Soil Biology & Biochemistry xxx (2017) 1–17

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Microbial energy and matter transformation in agricultural soils

Damien Finn [a, *], Peter M. Kopittke [a], Paul G. Dennis [a], Ram C. Dalal [a, b]

[a] School of Agriculture and Food Sciences, The University of Queensland, St Lucia 4072, Australia
[b] Department of Science, Information Technology and Innovation, Queensland Government, 4001, Australia

ARTICLE INFO

Article history:
Received 2 November 2016
Received in revised form
21 March 2017
Accepted 15 April 2017
Available online xxx

Keywords:
Soil organic carbon
Environmental microbiology
Microbial ecology
Microbial physiology

ABSTRACT

Low bioavailability of organic carbon (C) and energy are key constraints to microbial biomass and activity. Microbial biomass, biodiversity and activity are all involved in regulating soil ecosystem services such as plant productivity, nutrient cycling and greenhouse gas emissions. A number of agricultural practices, of which tillage and fertiliser application are two examples, can increase the availability of soil organic C (SOC). Such practices often lead to reductions in soil aggregation and increases in SOC loss and greenhouse gas emissions. This review focuses on how the bioavailability of SOC and energy influence the ecology and functioning of microorganisms in agricultural soils. Firstly we consider how management practices affect the bioavailability of SOC and energy at the ecosystem level. Secondly we consider the interaction between SOC bioavailability and ecological principles that shape microbial community composition and function in agricultural systems. Lastly, we discuss and compare several examples of physiological differences that underlie how microbial species respond to C availability and management practices. We present evidence whereby management practices that increase the bioavailability of SOC alter community structure and function to favour microbial species likely to be associated with increased rates of SOC loss compared to natural ecosystems. We argue that efforts to restore stabilised, sequestered SOC stocks and improve ecosystem services in agricultural systems should be directed toward the manipulation of the microbial community composition and function to favour species associated with reduced rates of SOC loss. We conclude with several suggestions regarding where improvements in multi-disciplinary approaches concerning soil microbiology can be made to improve the sustainability of agricultural systems.

1. Introduction

Soils provide essential ecosystem functions and services such as food production, regulation of atmospheric concentrations of greenhouse gases, prevention of soil erosion, regulation of the quality and quantity of water availability, and the maintenance of animal, plant and microbial biodiversity (Ciais et al., 2013; Diaz et al., 2006; Pimentel, 2000; Tilman et al., 1997). Soil organic carbon (SOC) dynamics play a fundamental role in regulating ecosystem functions and services (Lorenz and Lal, 2014). The benefits of SOC are many and include: a source of associated essential elements for biological activity, such as nitrogen (N), phosphorus (P) and sulphur (S), collectively termed soil organic matter (SOM); improved ion exchange capacity; soil water retention; improved soil aggregation and reduced erosion; and as a sink for potential greenhouse gases (Lal, 2014). It is well documented that the conversion of native vegetation to soils used for agricultural purposes results in losses of 25–50% of SOC (Lal, 2008). Continual reductions in SOM pose a significant threat to future food security, atmospheric concentrations of greenhouse gases and biodiversity maintenance (FAO, 2015). Over the past two decades, a number of excellent reviews describing the physical and chemical factors involved in the stabilisation and turnover of SOM have been written (Baldock and Skjemstad, 2000; Cotrufo et al., 2013; Dungait et al., 2012; Schmidt et al., 2011; Sollins et al., 1996; von Lützow et al., 2007). However, a notable component lacking in these reviews has been that of microbiology, which is interesting when one considers that microbiologists were among the first to describe Earth's biogeochemical cycles (Beijerinck, 1888, 1895; Winogradsky, 1887, 1890). The purpose of this review is to better integrate concepts such as microbial ecology and physiology into the soil physico-chemistry governing SOM turnover. We aim to dispel the supposition of the soil microbial 'black box' by discussing

* Corresponding author.
E-mail address: damien.finn@uqconnect.edu.au (D. Finn).

http://dx.doi.org/10.1016/j.soilbio.2017.04.010
0038-0717/

several physiological properties that contribute to a cellular mechanistic basis for decreases in SOC in agricultural systems. Consequently, we address the key soil physico-chemical factors controlling SOC turnover in relatively less depth than the impact of land management practices on soil microbial ecology and physiology. We conclude by arguing that the aim of restoring stabilised, sequestered SOC stocks would be improved by considering the responses of microbial ecology and physiology to the effects of specific management practices, ideally leading to methods for the targeted manipulation of the system to favour specific phylogenetic and functional taxa.

2. Bioavailability and processing of potential energy in agricultural systems

Agricultural ecosystems across the globe are incredibly diverse in terms of edaphic and climatic properties, land use (e.g. cropping, pasture), and land management (e.g. tillage, type and quantity of fertiliser application, crop rotation, cropping intensity, mono- versus polyculture) (Matson et al., 1997; Reeves, 1997; Tilman et al., 2002; West and Post, 2002). Furthermore, there is substantial spatial variability, not only across landscapes but also with soil depth. Despite this variability, there are several characteristics which soils tend to develop after transitioning from native vegetation to agriculture, such as: a) loss of aggregate stability and increased erosion; b) acidification; c) over-supply or insufficient replacement of N and P relative to crop removal; d) changes in the molecular composition of plant biomass input; e) reductions in both composition and abundance of functional biodiversity of local plant, animal and micro-organisms; and f) SOM loss (Don et al., 2011; FAO, 2015; Flynn et al., 2009; Matson et al., 1997; Pimentel et al., 1992; Sala et al., 2000; Smith et al., 2016; Vitousek et al., 2009). Each of these has the potential to change the quantity and/or composition of SOM which is available for microbial metabolism. The predominant factor limiting the activity of heterotrophic microorganisms is the availability of organic C (Blagodatsky and Richter, 1998). For this reason, changes in organic C availability have profound consequences for soil biological processes (Schmidt et al., 2011). Fig. 1 provides a conceptual framework illustrating the interactions between the environment, SOM, edaphic properties and microorganisms which will be continuously referred to in this section.

2.1. Soil physical properties affecting SOM bioavailability

A number of soil physical properties are important in regulating SOM bioavailability for microbial metabolism, such as the rate of aggregate formation, the distribution, size and network connectivity of pore space, soil mineralogy and surface area to volume ratio of soil minerals. Aggregate formation follows a complex cycle whereby macroaggregates (>250 μm in diameter) are formed by free microaggregates (<250 μm in diameter) binding together via a combination of electrostatic interactions between clay minerals, polyvalent cations, particulate organic matter (>53 μm particle diameter, POM) and fungal mycorrhizal and root structures (Edwards and Bremner, 1967; Gupta and Germida, 2015; Tisdall and Oades, 1982). Once this occurs, new microaggregates are formed within macroaggregates as microorganisms convert encapsulated POM into 'microbial-derived binding agents' such as extracellular polymeric substances (EPS) necessary for biofilm formation and particle aggregation (Angers et al., 1997; Flemming and Wingender, 2010; Sandhya and Ali, 2015; Six et al., 2000a; Tisdall and Oades, 1982). Finally, the macroaggregate structure is destabilised once the original organic binding agents are sufficiently degraded, freeing microaggregates which can repeat the cycle (Six et al., 2000a). The importance of this process for regulating SOM bioavailability is made evident by physical disturbance of macroaggregates. Land management practices such as conventional tillage result in significant decreases in SOM despite similar inputs of plant biomass to non-tilled soil (Hutchinson et al., 2007; McLauchlan, 2006; Six et al., 2000a, 2000b). Aggregate integrity and SOC stocks can be recovered, at least partially, by conversion of cropping soils to pasture (Conant et al., 2001; Don et al., 2011; Gebhart et al., 1994) or by adopting no-till management practices (Reeves, 1997; West and Post, 2002). Furthermore, aggregate formation through particle flocculation can be disrupted by

