside hydrolases in the organic horizon compared to the mineral horizon that was significantly enriched in glycoside transferases | [11] |
| Various countries and continents | Various biomes | Illumina paired end sequencing (390–1000 Megabase per sample) | Microbial communities of plant-free cold desert soils had the lowest levels of phylogenetic and taxonomic diversity | The desert communities had higher relative abundances of genes associated with osmoregulation and dormancy, but lower relative abundances of genes associated with nutrient cycling, catabolism of plant-derived organic compounds, and antibiotic resistance | [12] |
| Park experiment at Rothamsted Research, UK | Grassland | 454-FLX Titanium (4.88 Gigabase) | The most abundant taxa identified from Rothamsted soil were members of Alphaproteobacteria (*Bradyrhizobium*, *Rhodopseudomonas*, and *Nitrobacter* genera), Acidobacteria (*Solibacter* and *Acidobacteria* genera), Gammaproteobacteria (*Pseudomonas* genus), and Betaproteobacteria (*Burkholderia* genus) | Major functional categories included carbohydrate metabolism, cAMP signalling, and the Ton and Tol transport systems | [13] |
| Hess Creek, Alasksa, USA | Permafrost | Illumina paired end sequencing (39.8 Gigabase) | Core specific shifts in some community members including *Proteobacteria, Bacteriodetes*, and *Firmicutes* orders; *Actinobacteria* increased in both cores during thaw | Multiple genes involved in cycling of C and N shifted rapidly during thaw | [14] |
| Eureka, in the Canadian high Arctic | Permafrost | 454-FLX Titanium (1 Gigabase) | The active layer soil and the 2-m permafrost microbial community structures were very similar; Actinobacteria was the dominant phylum | Key genes related to $CH_4$ generation and oxidation and organic matter degradation were highly diverse for both permafrost and active soil layer whereas genes related to nitrogen fixation and ammonia oxidation showed low diversity but high abundance | [15] |
| Solvatn and Knudsenheia, Norway | Peat soil | 454-FLX Titanium (230 Megabase) | The phylogenetic diversity of both the peat soils were similar and the dominant groups belonged to Proteobacteria, Actinobacteria, Planctomycetes, Verrucomicrobia, Acidobacteria, and the Chloroflexi | Deduced the main degradation pathways of plant polymers in the high-Arctic peatlands of Svalbard | [16] |

[a]Selected cultivation-independent studies are based on large-scale sequence dataset analysis, derived from DNA that has not been subjected to targeted PCR amplification and selective sequence analysis.

low C turnover and, consequently, low $CO_2$ emissions and thus higher C sequestration [8]. This notion has been substantiated by metagenomic studies, which have reported a significant contrast in copiotroph versus oligotroph populations in land use management practices that influence SOC accumulation [19–21]. By contrast, it could also be argued that soil dominated with copiotrophs will have more soil carbon because they consume more labile forms over recalcitrant organic C, which makes up the bulk of the soil organic pool [10]. We suggest that because of enormous phylogenetic

and physiological diversity within each bacterial phylum, it is unlikely that an entire phylum demonstrate the same ecological characteristics. As with other microbiomes [22], deep branching clades could be ecologically coherent. Further improvement to culturing techniques and an increase in sequencing efforts are needed for each bacterial linage within soil bacterial phyla to broaden our knowledge of the ecological role of soil microbes.

The fungal:bacterial ratio in soils has been associated with C sequestration potential with greater fungal abundance being related to greater C storage [23]. Evidence relating fungal:bacterial ratio to C sequestration has mainly been gained from the intensively and less intensively managed systems [24]; however, contrasting observations have been reported [25]. Fungal:bacterial dominance can be predicted reasonably well from soil pH and soil C:N ratios [26,27]. A cross biome metagenomic study has recently shown that the ratio of fungal:bacterial rRNA reads varied across soils, with temperate and boreal forests having the highest fungal:bacterial ratios [12]. Higher C storage in fungal-dominated soils can be attributed to higher C use efficiency; longer retention of C in living biomass; and recalcitrant necromass resulting in longer resident time of C [23]. However, these observations are only correlative and it is still debated whether fungal dominant communities promote soil C storage or whether soil with high organic C favours soil fungi. Additionally, it can also be argued that fungi can negatively affect C storage because of their higher efficiency to decompose recalcitrant litter [28–30]. Although fungal:bacterial dominance is a widely used metric that provides soil ecologists with a means to assess the functional implications of soil microbial communities, the use of this ratio to accurately predict the C storage potential of soils is controversial [29,31]. Fungal communities represent a significant portion of the active biomass pools but are poorly represented in most of the metagenome studies [12,28]. High-throughput sequencing combined with stable isotope analyses have shown that in boreal forests fungi are responsible for stabilizing C and retaining it in soils [32]. Further advances in understanding links between microbial community structure and function in soils clearly relies on the development of methods to independently assess the functioning of bacterial and fungal assemblages in intact microbial communities or molecular tools that permit simultaneous characterization of the whole community at resolutions proportional to bacterial and fungal activities.

Autotrophic microorganisms are known to contribute significantly to $CO_2$ assimilation in aquatic systems but have not generally been thought to play a key role in $CO_2$ fixation and sequestration in soils. Recently it has been suggested that microbial autotrophy could account for up to 4% of the total $CO_2$ fixed by terrestrial ecosystems each year [33]. Complete genetic machinery for photosynthesis and carbo-oxidotrophy (ability to use $CO_2$ as a C source) has been elucidated for a few members of β-Proteobacteria [34,35]. Microbial autotrophs are difficult to culture and despite the indications of widespread presence of Ribulose 1,5-bisphosphate carboxylase/oxygenase (RubisCO) genes in various soil environments [33,35], only a few bacterial isolates showing $CO_2$ fixation have been isolated from soils. The diversity and abundance of autotrophic bacterial community in soil correlate with soil use and SOC content suggesting that soil management and cropping regime might be manipulated to enhance soil C sequestration by the growth of autotrophic bacteria [33,36]. This tantalising prospect demands improved culturing methods and genomic data to offer new insights into the importance of microbial autotrophy in terrestrial C cycling.

## Soil–microbial interactions and C sequestration

In recent years, a wealth of information has been uncovered by metagenomics, such as incredible diversity, vast swathes of uncharacterized metabolism, increased complexity of biogeochemical pathways, and even some paradigm shifts in our understanding of soil microbial ecology. Here, we present recent metagenomic-derived information on microbial interaction and feedbacks with soil and other environmental variables and their influence on C storage.

### *Microbial interactions and soil physicochemical properties*

Soil structure is an important regulator of microbially-mediated C storage or decomposition [37]. Various groups of microbes facilitate formation and stabilization of microaggregates [4,38–40]. Soil organic matter (SOM) is preferentially stabilized in these microaggregate fractions and aggregate stability increases linearly with C input [38]. Considering that the degradation of SOM is mainly a microbiological process, it can be suggested that different substrates and surface properties will select for specifically adapted microbial communities [1,37,38]. The only metagenomic study addressing the effect of aggregate stratification shows the association of specific bacterial assemblages with particular soil chemistries within the soil microenvironment [41]. Metagenomic analysis of forest soils has shown that the active and total microbial communities in different horizons are different and highly stratified during decomposition [11,28]. Carbon sequestration in a given system may comprise a hierarchy of biological processes at the spatial dimension of soil physical structure. There is thus an urgent need for the application of 'omics' techniques to understand soil C accumulation driven by biological processes within the micro-niche of soil space. However, these studies will require access to, and efficient extraction of, microbial cells and genomes from these very stable local micro-environments.

### *Land management practices and soil C storage*

A range of manipulation approaches for land management (Box 1) that influences soil decomposition processes has been proposed to enhance C sequestration [4,8]. Metagenomic-based insights have provided strong evidence that microbial community composition responds significantly to land use and management practices and are correlated with soil parameters including SOM [19–21]. In some of these studies, selected microbial communities may serve as a potential management indicator to discriminate between sustainable versus nonsustainable management practices [20,21]. Many developed countries now have established soil survey programmes that mine the data for linkage between soil management practices and microbial communities. Systematic exploration of soil processes

**Box 1. Harnessing plant–microbe interaction for C sequestration**

Terrestrial ecosystem conservation and restoration by manipulating plant assemblages provide a multitude of options for creating and optimizing inventories of stable C. Efforts have also been made to make designer plants (notably energy crops needed to produce bioethanol) in ways that stimulate them to produce larger fractions of more-recalcitrant organic matter that would lead to increased C sequestration [8,79]. Plants live in close association with microbial communities whose individual members can contribute to plant growth and development, plant productivity, and phytoremediation [56,80–82]. Various independent metagenomic studies have shown that there is a typical 'core' microbiome for the plant host, which is recruited from the common soil bacteria and selected by the ability of community members to grow in root exudates and provide benefits to the plant through direct or indirect mechanisms [80,81]. The analysis of genes and metabolically important gene products from plant-associated bacteria has resulted in the identification of many possible mechanisms that could help these microbes thrive within a plant environment, and potentially affect the growth and development of their plant host [58]. This has laid the basic foundation to genetically engineer desired bacteria for increased colonization ability; beneficial traits; biocontrol ability; manipulation of native microbial community; and/or altered production of extracellular enzymes involved in C degradation and storage. Manipulation of the C storage regulator (Csr) system could result in metabolite remodelling for the production, storage, or utilization of specific C substrates in soil. A recent study has also suggested that when faced with environmental change, plants may not be limited to adapt or migrate strategies; instead, they also may benefit from association with interacting species, especially diverse soil microbial communities, that respond rapidly to environmental change [82]. This further substantiates the importance of priming plants with beneficial soil microbes for predictive interventions that will increase plant health and productivity, C sequestration, and disease resistance through the rational utilization of the probiotic capacity of soils and the local environment. Interestingly, the shift in patterns of rhizo-deposition and changes in C utilization and fixation potential of the microbial community in response to disease is being postulated to have long-term effects on C storage and sequestration [83]. Further studies are required for understanding the relative importance of perturbations caused by phytopathogens on the microbial biodiversity and activity and the effect of these shifts in local and global-scale ecological phenomenon.

and metabolic properties of soil microbial communities will help to identify the ecological consequences of various land use practices and the development of management practices that increase net productivity and C sequestration.