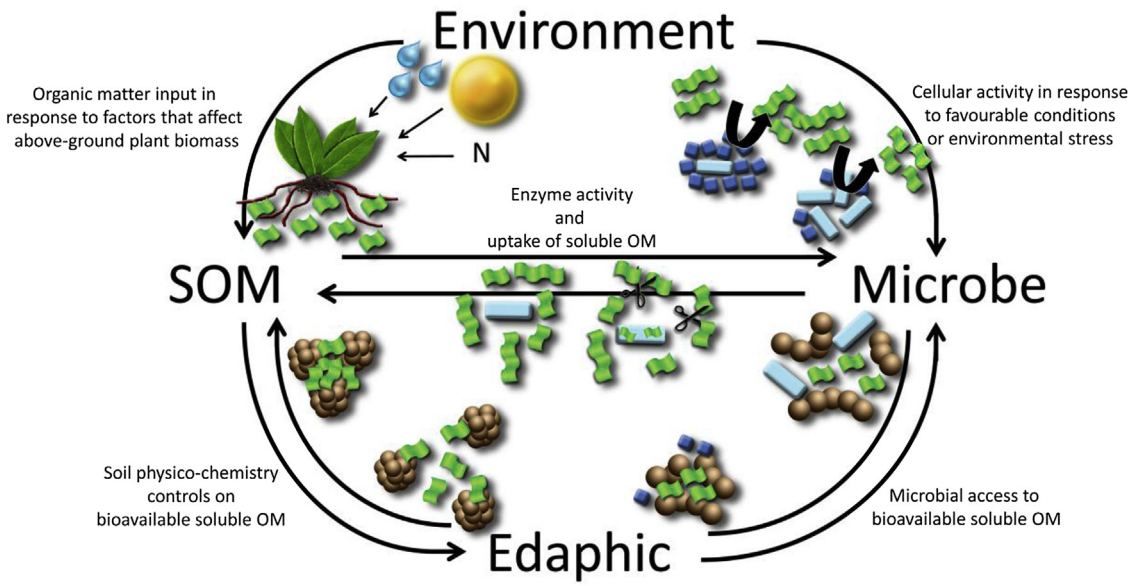

Fig. 1. A conceptual diagram of important interactions between: the environment and SOM, primarily as factors affecting plant biomass input; microorganisms and the environment, which affect cell viability and activity; SOM and microorganisms, such as relative molecular complexity of SOM; SOM and edaphic properties, including aggregate integrity controls on SOM bioavailability; and finally edaphic properties and microorganisms, such as pore size and connectivity restricting access to SOM or cell movement.

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

management practices which affect soil pH, such as liming and use of ammonium nitrate fertilisers (Haynes, 1999). Fig. 1 depicts an interaction between SOM bioavailability and edaphic properties, whereby the protection of SOM (in green) is partially dependent on aggregate formation or disruption (in brown).

Another important physical aspect is the distribution, size and network connectivity of pore spaces within and between aggregates, which can vary from micropores (<0.1 μm in diameter) to macropores (≥20 μm to centimetres in diameter) (Adu and Oades, 1978; Baldock and Skjemstad, 2000; Foster, 1988). This is particularly dependent on soil clay content (physical particle diameter of <2 μm), whereby increasing soil clay content increases micropore abundance and in turn can reduce the rate of OM decomposition (Chenu and Plante, 2006; Chotte et al., 1998; Killham et al., 1993). Where SOM is protected within pores inaccessible to microbial cells, C bioavailability is dependent upon abiotic factors which regulate diffusion of extracellular enzymes and soluble substrate, such as temperature, water-filled pore space (WFPS) and low water potential arising from low pore connectivity (Kemmitt et al., 2008). For example, where low pore connectivity results in low water potential, biodiversity of bacterial communities increase likely due to reduced diffusion of SOM, extracellular enzymes and increased spatial separation of microbial cells (Carson et al., 2010). However, increasing WFPS can also decrease the rate of decomposition of bioavailable SOM by limiting oxygen (O_2) diffusion and therefore aerobic heterotrophic metabolism, for example reduced turnover of SOM in pores < 6 μm in diameter relative to 6–30 μm in diameter (Baldock et al., 2004; Killham et al., 1993). Although soils of increasing clay content are often associated with both increasing amounts of microbial biomass C (MBC) and SOC (Banu et al., 2004; Constancias et al., 2015; Dalal, 1998), this correlation does not necessarily result in greater rates of C mineralisation (Wardle, 1992). This is indicative of the role of clay in hindering SOM bioavailability. Fig. 1 depicts an interaction between microbial cells and soils of differing pore connectivity (as an edaphic property), whereby increased pore connectivity affects SOM bioavailability and increased microbial cellular activity, with active cells in light blue and inactive cells in dark blue.

Soil mineralogy, and again in particular clay minerals, contribute further to SOM protection through increasing the surface area to volume ratio of potential sites where organo-mineral complexes can be formed. Extensive investigations with cross polarisation-nuclear magnetic resonance spectroscopy have identified strong associations of ^{13}C carbohydrate, aliphatic, carbonyl, alkyl and O-alkyl C functional groups with clay and silt particles (Baldock et al., 1990; Barron et al., 1980; Golchin et al., 1994). Such organo-mineral complexes are the predominant control on long-term stabilisation of SOM (Kogel-Knabner et al., 2008). Amorphous non-crystalline minerals with high surface area (such as allophane, imogolite and ferrihydrite) are particularly efficient at protecting SOM (Kramer et al., 2012; Torn et al., 1997) compared to crystalline clays (such as halloysite, kaolinite, gibbsite, goethite and hematite). However, soils of increasing crystalline clay content remain relatively more efficient at limiting the bioavailability of SOM than soils of increasing sand and silt content (Badgery et al., 2013; Hassink, 1997). The mineralogy itself also determines SOM bioavailability, which is dependent on polyvalent cations at the mineral surface. Adsorption of SOM to aluminium, iron and manganese oxides via ligand exchange is preferential in acidic soils, whereas polyvalent cation bridges are formed between SOM and calcium and magnesium in neutral or alkaline soils (von Lützow et al., 2007). Thus, depending on the soil mineralogy, land management practices that affect soil pH will alter the adsorption of soluble SOM to soil minerals and thereby influence SOM bioavailability (Haney et al., 2001; Jardine et al., 1989; Zech et al., 1994).

2.2. Bioavailability dependent on SOM chemical properties

While the view that SOM turnover is dependent on the inherent quality of SOM is developing into the view that turnover is more dependent on the ecosystem as a whole (Schmidt et al., 2011), some degree of recalcitrance to microbial metabolism due to chemical structure cannot be ruled out (Dungait et al., 2012). For example, the initial stage of POM mineralisation is primarily dependent on plant litter chemistry, which can be plant species specific (Bejarano et al., 2014; Finn et al., 2015; Hobbie, 2005; Mathers et al., 2007). This is attributed to the relative abundance of alkyl, N-alkyl, methoxyl and carboxyl C functional groups (associated with labile amino acids, organic acids and lipids) and O-alkyl and di-O-alkyl C functional groups (associated with cellulose, hemicellulose, tannin and lignin) that comprises plant litter. The composition of POM determines its bioavailability by controlling the enzymatic rate of a specific reaction or the multitude of reactions required to solubilise it for cellular uptake (Bosatta and Ågren, 1999). Fig. 1 depicts the final stage of cellulose catabolism in an interaction between SOM and microbe: cellobiose is hydrolysed to glucose by cellobiohydrolase, as cleaving of disaccharides to monosaccharides (in green) and subsequent uptake of soluble substrate by the cell (light blue). Conversion or rotation to pasture improves SOM stocks within the top 15 cm of soil by increasing relatively recalcitrant below-ground plant biomass, with greater improvements when specific grass species are present, for example greater SOM stocks under native pasture than exotic grass species (Allen et al., 2013; Conant et al., 2001; Pineiro et al., 2010; Skjemstad et al., 1990). This could be a consequence of specific species either allocating greater C and N to relatively more recalcitrant root structures, or perhaps if certain native grasses demonstrate improved rates of primary productivity compared to exotic grass species. Similarly, agroforestry management practices with tree species that have a high root biomass: above-ground biomass ratio can significantly increase SOM stocks (Lorenz and Lal, 2014).

Quantitatively, the majority of SOM is within the <53 μm silt + clay fraction, herein termed humus (Skjemstad et al., 2004). Humus is chemically distinct from POM, with a lower abundance of carbohydrate and cellulose and an enrichment of amides, lipids and organic acids (Baldock et al., 1997, 2013; Grandy and Neff, 2008). This indicates that the majority of SOM consists of microbially-derived OM or as the products of microbial metabolism. In bulk soil, humus is the primary source of energy for micro-organisms (Kuzyakov and Blagodatskaya, 2015) and a diverse range of micro-organisms are capable of metabolising aromatic humic compounds (Park and Kim, 2015). However, the turnover of the humus C pool is considerably slower (and presumably less bioavailable) than POM (Balesdent et al., 1988; Coleman and Jenkinson, 1996; Jenkinson and Rayner, 1977). As described above, a number of soil physical properties restrict the bioavailability of SOM. Furthermore, the sheer complexity of the chemical structures that comprise humus, and the low volume of soil inhabited by microorganisms (<1%), means there is considerable separation between microorganism, extracellular enzyme and specific substrate in space (Foster, 1988; Schmidt et al., 2011). Finally, the relatively 'low-quality' (considered as less uptake of soluble SOM per enzymatic reaction due to structural complexity) of humus is a major limiting factor in the rate of humus decomposition (Bosatta and Ågren, 1999). In short, humus represents a less bioavailable pool of SOM than POM. As a management practice, the addition of low-quality decomposed or composted OM (i.e. manure, biosolids) has been shown to significantly improve SOM stocks compared to the addition of the equivalent amount of fresh POM (Haynes, 1999; Jenkinson, 1990; Johnston, 1975; McLauchlan, 2006; Powlson et al., 2011).