N availability is likely to impact C storage through a variety of feedbacks with different timescales. A few studies have shown that N deposition significantly reduce the richness and diversity of genes involved in the production of extracellular enzymes involved in the degradation of recalcitrant C, which has a positive effect on C storage [42–44]. Nitrogen amendment causes a consistent shift in the predominant microbial life history strategies, favouring a more active, copiotrophic microbial community [10,43,44]. Studies have further suggested that N deposition-related decreases in soil C decomposition support enzyme inhibition and N mining hypotheses that explain decreased microbial activity in response to N amendments [10,43]. However, further studies are needed to confirm applicability of the enzyme inhibition hypothesis and to determine if the presumed oligotroph–copiotroph switch is a consistent response to N additions.

### *Climate change and soil C storage*

Continued increases in atmospheric $CO_2$ may have a variety of different consequences for soil C inputs via controls on photosynthetic rates and C losses through respiration and decomposition. Enhanced heterotrophic respiration due to an increase in rhizodeposition under elevated (e)$CO_2$ may also accelerate decomposition of SOM through increased microbial activity [45]. However, manipulated experiments did not show consistent effects of elevated $eCO_2$ on bacterial biomass, richness, and community composition across six contrasting terrestrial ecosystems, although significant responses were observed in individual ecosystems [46]. In grasslands, comprehensive metagenomics-based surveys of microbial richness and composition have revealed that $eCO_2$ significantly alters microbial community diversity, composition, structure, and their functional potential [47–49]. Increases in the abundance of genes involved in degradation of labile forms of C is in line with the previous observation that $eCO_2$ increase the inputs of organic C in soil. Also, the abundance of genes involved in recalcitrant C degradation do not significantly change at $eCO_2$, indicating that soil C storage may remain largely unaffected in the long term, which is consistent with the fact that $eCO_2$ has little effect on soil C storage [47].

Warming typically accelerates soil microbial respiration rates due to increased soil enzyme activities, which drive decomposition [50]. Primarily as a result of this response, a 2°C global average temperature increase is predicted to stimulate soil C loss by 10 Gt/year [8]. However, this stimulation of soil C loss could be entirely mitigated by a decline in the temperature sensitivity of microbial activity [51]. Metagenomics-based studies have provided a mechanistic understanding of microorganism responses and its impact on ecosystem C storage including (i) shifting microbial community composition, most likely led to the reduced temperature sensitivity of heterotrophic soil respiration [52,53], (ii) differentially stimulating genes for degrading labile but not recalcitrant C so as to maintain long-term soil C stability [14,52,53], and (iii) enhancing nutrient cycling processes to promote plant nutrient availability and hence plant growth [52,53]. We suggest that the effect of warming on microbial communities and their related functions will be variable between biomes and are likely to have strong effects on decomposition processes in alpine and arctic regions.

## Evidence of microbial potential to influence C storage from whole genome sequencing

Although both bacteria and fungi are important in the context of soil C sequestration, genomic and metagenomic studies aimed at interrogating the role of microbial communities in soil C dynamics has mainly been undertaken for bacteria due to a rapidly increasing number of bacterial genome sequences becoming available. Because fungi play central roles in terrestrial ecosystems, both as decomposers of organic matter and as root-associated mediators of below-ground C transport and respiration, there exists an urgent need for systematic sampling and genome sequencing of the fungi. A recent comparative analysis of 31 fungal genomes does provide insights into the evolution of

enzymes capable of degrading lignin [54]. As data become available from a current initiative of genome sequencing for fungi (http://genome.jgi.doe.gov/programs/fungi/1000fungalgenomes.jsf), our understanding of the role of fungi in global C cycling will improve.

Microbial diversity of enzyme genotype may be associated with lifestyle strategy and can influence C storage in terrestrial ecosystems. The genetic potential to produce extracellular enzymes involved in the degradation of relatively labile forms of C, including most abundant plant structural C polymers such as cellulose and hemicellulose, seems to be less conserved among different phylum of the soil bacteria (Figure 2) [55]. However, the number of genes per genome involved in the degradation of moderately labile C seems to be higher in typical soil-inhabiting bacteria belonging to Actinobacteria and Acidobacteria as compared to most of the Proteobacterial members (Figure 2) [56]. Members of Actinobacteria and Acidobacteria seem to possess well-equipped genetic machinery for the production of enzymes (including chitinase) involved in degradation of cell wall materials, which possibly can impact these important sources of C and N for long-term stabilization (Figure 2). This supports the argument that these bacteria mainly survive on SOC. Only a few bacteria encode genes for the production of enzymes involved in degradation of recalcitrant C forms, especially lignin (Figure 2). This might be the reason for the stimulation of only a few selected bacterial groups by the addition of lignin to soil samples [57]. Linking phylogenetic and trait-based patterns of biogeography of soil microbial communities based on enzyme production is difficult considering the role of 'cheaters' (microbes that take up the byproducts of polymer breakdown but do not contribute to the pools of extracellular enzymes that catalyse the breakdown process), horizontal gene transfer, and different ecological function(s) of a single enzyme.

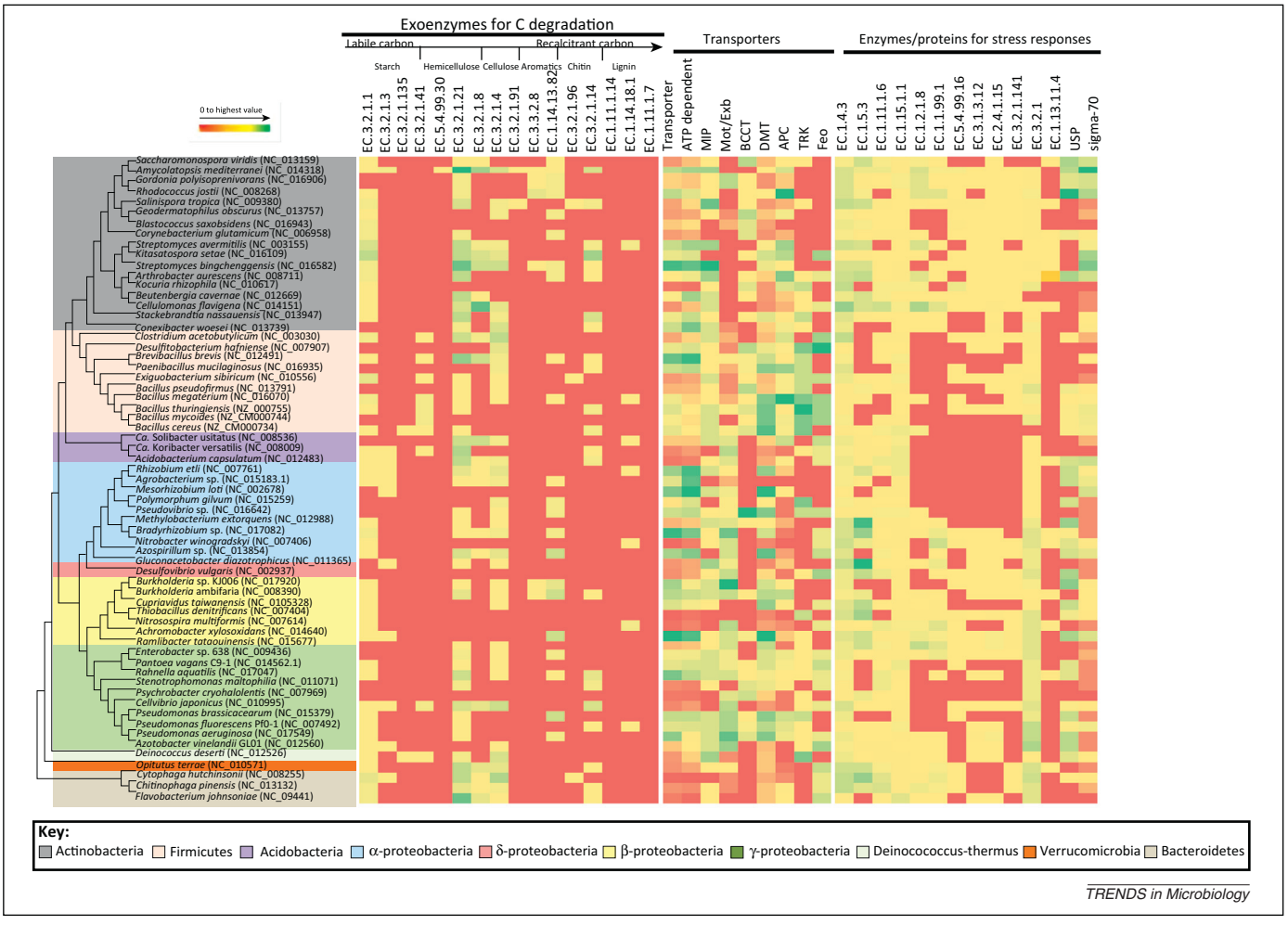


**Figure 2**. Distribution of genes involved in the production of exoenzymes for C degradation, transporters, and enzymes/proteins for stress tolerance from selected bacteria associated with the terrestrial ecosystem. On the left, different coloured boxes represent different phyla or groups. The phylogenetic tree on the left was constructed using the neighbour-joining algorithm to evaluate the distance between 16S rRNA gene sequences of selected bacteria. Numbers in brackets represent the accession numbers of complete genomes. Enzymes: EC 3.2.1.1 – α-amylase; EC 3.2.1.3 – glucan 1,4-α-glucosidase; EC 3.2.1.135 – neopullulanase; EC 3.2.1.41 – pullulanase; EC 5.4.99.30 – UDP-arabinopyranose mutase; EC 3.2.1.8 – endo-1,4-beta-xylanase; EC 3.2.1.4 – cellulose; EC 3.2.1.91 – cellulose 1,4-beta-cellobiosidase; EC 3.3.2.8 – limonene-1,2-epoxide hydrolase; EC 1.14.13.82 – vanillate monooxygenase; EC 3.2.1.96 – mannosyl-glycoprotein endo-β-N-acetylglucosaminidase; EC 3.2.1.1.14 – chitinases; EC 1.11.1.14 – lignin peroxidase; EC 1.14.18.1 – monophenol monooxygenase; EC 1.11.1.7 – peroxidase. Transporters: MIP – major intrinsic protein; BCCT – betaine/carnitine/choline transporters; DMT – drug/metabolite transporter; APC – amino acid/polyamine/organocation superfamily transporter; Trk – potassium transport proteins; Feo – iron(II) transport system; Mot-Exb – $H^+$- or $Na^+$-translocating bacterial flagellar motor/outer membrane transport energizer superfamily. Enzymes/proteins for stress response: EC 1.4.3 and 1.5.3 – oxidases that use molecular oxygen to metabolize amino groups; EC 1.11.1.6 – catalase/peroxidase; EC 1.15.1.1 – superoxide dismutase; EC 1.2.1.8 – betaine-aldehyde dehydrogenase; EC 1.1.99.1 – choline dehydrogenase; EC 5.4.99.16 – maltose α-D-glucosyltransferase; EC 3.1.3.12 – trehalose-phosphatase; EC 2.4.1.15 – α,α-trehalose-phosphate synthase; EC 3.2.1.141 – 4-alpha-D-{(1->4)-alpha-D-glucano} trehalose trehalohydrolase; EC 3.2.1 – glycosidases; EC 1.13.11.4 – gentisate 1,2-dioxygenase; USP – universal stress protein.

Physiological responses to stress have costs at the organismal level that can result in altered ecosystem level C, energy, and nutrient flow [39,58,59]. Genomic information provides evidence that most soil bacteria, irrespective of their phylogenetic groupings, possess different genes involved in relieving stresses caused by temperature, osmotic potential, oxygen concentration, and metabolism (Figure 2) [34,39,58,59]. This can explain the resilience of soil microbial communities to moderate fluctuations in abiotic variables [60]. Based on the information gathered from full genome sequences, we infer that bacteria belonging to Acidobacteria and Actinobacteria possess an impressive array of genes allowing breakdown, utilization, and biosynthesis of diverse structural and storage polysaccharides and resilience to stressful soil conditions making them truly ubiquitous in terrestrial ecosystems (Figure 2). This finding supports the metagenomic evidence of higher SOC in Acidobacteria- and Actinobacteria-dominated communities and suggest that these groups promote soil C storage not only due to life style (slow growth and lower metabolic activities), but also by producing polysaccharides for soil structural stability.