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

2.3. Bioavailability dependent on POM input and retention

To maintain SOM stocks and soil aggregates, POM must be degraded to humus and subsequently stabilised via edaphic factors (Cotrufo et al., 2013; Dungait et al., 2012). Energy starvation due to poor bioavailability of POM is itself a control on SOM turnover, and is the predominant factor limiting microbial activity (Blagodatsky and Richter, 1998). During starvation, the number of viable microbial cells within a population decreases rapidly, which is not necessarily coupled to cell lysis or loss of MBC (Morita, 1993). A viable subpopulation of cells remains active, often in a dormant state resistant to environmental stress. Starved cells can respond immediately to the input of energy (even after starvation periods of eight months) (Amy and Morita, 1983) with the lag phase prior to the resumption of exponential growth dynamics dependent on the length of the starvation period. *In situ* these irregular bursts of bioavailable energy are termed pulse events and can last hours–-days in the rhizosphere or weeks–months in the bulk soil, dependent on environmental factors such as soil moisture, temperature and plant biomass input (Kuzyakov and Blagodatskaya, 2015; Matzner and Borken, 2008; Rousk and Baath, 2011). The frequency of these events, and the activity of the microbial community, will determine cell viability and therefore the turnover of SOM. The interaction between environment and microbe in Fig. 1 depicts different rates of SOM processing (in green) between microbial communities with varying numbers of viable (light blue) and non-viable (dark blue) cells. Under favourable conditions, POM is partially decomposed. Presuming these compounds are stabilised via organo-mineral interactions, or become physically inaccessible to further decomposition, or the relative recalcitrance of microbial products makes their further decomposition less favourable, partially decomposed POM will promote soil aggregation and increased SOM stocks.

Stubble or crop residue retention, coupled with reduced tillage, as a source of POM is a well-proven method for maintaining soil aggregation and SOM stocks in agricultural soils by maintaining the viability and biological function of soil microorganisms (Jordan et al., 2010; Mulumba and Lal, 2008; Prove et al., 1990). Conversely, fallow periods with crop species that demonstrate a low input of plant biomass to soil result in significant losses of SOC (Campbell et al., 2000).

2.4. Effects of ecological stoichiometry and biodiversity

Plant biomass as litter (leaf, root and wood) or rhizodeposits are the primary source of humus (Kogel-Knabner, 2002). The differential allocation of C, N and P in biomass, dependent on plant species, can affect humus formation and SOM turnover by influencing the ecological stoichiometry of the system (Zechmeister-Boltenstern et al., 2015). Ecological stoichiometry controls microbial and fungal CUE, as a measure of the ratio of C anabolism *versus* catabolism (Manzoni et al., 2012). For example, there is a large discrepancy between the C:N ratio of plant biomass (15–300) compared to fungal and microbial biomass (<10) (Anderson and Domsch, 1980; Bertrand et al., 2011; Gleixner, 2013; Mouginot et al., 2014; Shen et al., 1984; Zechmeister-Boltenstern et al., 2015). This discrepancy can result in reductions in humus immobilisation relative to mineralisation, with greater C mineralisation when plant material of increasing C:N ratio is decomposed (Craine et al., 2007; Manzoni and Porporato, 2009; Moorhead and Sinsabaugh, 2006). Furthermore, when nutrients such as N and P are limiting, pre-existing SOM can be preferentially mineralised as a resource for limiting nutrients, known as SOM priming (Kuzyakov, 2010).

Above and belowground biodiversity of plant, soil fauna, fungal and bacterial species plays a role in decomposition and humus formation. Fungal activity (often assumed to have a relatively high CUE compared to bacteria) contributes to SOM gains in no-till systems, whereas bacterial decomposition (assumed to have a relatively low CUE compared to fungi) predominates in tilled systems (Beare et al., 1992), however a relationship between CUE and the ratio of fungal biomass to bacterial biomass is not always present (Thiet et al., 2006). In environments with increasing aboveground plant species diversity, there are improvements in soil biological function of carbohydrate, carboxylic acid, amine and protein cycling (Loranger-Merciris et al., 2006), total plant C and N inputs (Tilman et al., 1997; Zak et al., 2003) and agroforestry management significantly improves ecosystem properties such as C and N turnover (Wood et al., 2015). In agricultural systems, incorporation of crop rotations and increasing the diversification of crop rotations can also yield benefits to soil function (McDaniel et al., 2014; Reeves, 1997; West and Post, 2002). Rotation benefits are crop species specific, with species that demonstrate low biomass inputs and elicit poor CUE (e.g. flax, *Linum usitatissimum* L.) contributing less to SOC gains than species with low plant C:N ratio and which elicit higher CUE (e.g. lentil, *Lens culinaris* L.) (Campbell et al., 2000). Thus management practices which affect the efficiency of biological humus formation will ultimately affect the quantity and quality of bioavailable SOM. Fig. 1 depicts environmental affects (water availability as blue droplets, temperature as the sun and N availability as N, but environmental affects also include management practices such as fertilisation and aboveground plant species biodiversity) on SOM by controlling the amount of SOM provided by aboveground plant species.

2.5. Fertilisation effects on SOM turnover

Fertilisation practices aim to prevent reductions in soil N and phosphorous (P) in agricultural systems, however fertilisation can alter the stoichiometry of the system through oversupply or insufficient replacement of N and P relative to crop removal (Matson et al., 1997; Vitousek et al., 2009). This has the potential to significantly alter microbial viability and activity (Berg and Matzner, 1997; Carreiro et al., 2000; Fog, 1988; Sinsabaugh et al., 2002). The consequences of this can be either increases in SOM stocks (Cusack et al., 2010, 2011; Frey et al., 2014) or decreases (Khan et al., 2007) or no interactions at all (Grandy et al., 2013; Robertson et al., 2015). These variable results are presumably due to CUE and priming system properties, dependent on stoichiometry (including both plant biomass input and SOM) that vary between soils. For example, N fertilisation of low TOC and high C:N ratio soils can lead to priming and SOM loss, whereas N fertilisation of high TOC and low C:N ratio soils can have minimal change in C mineralisation (Finn et al., 2015). By standardising input plant residue ratios of C, N, P and sulphur with inorganic forms in order to match stoichiometric ratios of soil humus (10 000: 833: 200: 143 for C, N, P and sulphur, respectively) Kirkby et al. demonstrate significant improvements in humification efficiency *in vitro*, and thus increases in SOM (Kirkby et al., 2013). The variation in how SOM stocks respond to fertilisation is also dependent on cropping practices and whether soil pH is affected by long-term inorganic N fertilisation (Geisseler and Scow, 2014). An alternative to fertilisation is the use of rotations with N fixing legumes with low plant C:N ratio, which can contribute to improved soil N, however this is dependent upon the quantity of N-rich plant residue input (Conant et al., 2001; Drinkwater et al., 1998; Peoples and Baldock, 2001). Comparisons of soils under forest, corn/soybean/wheat rotation and soybean monoculture demonstrate increasing microbial CUE with increasing N input and most markedly under N fixing soybean monoculture (Lee and Schmidt, 2014). As in Section 2.3, insufficient

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

or oversupply of N and/or P can affect the interaction between both environment and microbe and environment and SOM, through plant species (Fig. 1) by influencing the viability and activity of the microbial and plant communities.

3. Soil microbial ecology in agricultural systems

Microbial biodiversity and community composition play a significant role in a number of processes of agricultural importance, such as: a) a significant positive effect on ecosystem functions including plant productivity (Delgado-Baquerizo et al., 2016; Hartmann et al., 2008); b) regulation of soil C and N cycling, particularly in the rhizosphere (Bender et al., 2016; Delgado-Baquerizo et al., 2016; Schimel and Schaeffer, 2012); and c) regulation of live-weight gain in ruminant livestock production (Hungate, 1966; Russell and Rychlik, 2001). A thorough discussion of microbial ecological theory is beyond the scope of this review. Here we focus on hypotheses relevant to how microbial communities are shaped by SOC bioavailability. We discuss examples of how microbial communities are affected by conversion of natural to an agricultural ecosystem, and effects of specific land management practices.