Genomic analysis shows that fast growing bacteria (especially those belonging to the phyla Proteobacteria and Firmicutes) have a higher number of total transporters including ATP-binding cassettes, phosphotransferase systems, and drug/metabolite transporters that could import or export a broad range of compounds (Figure 2) [61]. The presence of low affinity transporters allows fast growth in periods of feast, while enduring starvation in periods of famine. Bacteria belonging to the phyla Proteobacteria and Firmicutes also possess higher numbers of flagellar motor/ExbBD outer membrane transport energizer (Mot-Exb) (Figure 2) transporters involved in motility that, together with a higher number of substrate transporters, can explain the dominance of these bacterial groups in the nutrient rich soil environments such as the rhizosphere. However, slow growing bacteria in the Acidobacteria and Actinobacteria taxa possess a low number of total transporters that have high affinity to a specific substrate allowing them to thrive in low nutrient concentrations, but become saturated at high nutrient concentration leading to their selective exclusion by fast growers in rich environments (Figure 2). We propose that insights into substrate specificity and diversity of transporters in genome sequences could provide useful and relevant clues for the C substrate utilization of a bacterium, bacterial group, or even a microbial community. This information can also provide direct evidence in support of bacterial lifestyles such as oligotroph or copiotroph. However, whole genome sequences are available only for limited soil bacteria and in the future many more genomes need to be included, either from whole genome sequencing or from constructing genomes from metagenomic sequences, in order to provide conclusive and consistent evidence.

Overall genomic features of individual bacteria provide an indication of their possible role in C turnover based on the battery of genes responsible for producing extracellular enzymes; their survival strategies in different microenvironments; or utilization of specific substrates. However, the presence of a gene does not mean that the feature will be reflected in actual environmental conditions. To add another layer to the complexity, soil bacterial genomes include several novel features that in most cases are not known or described. Further investigation of protein structure and function is needed to link them to physiology and environmentally relevant functions. Information provided by the genome sequence of individual bacteria and subsequent searching for the abundance of ecologically important genes by metagenomic analysis can become a powerful approach for revealing ecological and evolutionary forces that influence microbial traits in a changing environment.