3.1. Carbon and energy flow measured as CUE

Describing ecological systems through metabolism and energy flow is a concept that has been favoured over time (Odum, 1968). This is because, at its foundation, energy flow is unidirectional due to the second law of thermodynamics. This makes measurements of energy flow more informative of ecosystem dynamics than measurements of constantly cycling pools of OM, i.e. MBC (Odum, 1968). For example, OM input as rhizodeposits to a rhizosphere microbial community may have no net effect on total MBC, and so would appear to be a rather static system, despite active uptake, catabolism and anabolism of OM. Of particular interest to C and energy flow in terrestrial systems is CUE, considered as a ratio of C anabolism *versus* catabolism. It is likely that soil microbial CUE *in situ* converges at approximately 0.3, which is roughly half of the estimated thermodynamic maximum for microbial growth (Sinsabaugh et al., 2013). However this figure varies greatly between studies, dependent on temperature, molecular composition of substrate, water, C:N:P, O_2 availability, protozoal grazing of microorganisms and potentially the ratio of fungal biomass to bacterial biomass, however this is currently unclear (Frey et al., 2001; Lee and Schmidt, 2014; Manzoni et al., 2012; Thiet et al., 2006). An increase in the quantity of easily decomposable C, as in cropping systems relative to forestry systems, demonstrates a negative relationship with CUE (Sinsabaugh et al., 2016). Decreases in the relative CUE of an ecosystem leads to loss of SOC stocks (Zechmeister-Boltenstern et al., 2015).

The CUE is often measured as a ratio of microbial biomass production: biomass production + C mineralisation (Equation (1)) (however see Manzoni et al., 2012 for more methods of measuring CUE).

$$CUE = \Delta MBC / \Delta MBC + R_C \quad (1)$$

whereby CUE is the carbon use efficiency of the system, ΔMBC is the change in microbial biomass C (typically measured as mg C kg^{-1} soil by techniques such as chloroform-fumigation (Vance et al., 1987)) and R_C is cumulative respiration by the MBC (typically measured as mg C kg^{-1} soil by techniques such as alkali traps or gas chromatography (Singh et al., 2012; Wang et al., 2004)). Note that this approach cannot be used where plant roots are also actively respiring.

A limitation of measuring CUE is that only the C retained by the system is measured rather than individual steps in the flow of C. Consequently, CUE calculations can be underestimated depending on the degree of protozoal grazing of microbial cells and/or macropod predation of fungi, or by cryptic growth on microbial necromass (Beare et al., 1992; Chapman and Gray, 1986; Frey et al., 2001). This can pose difficulties in describing CUE in terms of microbial ecological significance. A possible means to disentangle these interactions is with stable isotope probing approaches, which track the flow of ^{13}C, ^{15}N and/or ^{18}O through the nucleic acids of individual microbial taxa (and potentially through trophic levels) to determine organisms involved in the metabolism of a specific substrate, or to identify ecological interactions such as co-metabolism between taxa or predation due to dissemination of labelled elements throughout the community over time (Neufeld et al., 2007; Whiteley et al., 2007).

3.2. Ecological coherence at high taxonomic rank

Ecological coherence suggests that more closely related taxa share a greater similarity of specific traits relative to more distantly related taxa (Philippot et al., 2010). Large-scale (1374 bacterial genomes) distance-based network analyses comparing functional traits predicted from annotated genomes support strong clustering of shared function in specific phyla, such as Firmicutes, Chlamydia and Acidobacteria (Zhu et al., 2015). Ecological coherence at high taxonomic rank has been used to describe ecological groupings of soil bacterial taxa, with the relative abundance of 'copiotrophic' Beta-Proteobacteria and Bacteroides linked to increased rates of soil C mineralisation and 'oligotrophic' Acidobacteria linked to decreased rates of soil C mineralisation (Fierer et al., 2007). Copiotrophs are defined as species with a high maximum growth rate in energy rich environments yet relatively poor CUE, whereas oligotrophs are considered as species with a low maximum growth rate, high CUE and tend to dominate energy poor environments. A number of studies appear to support ecological coherence of Proteobacteria, Actinobacteria and Bacteroides as generally associated with copiotrophic behaviour, and Verrucomicrobia, Firmicutes and Acidobacteria as associated with oligotrophic behaviour (Fierer et al., 2012; Goldfarb et al., 2011; Wessen et al., 2010). Thus, soils which favour the enrichment of copiotrophs will demonstrate a relatively low CUE over the same period of time as a soil dominated by oligotrophs, and subsequently higher rates of C mineralisation and reduced SOC stocks over time would be predicted.

There are potential limitations to the ecological coherence hypothesis. These include: a) phyla do not always demonstrate the same ecological behaviour between studies, for example Actinobacteria and Firmicutes have also been reported to have no relationship with C mineralisation (Fierer et al., 2007); b) specialised functions, such as lignin catabolism and denitrification, can be widely dispersed across phyla and so ecological coherence is function specific (Goldfarb et al., 2011; Schimel and Schaeffer, 2012); c) high levels of functional diversity can be present within a phylum, such as the Gamma, Alpha and Beta-Proteobacterial classes (Zhu et al., 2015); and d) our understanding of the distribution of functional traits related to C and nutrient turnover remains quite poor. This is evident from the recent discoveries of aerobic methane oxidation in Verrucomicrobia and the importance of aerobic ammonia oxidation by Archaea, which were functions historically thought specific to Proteobacteria (Dunfield et al., 2007; Prosser and Nicol, 2012), and non-photosynthetic Cyanobacteria (Soo et al., 2014). In plant ecology, an alternative to the arguably simplistic copiotroph/oligotroph hypothesis has been proposed. The competitor-stress tolerator-ruderal (or universal adaptive strategy) hypothesis not only considers maximum growth rate in

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

response to energy availability but also adaptive capacity to environmental perturbation and/or stress (Grime and Pierce, 2012). There may be value in testing such a hypothesis in soil microbial ecology, as the Actinobacteria in particular demonstrate rapid adaptation to soil perturbation (as described below). Indeed, the competitor-stress tolerator-ruderal hypothesis has been used to convincingly argue ecological coherence within aerobic methanotrophic Proteobacterial species (Ho et al., 2013).

3.3. Broad versus narrow functional biodiversity

Understanding the role of functional biodiversity on geochemical processes to develop a predictive framework is of practical interest for microbial ecologists and biogeochemists alike. Currently, many geochemical models express microbial functionality as a single parameter which is assumed to remain constant under all environmental conditions and also assumes that all microbial communities function identically (Allison and Martiny, 2008). Biodiversity (either taxonomic diversity of the entire community or functional diversity of specific taxa that comprise a function) is commonly measured as the Shannon-Weaver diversity index (H′), which is a function of the total number of taxa (richness) and their abundance distribution (evenness) (Prosser, 2012). A growing body of literature appears to suggest that the relationship between biodiversity and the rates of individual functions is sometimes significant and other times not. However, there is general consensus that biodiversity is positively related to function at the ecosystem level, and this has been demonstrated across national and international scales with strong correlations for functions such as N mineralisation and with system properties such as plant productivity, net primary productivity and litter decomposition (Delgado-Baquerizo et al., 2016; Wagg et al., 2014). The interaction between biodiversity and ecosystem function is of relevance to agricultural ecosystems, as land management significantly affects taxonomic and functional biodiversity (Constancias et al., 2015; de Menezes et al., 2015; Mendes et al., 2015).

Microbial functions can be categorised as either: a) 'broad' functions which a relatively large proportion of the community can carry out, i.e. disaccharide hydrolysis; or b) 'narrow' functions which are performed by a relatively small proportion of the community, i.e. nitrification, nitrogen fixation and methane oxidation (Schimel and Schaeffer, 2012). Differentiating these functional categories is important as narrow functions may demonstrate greater sensitivity to environmental perturbation, possibly due to functional redundancy, resilience or resistance, or a combination of these. Functional redundancy is defined as a function which multiple distinct taxa can perform; resilience is the capacity for a function to remain stable despite perturbation; and resistance is the rate at which a function recovers from perturbation (Allison and Martiny, 2008). Narrow functions can be knocked out in low diversity soils. For example, comparative analyses of soils with relatively low and high 16S rRNA gene biodiversity ($H' = 3.25 \pm 0.02$ and 3.68 ± 0.04, respectively, as measured with denaturing gradient gel electrophoresis) perturbed with benzene lost the capacity to metabolise the organic pollutant 2,4-dichlorophenol in the lower diversity soil, whereas the higher diversity soil recovered 2,4-dichlorophenol metabolism by nine weeks of incubation (Girvan et al., 2005). Broad functions can show significantly reduced resistance in low diversity soils. For example, by decreasing diversity in soils with chloroform incubation ($H' = 2.03–2.36$ and $1.83–1.95$ of non-treated and treated soils, respectively), or mercury exposure ($H' = 3.83 \pm 0.02$ and 3.48 ± 0.02 for non-treated and treated soils, respectively) and then perturbing with copper sulphate or heat shock, the lower diversity soils demonstrated significantly greater lag periods before the recovery of OM decomposition (Griffiths et al., 2000; Muller et al., 2002).

However, it should be noted that examples of no perturbation effects on narrow (nitrite oxidation) or broad (denitrification) functions across biodiversity gradients also exist (Wertz et al., 2007). Additionally, community reconstruction experiments comparing diversity effects of broad groups of soil organisms (including microorganisms only, microbes + mesofauna and microbes + mesofauna + macrofauna) can show no diversity effects on broad functions such as OM decomposition, plant biomass production and plant carbon dioxide uptake (Fitter et al., 2005). These contradictory results may be due to methodological limitations in appropriately assessing microbial diversity with culture-based or 16S rRNA gene fingerprinting techniques. Furthermore, many studies have assumed a relationship between taxonomic diversity and function, as opposed to the diversity of a specific functional gene and a function, again likely due to methodological limitations or poor understanding of the distribution of certain functions. This may be further complicated in that phenotypic activity can indeed be dependent on taxonomy. For example only specific methanotroph species, such as those within the Upland Soil Cluster-α group, appear to actively oxidise methane at atmospheric concentrations whereas other species, such as *Methylosarcina* spp., only actively oxidise atmospheric concentrations of methane after being induced with high concentrations of methane, for example in water-saturated rice paddy soils that favour methanogenesis (Baani and Liesack, 2008; Cai et al., 2016). Thus for certain ecosystem functions a combination of functional gene diversity, taxonomic diversity and knowledge of the conditions which induce protein expression between species may be necessary to elucidate a relationship between function and diversity. This may explain why relationships are more readily apparent for some functions, such as enzymes involved in decomposition (Trivedi et al., 2016) but not necessarily with others, such as methane oxidation (Rocca et al., 2015). In short, much scope remains for appropriate ecological hypothesis testing of the role of functional diversity in soil geochemical processes (Prosser et al., 2007).

3.4. The impacts of land management on soil microbial communities

Fig. 2 is a visual example of significant changes in the relative abundance of microbial species upon slash and burn conversion of a tropical forest soil to a soybean (*Glycine max*) cropping agricultural soil in the top 0–20 cm soil layer. Please consult the Supplementary Material for further information regarding the source material and statistical methods applied. Upon conversion of forest to agriculture, there is an enrichment of microorganisms primarily belonging to the Actinobacteria, Proteobacteria and Firmicutes, and to a lesser extent Bacteroides, Planctomycetes, nitrite-oxidising Nitrospirae and ammonia-oxidising Archaea (Table 1). The enrichment of phyla considered to be copiotrophic, such as Actinobacteria, Proteobacteria and certain N-cyclers, is consistently seen in response to nutrient input, such as N fertilisation (Fierer et al., 2012; Frenk et al., 2015; Hartmann et al., 2015; Jimenez-Bueno et al., 2016; Wessen et al., 2010). Soil acidification due to the over-application of inorganic N fertilisers, such as ammonium sulphate, has a significantly negative impact on all phyla, particularly Verrucomicrobia (Wessen et al., 2010). Verrucomicrobia can be highly abundant in oligotrophic soils and their abundance is positively correlated with cycling of recalcitrant C compounds and negatively correlated with N metabolism (Fierer et al., 2013). Tillage, which as described in Section 2 has a great influence on SOM bioavailability and leads to large SOC losses, favours the abundance of Proteobacteria (de Vries et al., 2015; Souza et al.,

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

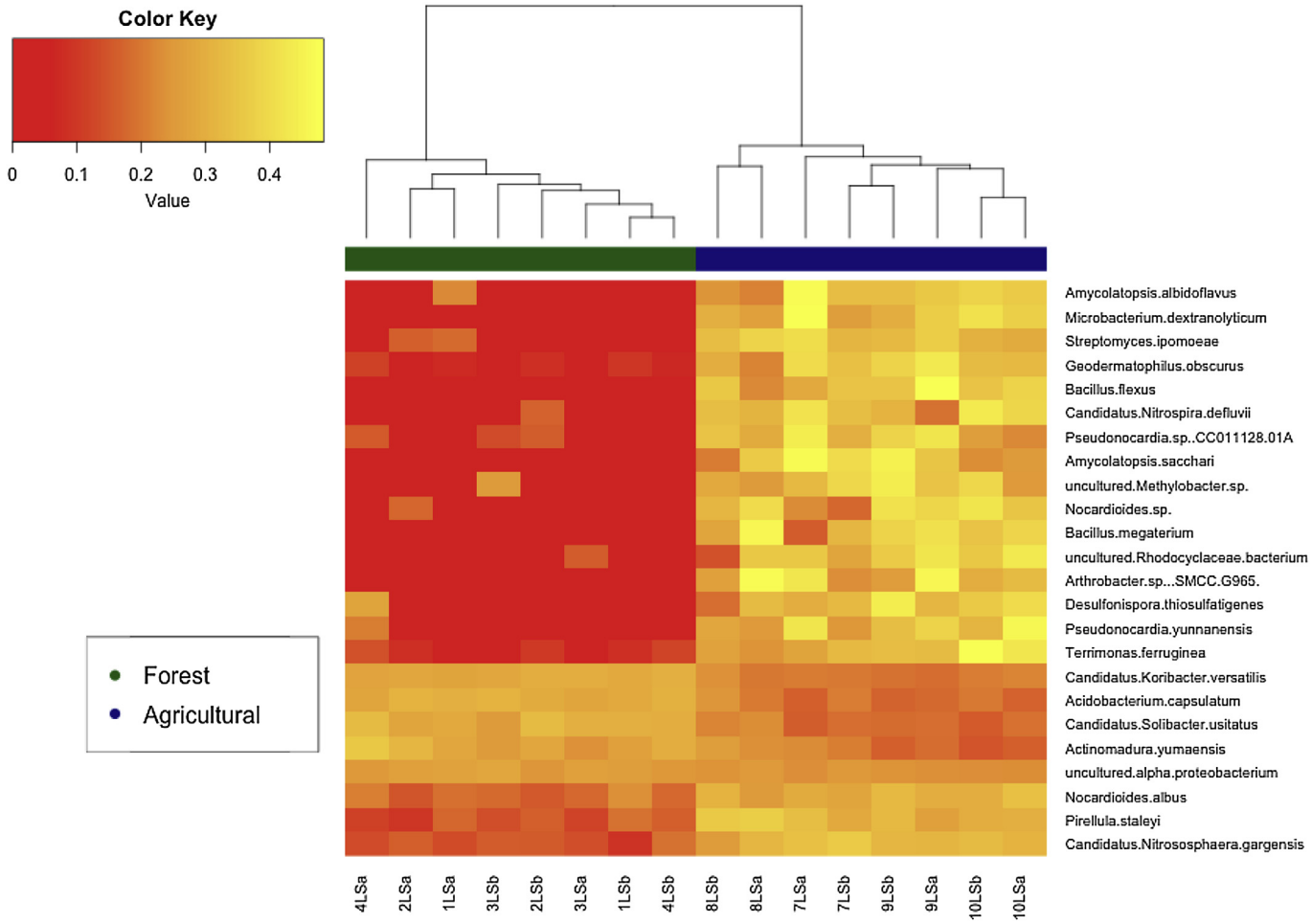

Fig. 2. Heatmap of significantly different microbial species (y axis) after conversion from a tropical forest (green bar) to a soybean cropping agricultural (blue bar) soil. The color key indicates relative abundance. The dendrogram indicates similarity between samples, labelled on the x axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2013) while zero till systems favour oligotrophic N fixing microorganisms and Acidobacteria (Jimenez-Bueno et al., 2016; Souza et al., 2013). Interestingly, Actinobacteria are diverse in both tilled and zero till systems (de Vries et al., 2015; Jimenez-Bueno et al., 2016; Souza et al., 2013), which suggests if there is ecological coherence within the Actinobacteria, their ecological behaviour may be better explained by the ruderal framework than the copiotrophic framework. Fig. 2 and Table 1 also indicate significant decreases in Acidobacteria upon conversion from natural to agricultural ecosystems. The Acidobacteria are considered to be oligotrophic, favouring the nutrient poor bulk soil (Uksa et al., 2015). In agricultural systems, decreasing soil C:N ratio, changes in soil acidity and changes in above-ground plant species have been associated with a decrease in the relative abundance of certain Acidobacteria (Fierer et al., 2012; Navarrete et al., 2015). Thus, agricultural management practices which perturb soils and increase the bioavailability of C have a profound effect on microbial community composition. The result is that agricultural systems tend to enrich for ecologically coherent groups at high taxonomic rank that favour nutrient rich environments and which have relatively poor CUE (copiotrophs). Conversely, the relative abundance of ecologically coherent groups that have a relatively high CUE tends to decrease in agricultural systems (oligotrophs). These changes will lead to poorer CUE of the system and subsequent decreases in SOC stocks.