## Modelling microbial communities

Because microbes affect biogeochemical feedbacks to global change, there have been many calls to integrate microbial communities into broad scale ecosystem and climate models [62,63]. Such integration would require direct evidence of microbial control of biogeochemical processes and a quantitative relationship between changes in microbial composition and the rate of the biogeochemical cycle [17,62–65]. For terrestrial ecosystems, modelling the spatial and temporal characteristics of microbial community structure is extremely difficult, primarily because of the perceived heterogeneity that results in the patchiness of predictive capability. However, 'parts lists' provided by metagenomics studies have started to elucidate the level of overlap in the taxonomic composition between different terrestrial systems across different scales and begun to show that the perceived heterogeneity might not be as patchy [64]. The integration of microbial-mediated functions in terrestrial ecological models has already begun at a small scale [65], but has not yet influenced the structure of coupled climate change models at the global scale. In this section, we discuss various types of microbial-based modelling approaches that have provided deeper insights into the coupling between microbial community functional traits, the environmental context, and the ecosystem processes that occur.

### *Individual-based models*

Individual-based models (IBMs) attempt to capture the properties and dynamics of a population by describing all the actions of its constitutive individuals and their interaction with the environment and with each other [66–68]. Recently, few studies have attempted to use IBMs to predict the interaction between diversity, population dynamics, and community function in soil and how these are linked to events at the individual level, including cell adaptation and evolution [66–69]. INDividual DIScrete SIMulations (INDISIM) uses a number of state variables and parameters related to SOM and microbial activity to model the dynamics and evolution of C and N associated with organic matter in soils [67]. The Model SEED platform developed using metabolic interactions to 6903 species pairs derived from 118 bacteria provides a conceptual framework for predicting possible interactions depending on the sum of growth rates when grown together compared to separately on the same media [68]. A dynamic Multi-Species Metabolic Modelling framework that integrates genome scale metabolic models within the dynamic Flux Balance Analysis (dFBA) framework has been developed to

predict metabolic flux distributions and biomass concentration of individual species in the extracellular environment [69].

### Heterogeneous network models

Although a network approach is powerful in describing ecological interactions among species, defining the network structure in microbial communities is a huge challenge. Recently, such correlative systems analyses are scaling up to link biomolecular networks to ecological networks. Both phylogenetic (dataset from 16S rRNA gene pyrosequencing) and functional (dataset from GeoChip hybridizations) molecular ecological networks (MENs) of soil microbial communities based on random matrix theory (RMT) under different climate change scenarios ($eCO_2$ or warming) possessed the general characteristic of complex systems such as scale free, small world, modular, and hierarchical [70,71]. The structure of identified MENs under different environmental conditions differed substantially in terms of overall network topology, network composition, node overlap, module preservation, module-based higher order organization, topological roles of individual nodes, and network hubs, suggesting that altered climate variables dramatically change network interactions among different functional and phylogenetic groups or populations.

Although we expect that IBM and network-based models can provide us with the mechanistic descriptions of soil microorganisms interactions at the fine scale, synthetic network modelling approaches are needed for scaling up to the ecosystem level in order to explain more important soil functions.

### Trait-based microbial models

Trait-based microbial models parameterize specific traits that determine the relative fitness of an organism in a given environment, and represent the complexity of biological systems across ecosystem gradients [72]. Previous applications of the microbial trait-based approach have been successful in predicting rates of litter decomposition [73] and biological nitrification [74] in terrestrial ecosystems. The decomposition model of enzymatic traits (DEMENT) accounted for 69% of the variation in decomposition rates of 15 Hawaiian litter types and up to 26% of the variation in enzyme activities, providing evidence that microbial interactions in the decomposing litter vary with community investment in extracellular enzyme production and the magnitude of trade-offs among traits that represent alternative microbial strategies for resource acquisition [73]. Limited reports using trait-based models show their ability to describe the ecological community or the ecosystem as a whole entity thus making them also suitable for studying feedback between life and its environment on evolutionary time scales [72–74]. An important avenue for future research will be to focus on whether the integration of these microbial diversity modules into ecosystem models can improve site, regional, and global predictions of carbon and nutrient cycling. However, using a metagenomic 'parts lists' to infer global patterns on microbial ecology is a significant challenge. To deduce important ecological indicators such as environmental adaptation, molecular trait dispersal and diversity variation from a gene pool of an ecosystem, omics-derived datasets should be integrated with geochemical, meteorological, and ecological measurements. This information should further be used to investigate the relationship between the environment and the metagenome-derived gene or pathway repertoire of an ecosystem and the interplay between functional composition and ecosystem processes such as decomposition.

### Bioclimatic models

Predictive bioclimatic models define the habitable geographical or temporal range of a species as a function of environmental parameters [17,65]. An artificial neural network approach has been employed to develop a bioclimatic model that can predict the climate-dependent abundance of microbial taxa in space and time [17]. Although the model proposed by Larsen *et al.* [17] focused on predicting taxon distributions, a similar approach using shotgun metagenomics data could be leveraged to predict the abundance of functional genes that are critical to global biogeochemical cycles. The use of this modelling approach to terrestrial ecosystems has many caveats mainly because of the heterogeneity of soils. However, the relationship(s) between microbial taxa shape the structure of microbial communities, and thus, it can be expected that nonrandom co-occurrence patterns and significant inter-taxa relationship may occur in soils. In fact a recent study using the metagenomics data from a broad range of environments has revealed co-occurrence patterns including general nonrandom association, common life history strategies at broad taxonomic levels, and unexpected relationships between community members [64]. Bioclimatic model approaches can be used to document new microbial interactions, identify shared niche spaces, reveal the natural histories of microbial taxa, and possibly predict how global climate change may impact microbial communities.