4. A physiological basis for SOM loss in agricultural systems

The discussed ecological shifts in response to a conversion of soil to agriculture are a consequence of how microorganisms respond to C bioavailability. This is dependent on their physiology. Fig. 3 and Table 2 show significant shifts in functional subsystems after slash and burn conversion of a tropical forest soil to a soybean cropping agricultural soil. While the shift in many functions is less pronounced than species shifts in Fig. 2, several important trends should be noted. In the agricultural soil, the relative abundance of functions involved in DNA, RNA and protein biosynthesis are significantly higher. Of particular interest are increases in the relative abundance of protein chaperones above detection limits ($P < 0.001$) and universal GTPases ($P = 0.016$) which are essential for a variety of functions including conformational changes in proteins, tRNA function, ribosome assembly, cell replication, sporulation, cell elongation and filamentous growth (Caldon and March 2003). Unsurprisingly, following an increase in functions involved in biosynthesis is an increase in functions involved in conversion and generation of potential chemical energy, such as cytochrome biogenesis ($P = 0.007$) and the relative abundance of bacterial species which utilise the F_0F_1 ATP synthase ($P = 0.004$) as opposed to Archaea and some Firmicutes which utilise a V_0V_1 or A_0A_1-type ATP synthase (Koumandou and Kossida, 2014). Finally, of interest in the agricultural soil is a large increase in *dnaK* ($P < 0.001$) which is

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

Table 1
Relative species abundance (10^{-3}, %) of bacteria and archaea identified as significantly different ($P < 0.05$) between forest and agricultural soils in a paired site study from the Amazon.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Relative Abundance (10^{-3}, %)		*P* value
							Forest	Agricultural	
Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Pseudonocardiaceae	*Amycolatopsis*	*albidoflavus*	0.11 ± 0.29	1.57 ± 0.67	0.01
						sacchari	0	1.13 ± 0.56	0.047
				Nocardioidaceae	*Nocardioides*	sp.	0.09 ± 0.24	2.28 ± 0.99	0.006
						albus	3.32 ± 1.01	6.79 ± 1.01	0.046
				Micrococcaceae	*Arthrobacter*	sp. SMCC.G965	0	0.67 ± 0.33	0.028
				Thermomonosporaceae	*Actinomadura*	*yumaensis*	7.06 ± 1.61	2.73 ± 1.04	0.039
					Pseudonocardia	sp. CC011128.01A	0.35 ± 0.46	4.07 ± 1.63	0.015
						yunnanensis	0.12 ± 0.33	2.26 ± 0.92	0.003
				Microbacteriaceae	*Microbacterium*	*dextranolyticum*	0	1.04 ± 0.45	0.008
				Streptomycetaceae	*Streptomyces*	*ipomoeae*	0.2 ± 0.35	2.43 ± 0.53	0.02
				Geodermatophilaceae	*Geodermatophilus*	*obscurus*	0.86 ± 0.65	15.3 ± 4.94	0
	Firmicutes	Bacilli	Bacillales	Bacillaceae	*Bacillus*	*flexus*	0	1.5 ± 0.56	0.005
						megaterium	0	2.48 ± 1.05	0.027
		Clostridia	Clostridiales	Peptococcaceae	*Desulfonispora*	*thiosulfatigenes*	0.12 ± 0.33	1.28 ± 0.49	0.047
	Nitrospirae	Nitrospira	Nitrospirales	Nitrospiraceae	Candidatus *Nitrospira*	*defluvii*	0.13 ± 0.35	3.75 ± 1.47	0.001
	Proteobacteria	Gamma-proteobacteria	Methylococcales	Methylococcaceae	Uncultured *Methylobacter*	sp.	0.09 ± 0.25	1.1 ± 0.44	0.02
		Beta-proteobacteria	Rhodocyclales		Uncultured *Rhodocyclaceae*	0.08 ± 0.21	2.3 ± 0.88	0.004	
		Uncultured Alpha-proteobacteria					104.23 ± 12.22	68.31 ± 6.29	0.025
	Bacteroides	Sphingobacteria	Sphingobacteriales	Chitinophagaceae	*Terrimonas*	*ferruginea*	0.77 ± 0.7	9.92 ± 4.85	0.016
	Acidobacteria	Acidobacteria	Acidobacteriales	Acideobacteriaceae	Candidatus *Koribacter*	*versatilis*	52.56 ± 5.2	21.2 ± 3.29	0
					Acidobacterium	*capsulatum*	27.7 ± 2.54	9.39 ± 2.67	0
		Solibacteres	Solibacteriales	Solibacteraceae	Candidatus *Solibacter*	*usitatus*	49.82 ± 7.13	15.81 ± 4.04	0
	Planctomycetes	Planctomycetacia	Planctomycetales	Planctomycetaceae	*Pirellula*	*staleyi*	1.83 ± 0.78	6.63 ± 1.48	0.003
Crenarchaeota	Thaumarchaeota	Nitrososphaeria	Nitrososphaerales	Nitrososphaeraceae	Candidatus *Nitrososphaera*	*gargensis*	4.08 ± 1.48	15.16 ± 3.09	0

important in the regulation of protein assembly and cellular growth between exponential and stationary phases in response to resource availability (van Elsas and van Overbeek, 1993). Conversely, in the presumably oligotrophic forest soil, there is a greater relative abundance of: a) σ factors ($P = 0.013$), suggestive of an emphasis on transcriptional regulation (Helmann and Chamberlin, 1988); b) formate hydrogenase ($P = 0.01$), suggestive of more efficient nicotinamide adenine dinucleotide (NAD(P)H) production from alternative electron donors (Fogal et al., 2015); and c) increases in anaplerotic reactions of phosphoenolpyruvate (PEP) metabolism ($P < 0.001$), suggestive of greater complexity in how C flux is distributed between catabolic and anabolic intermediates (Sauer and Eikmanns, 2005). Oddly, Respiratory Complex I (i.e. NADH dehydrogenase) is also more abundant in the forest soil ($P < 0.001$), which is an enzyme that is practically ubiquitous throughout organisms which perform aerobic metabolism (Friedrich and Scheide, 2000). As this enzyme is shared between mitochondria, bacteria and archaea, it is possible that the greater relative abundance of this enzyme in the forest soil is due to a greater relative abundance of eukaryotic DNA in forest *versus* agricultural soils, however this is speculative.

In summary, conversion from forest to agricultural soil favours a shift from microbial species physiologically adapted to low energy environments that require strict transcriptional regulation and allocation of C between energy generation and biosynthesis, to species physiologically adapted to rapid DNA, RNA and protein biosynthesis during periods of resource availability. The following section aims to explore the physiological mechanisms that may underlie these principles. Furthermore, we discuss how agricultural practices intended to manage SOC stocks affect the functional composition of soil microbial communities.

4.1. Physiological differences in electron transport chains

An electron transport chain (ETC), where electrons (e^-) are transferred by carriers from a low redox potential to a terminal e^- acceptor of higher redox potential, is necessary to create an electrochemical gradient across a membrane (Mitchell, 1961). In aerobic chemo-organotrophs which can utilise O_2 as the terminal e^- acceptor, this electrochemical gradient enables protons (H^+) to be pumped from the cytoplasm across the membrane, where they can generate an H^+ motive force (PMF) to drive the formation of chemical energy for cellular function (in the form of adenosine triphosphate, ATP) back through transmembrane ATP synthase. Microbial ETCs are malleable, and the expression of the e^- carriers that comprise them are regulated by the growth phase of the cell, reducing equivalents, pH, membrane potential and the ATP:adenosine diphosphate (ADP) ratio (Capaldi, 1990; Meyer and Jones, 1973).

Microbial ETCs demonstrate ecological coherence of terminal oxidases such as cytochrome *bd*, and A-, B- and C-type heme-copper cytochrome families at certain taxonomic ranks (Brochier-Armanet et al., 2009; Koumandou and Kossida, 2015). For example, genome comparisons across Proteobacterial classes suggest that the presence of A-type heme copper cytochromes is more widely distributed across Gamma (130/157 genomes), Beta (48/53 genomes) and Alpha-Proteobacteria (79/83 genomes) than Epsilon-Proteobacteria (0/19) (Brochier-Armanet et al., 2009). While the function of terminal oxidases is similar, their efficiencies in generating an electrochemical gradient can differ markedly. For example,

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

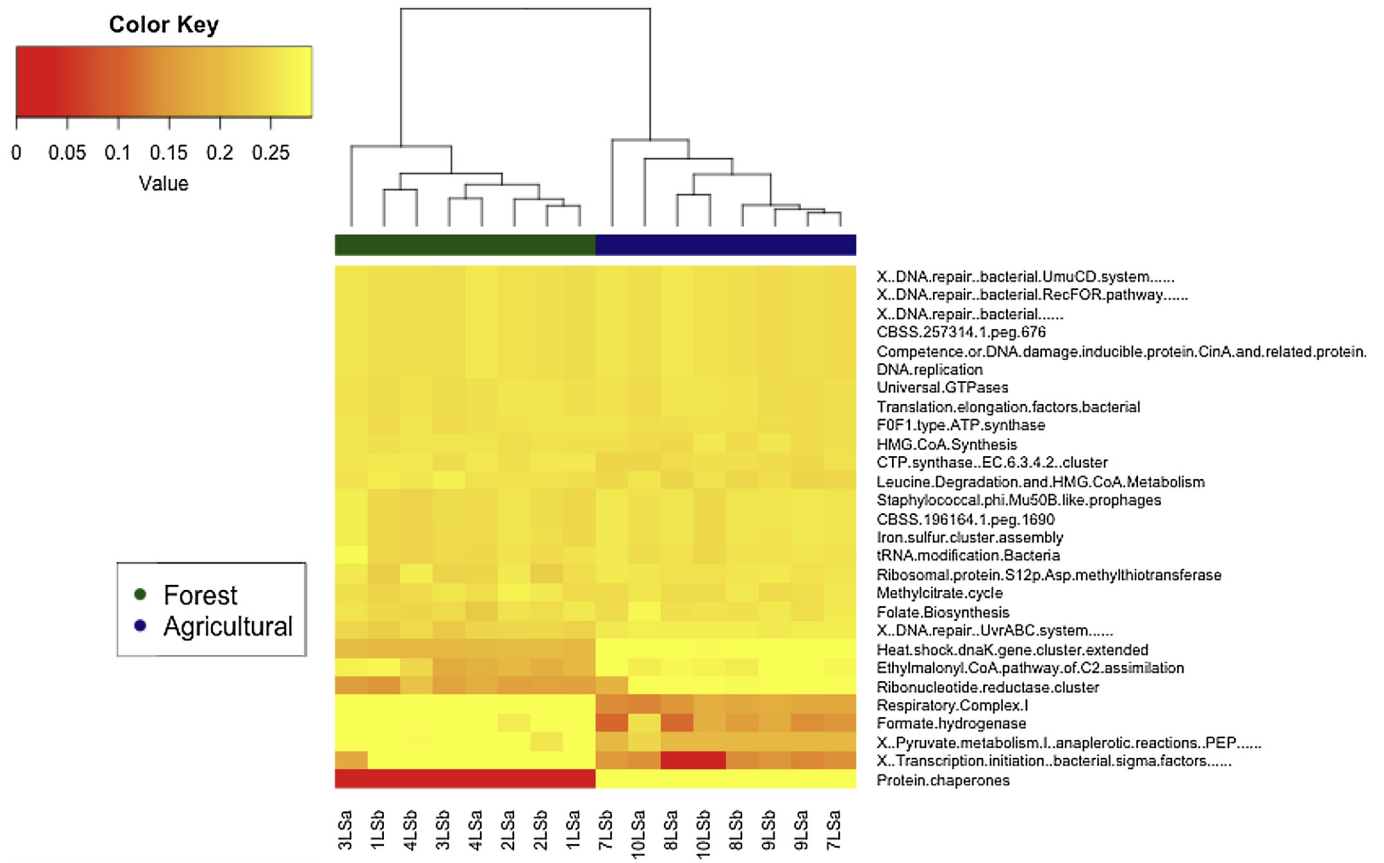

Fig. 3. Heatmap of significantly different functional subsystems (y axis) after conversion from a tropical forest (green bar) to a soybean cropping agricultural (blue bar) soil. The color key indicates relative abundance. The dendrogram indicates similarity between samples, labelled on the x axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in *Escherichia coli*, the A1-type cytochrome *bo* is more efficient at e^- transfer than cytochrome *bd* even though both can be expressed simultaneously and both contribute to total respiration (Calhoun et al., 1993; Sousa et al., 2011). Supplementary Fig. 1 is a comparison of ETCs in Beta-Proteobacterial *Burkholderia* spp., the Acidobacterium *Candidatus* Solibacter usitatus Ellin6076 and the Actinobacterium *Streptomyces coelicolor* A3(2). Electron transfer efficiencies are measured by H^+/e^- ratio, whereby a higher H^+/e^- ratio results in more H^+ transferred across the membrane per e^- and ultimately a higher production of ATP per e^- donor (Calhoun et al., 1993). The H^+/e^- ratios of cytochrome *bd* is 1, cytochrome *bo* is 2, cytochrome caa_3 is 1 and the $bcc\text{-}aa_3$ super complex is ≤ 2 (Borisov et al., 2011; Harold, 1972; Noor and Soulimane, 2013). Electron transfer efficiency also differs between the utilisation of ubiquinone and menaquinone as e^- carriers, with a relatively lower potential generated by menaquinone in Actinobacteria (Kao et al., 2016). As demonstrated in Supplementary Fig. 1, *Burkholderia* spp. have the highest potential rate of respiration and ATP production, *Can*. S. usitatus Ellin6076 has the lowest, and *S. coelicolor* A3(2) may have a greater capacity to adjust its ETC depending on its environment and energy requirements.

At the cellular level, *in vitro* physiological assays of O_2 consumption support phenotypical differences in microorganisms considered to be copiotrophic or oligotrophic, with aerobic respiration rates of 60–300 nmol O_2 min^{-1} mg dry $weight^{-1}$ and 8–15 nmol O_2 min^{-1} mg dry $weight^{-1}$ in copiotrophs and oligotrophs, respectively (Semenov, 1991). Competition assays with *E. coli* knockout mutants reliant on either high H^+/e^- membrane-bound nitrate reductase (NAR) or low H^+/e^- periplasmic nitrate reductase (NAP) for respiration demonstrate differential phenotypic properties. For example, NAR-mutants will outcompete NAP-mutants for C, whereas NAP-mutants will outcompete NAR-mutants if the e^- acceptor (nitrate) is limiting (Potter et al., 1999). Alternatively, expression of low H^+/e^- oxidases may be beneficial under certain conditions, such as a means for controlling the redox state of the cell when an oversupply of H^+ is likely to be produced during growth on reduced C substrates such as fatty acids (Richardson, 2000).

Agricultural soils and soils under native vegetation differ in their composition of microbial cytochromes. Specifically, significant decreases in the relative abundance of cytochrome *bd* and increases in low-O_2 affinity A-type heme copper cytochromes are observed in agricultural soils (Morris and Schmidt, 2013). Conversion of forest to agriculture, pasture or deforestation all lead to significant changes in the abundance of functional genes associated with respiration (Mendes et al., 2015). In regard to agricultural management practices, the relative abundance of respiratory functional genes increases in no tillage cropping systems compared to native ecosystem (Souza et al., 2016). However, where SOM and MBC had significantly decreased under 23 years of conventional tillage, decreases in the relative abundance of respiratory functional genes compared to native ecosystem occurred (Souza et al., 2016). Increasing N fertilisation (across gradients of 0–291 kg N ha^{-1} $year^{-1}$) increases the relative abundance of ubiquinone-cytochrome reductase complexes and F_0F_1 ATP synthase (Fierer et al., 2012), similar to shifts observed in Table 2. To the authors'

Table 2
Relative abundance (10^{-3}, %) of functional subsystems identified as significantly different ($P < 0.05$) between forest and agricultural soils in a paired site study from the Amazon.