### Incorporating microbial ecology to biogeochemical models

Many models have been developed to address questions related to feedbacks to global warming, C stocks across regional gradients, and N dynamics under different climate change scenarios or land-use management (such as the CENTURY, DAISY, DNDC, Roth-C, CANDY, DAYCENT, and others). Most of these models are regarded as process-oriented models and assume that microbial communities do not ultimately influence biogeochemical cycling either in time or space [63,65]. Combining these physical models with microbial diversity models, in which a number of microbial phenotypes are initialized and their interaction with the modelled environment determines their fitness, should enable accurate prediction for changes in ecosystem processes. Recent modelling efforts that have incorporated microbial dynamics in ecosystem models have simulated terrestrial C dynamics with global warming [51], altered moisture regimes [75], and N deposition [76]. Several models have also been developed to address microbial controls on decomposition [65]. Incorporation of microbial mechanisms have altered (but not necessarily improved) the predictions of conventional models

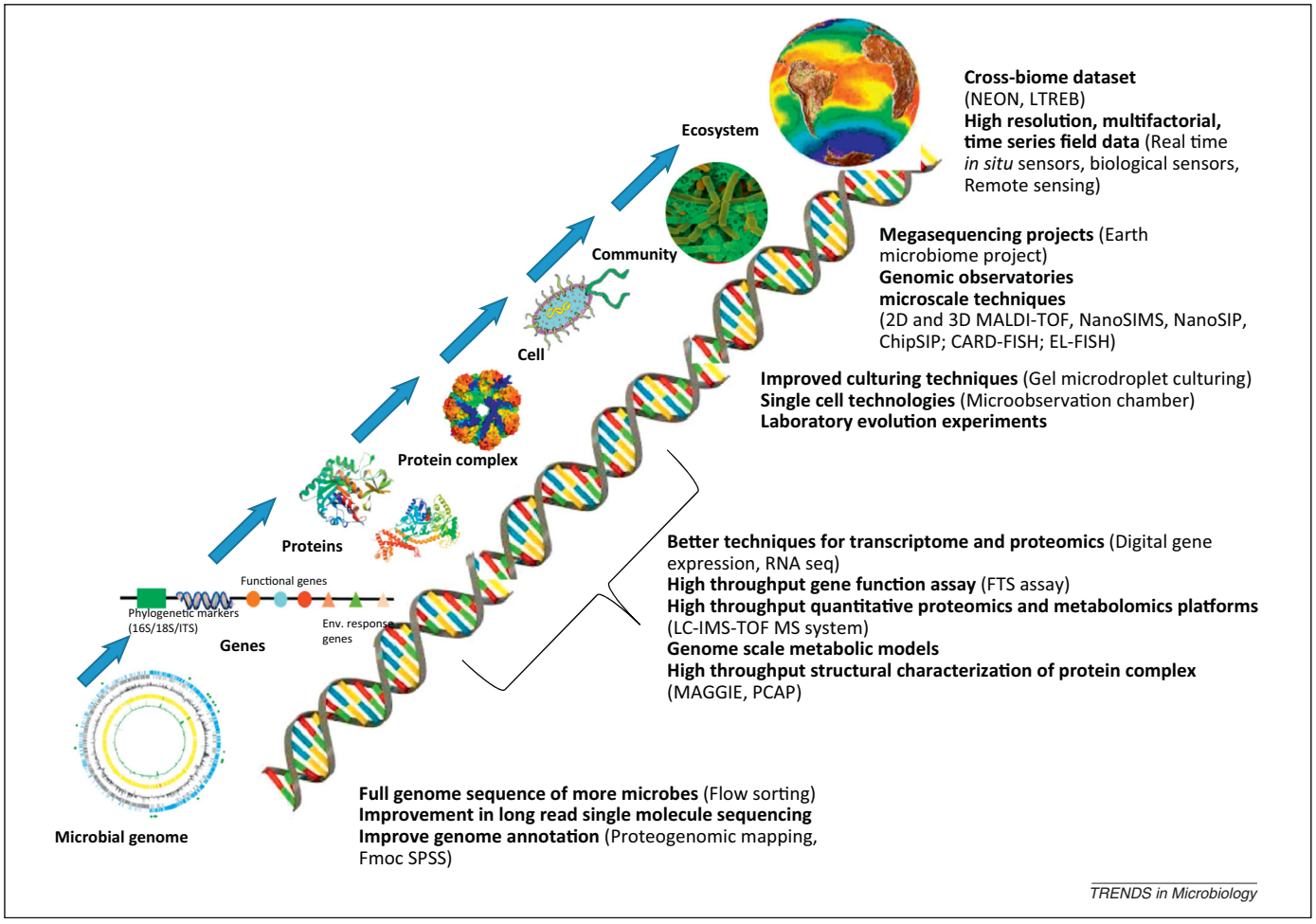


**Figure 3**. A road map of linking a microbial genome to ecosystem function. This scheme shows hypothetical linkages between the information encoded in a microbial genome and the community interactions that can drive ecosystem functions. The figure on the left shows the technical requirements needed at each level to provide linkage with the next level, and the text in brackets describes the newly developed tools or scientific initiatives to achieve the objectives. Each step will also require robust computational techniques for linkages to the higher level and ultimately to develop predictive ecosystem models (not shown). Abbreviations: internal transcribed spacer sequence (ITS); 9-fluorenylmethyloxycarbonyl (Fmoc)-solid-phase peptide synthesis (SPPS); Molecular Assemblies Genes, and Genomics Integrated Efficiently (MAGGIE) platform; Protein Complex Analysis Project (PCAP); fast capillary (LC)-ion mobility spectrometer (IMS)-time-of-flight mass spectrometer (TOF MS); fluorescence-based thermal shift (FTS) assay; matrix-assisted laser desorption/ionization-time of flight (MALDI-TOF); nano-scale secondary ion mass spectrometry (NanoSIMS); stable isotope probing (SIP); chip-stable isotope probing (ChipSIP) catalysed reporter deposition (CARD) and elemental level (EL) fluorescence *in situ* hybridization (FISH); National Ecological Observatory Network (NEON); Long Term Research in Environmental Biology (LTREB).

simulating broad ecological process under altered climate conditions [63,65]. In a recent breakthrough, Wieder *et al.* [77] created a new soil biogeochemistry module for use in the Community Land Model (CLM) that explicitly represents microbial mechanisms of soil C cycling on a global scale. CLM microbial model projects a much wider range of soil C responses wherein the ability of global soils to sequester C will depend on microbial growth efficiency and their adaptation to climate change. However, validation and parameterization of the performance of these models is challenging. To establish the advantages of microbial-based models in comparison to conventional models, benchmarking with multiple datasets and output parameters will be needed. In the future, experiments providing insights into microbial control over biogeochemical cycles and quantitative linkages between microbial diversity and/or community shifts and ecosystem functioning are essential requirements for successful incorporation of microbial functions in ecosystem modelling (Figure 3). The next challenge will be to develop physiological parameterizations that directly interface between molecular, genomic, and physiological datasets scaling the ecological models from the gene to ecosystem level.

## Concluding remarks and future directions

Microbial communities play a vital and undisputable role in soil C storage but microbial control over processes that facilitate soil C storage remains a topic of debate. Numerous questions remain to be addressed for understanding microbial control over C cycling in terrestrial ecosystems (Box 2). A comprehensive, mechanistic understanding of ecosystem responses to global change requires that responses at the organism level be directly related to responses of the genome, and these in turn be linked to higher levels of organization (Figure 3). In the future, we anticipate that advances in single-cell genomics, bioinformatics, and metabolic network modelling will enable the application of such methods to provide a genomic–mechanistic basis for biological feedbacks to the climate system brought about through the terrestrial C cycle. Linking

**Box 2. Outstanding questions**

- How to comprehensively determine the makeup and genetic potential of the terrestrial microbial community?
- How can we manipulate the soil microbial community to control C mobilization and storage in terrestrial ecosystems?
- How to incorporate microbial community patterns and process rates into a rigorous ecological framework when most ecosystem models often 'black box' microbiology?
- How to integrate knowledge from many different disciplines, and across different spatial scales, from genomes to biomes, in order to formulate sound energy and land management policies?

manipulative experimentation (i.e., mesocosm approaches) with computational and functional genomics will provide a way forward for linking genomes to biomes. Integrating the information gained from individual cells or simple microbial communities with comprehensive profiling of terrestrial microbial communities will provide evidence for microbial regulation of biogeochemical cycles [78] and feedback in response to climate change (Figure 3). A systems biology approach, which couples modelling and simulation with experiment and theory, will relate genome-based microbial ecophysiology to the assessment of global C sequestration strategies and climate impacts. As the technology develops, the combination of long-term and cross-biome microbial data will be used to inform the microbial role in soil C storage. The emerging field of global change microbial ecology will generate systematic, open access datasets that can be used for probing the morphological and molecular makeup, diversity, evolution, and ecology of soil microbial communities as well as their impacts on C sequestration. We envisage that unravelling of complex interspecies ecological interactions and metabolic networks by the quantification of molecular functions will provide both the parts and wiring diagrams for modelling microbial communities. Incorporation of microbial mechanistic behaviours (cellular, community, and ecosystem) in ecological models will result in the development of robust predictive models that can be used to interpolate or extrapolate observed interactions among microbes and their environment thus reducing the uncertainties in assessments of global change on terrestrial C stocks. Comprehensive understanding of terrestrial microbial communities and specific processes that determine the rate and fate of C dynamics will increase the likelihood of successful manipulation of the terrestrial ecosystem for increasing stable C inventories.

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