Level 1	Level 2	Level 3	Relative Abundance (10^{-3}, %)		*P* value
			Forest	Agricultural	
DNA Metabolism	DNA repair	DNA repair, bacterial UmuCD system	4.54 ± 0.3	6.13 ± 0.63	0.03
		DNA repair, bacterial RecFOR pathway	4.54 ± 0.3	6.13 ± 0.63	0.03
		DNA repair, bacterial	4.54 ± 0.3	6.13 ± 0.63	0.03
		DNA repair, UvrABC system	7.74 ± 0.67	13.21 ± 0.77	0
	DNA replication	DNA-replication	4.54 ± 0.3	6.14 ± 0.63	0.03
RNA Metabolism	RNA processing and modification	tRNA modification Bacteria	5.97 ± 0.75	8.26 ± 0.83	0.047
	Transcription	Transcription initiation, bacterial sigma factors	9.56 ± 2.83	1.78 ± 0.99	0.013
Protein Metabolism	Protein biosynthesis	Universal GTPases	16.03 ± 1.16	21.6 ± 2.03	0.016
		Translation elongation factors bacterial	16.03 ± 1.16	21.6 ± 2.03	0.016
	Protein processing and modification	Ribosomal protein S12p Asp methylthiotransferase	1.36 ± 0.16	2.01 ± 0.13	0.002
	Protein folding	Protein chaperones	0	15.88 ± 1.53	0
Amino Acids and Derivatives	Branched-chain amino acids	HMG CoA Synthesis	4.45 ± 0.24	5.87 ± 0.43	0.003
Respiration	Electron donating reactions	Respiratory Complex I	11.73 ± 1.51	4.16 ± 0.82	0
	Respiration	Formate hydrogenase	7.65 ± 1.37	2.71 ± 1.34	0.01
	ATP synthases	F0F1-type ATP synthase	11.58 ± 0.83	15.4 ± 1.2	0.004
Carbohydrates	Central carbohydrate metabolism	Pyruvate metabolism I: anaplerotic reactions, PEP	7.58 ± 0.61	4.96 ± 0.46	0
		Ethylmalonyl-CoA pathway of C2 assimilation	1.39 ± 0.49	3.19 ± 0.41	0.01
	Organic acids	Methylcitrate cycle	2.63 ± 0.32	3.53 ± 0.22	0.04
Cofactors, Vitamins, Prosthetic Groups, Pigments	Folate and pterines	Folate Biosynthesis	1.42 ± 0.14	2.08 ± 0.08	0.001
Clustering-based subsystems	Clustering-based subsystems	CTP synthase (EC 6.3.4.2) cluster	5.73 ± 0.36	7.03 ± 0.5	0.048
		Ribonucleotide reductase cluster	0.67 ± 0.15	3.1 ± 0.93	0.02
	Two related proteases	CBSS-257314.1.peg.676	4.54 ± 0.3	6.13 ± 0.63	0.031
	Cytochrome biogenesis	CBSS-196164.1.peg.1690	5.75 ± 0.56	8.26 ± 0.84	0.007
Stress Response	Heat shock	Heat shock *dnaK* gene cluster extended	9.65 ± 0.65	27.01 ± 2.19	0
Miscellaneous	Plant-Prokaryote DOE project	Competence or DNA damage-inducible protein CinA and related protein families	4.54 ± 0.3	6.13 ± 0.63	0.03
		Iron-sulfur cluster assembly	5.78 ± 0.59	8.26 ± 0.83	0.008
Phages, Prophages, Transposable elements, Plasmids	Phages, Prophages	Staphylococcal phi-Mu50B-like prophages	5.75 ± 0.56	8.26 ± 0.83	0.006

knowledge, comparative metagenomics considering the abundance and composition of microbial cytochrome genes under various management practices to improve SOC stocks (i.e. crop retention, crop rotation, agroforestry) and their role in these systems do not currently exist. As phenotypic assays suggest that low H^+/e^- oxidases preferentially outcompete high H^+/e^- oxidases when e^- acceptor is limiting (Potter et al., 1999) or during growth on reduced C substrates (Richardson, 2000), a closer look at whether no tillage systems and/or fertilisation with partially decomposed, reduced OM preferentially select for low H^+/e^- oxidases could be warranted. Due to the inherent difficulties in appropriately deriving *in situ* system properties from complex microbial communities, an initial approach could be validating the phenotypes observed from pure culture assays in sterilised soils under various agricultural practices.

4.2. Importance of DnaK during stress response

In situ, microorganisms must contend with a combination of stressors such as resource bioavailability, osmotic stress, temperature, oxidative stress and pH. Initially microorganisms will respond with specific response mechanisms to environmental stressors; however, if cell homeostasis is not maintained then a number of general adaptation and starvation response mechanisms involving DnaK, GroEL, OxyR, σ^S, σ^{54} and/or σ^B are initiated (Hecker and Volker, 2001; Segal and Ron, 1996). DnaK was first identified as a heat shock protein but its importance during starvation response became apparent over time (van Elsas and van Overbeek, 1993). This protein acts as a chaperone regulating protein folding under stress and plays a particularly important role in ribosome assembly (Alix and Nierhaus, 2003; Vorob'eva, 2004). The maximum growth rate of a microorganism can be limited by the 16S rRNA gene copy number encoded by its genome, which encodes for part of the small ribosomal subunit in bacteria (Bremer, 1975). On average, microorganisms considered to be copiotrophic have 5.5 16S rRNA gene copies genome^{-1} whilst those considered as oligotrophic have 1.4 16S rRNA gene copies genome^{-1} (Klappenbach et al., 2000). The species presented in Supplementary Fig. 1 demonstrate the general trend of copiotrophs having a significantly higher number of 16S rRNA gene copy number, with six copies present in *B. xenovorans* LB400, six copies in *S. coelicolor* A3(2) and two copies in *Can.* S. usitatus Ellin6076 (Markowitz et al., 2012). However using 16S rRNA gene copy number in isolation as a predictor for growth strategy is grossly over-simplistic. For example, while comparisons of 2900 bacterial and archaeal genomes have identified a strong relationship between 16S rRNA gene copy number and phylogeny, variation between relatively closely related Orders does exist, for example an average of six copies in Bacillales compared to three copies in Lactobacillales, both Orders within the Class Bacilli (Angly et al., 2014). This variation between relatively closely related taxa is supported by culture-dependent studies comparing oligotrophic and copiotrophic marine Gamma-Proteobacteria, and also at the Genus level with *Psuedomonas* spp. (Lankiewicz et al., 2016; Semenov, 1991). Furthermore, there is no definitive relationship between rRNA synthesis and decay, growth rate activity or cell maintenance activity (Blazewicz et al., 2013) thus attempts to predict overall cell physiology, such as a copiotrophic growth strategy, from 16S rRNA gene copy number is problematic.

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

Therefore while a high 16S rRNA gene copy number and rapid ribosome assembly due to DnaK/stress response stimuli may contribute to growth strategy, many other factors controlling cellular ribosome content and growth rate must be considered.

Soil C and N stocks appear to correlate with the ratio of functional gene abundance of stress response *versus* cell signalling and transcriptional regulation. Functional genes associated with stress response are higher in C rich organic soil layers, whereas regulation and cell signalling are higher in C poor mineral soil layers (Uroz et al., 2013). Similarly, N fertilisation has a negative effect on the abundance of functional genes associated with regulation and cell signalling (Fierer et al., 2012). It is possible that the dramatic increase in the relative abundance of *dnaK* in agricultural soils (Table 2, $P < 0.001$) is associated with rapid ribosome expression and assembly under nutrient rich conditions. Conversely, it is possible that there is a greater role for strict transcriptional regulation and specific stress responses with σ factors in forest soils where C and N may be less bioavailable (Table 2, $P = 0.013$). However, these are very general observations, and both σ factors and signal transduction in response to stress appear to make up a relatively large proportion of soil microbial genomes due to the heterogeneous nature of the soil environment (Bentley et al., 2002; Chain et al., 2006; Ward et al., 2009).

4.3. Extracellular enzyme activity

In terms of microbiology, enzymology is of primary interest in soil science. Enzymes involved in SOM turnover are diverse in regard to their location (e.g. intracellular enzymes within living cells, intracellular but released extracellularly upon cell death, actively exported extracellular enzymes or membrane-bound enzymes) and their function (e.g. oxidoreductases, hydrolases, lyases and transferases) (Skujins and Burns, 1976; Tabatabai, 1994). Historically there has been a focus on measuring the potential activity of actively exported extracellular enzymes involved in the synergistic decomposition of plant and microbial OM and acquisition of N, P and sulphur (Wallenstein and Weintraub, 2008). An important group of hydrolases involved in the catabolism of polysaccharides found in soil (e.g. cellulose, hemicellulose, pectin and chitin) are the glycosyl hydrolases (GH). The GHs are classified within families according to structural features, evolutionary relationship based on amino acid composition and mechanism of action (Cantarel et al., 2009). While complex, this system is necessary as attempts to classify a GH based on its substrate specificity are misleading because, for example, a single endoglucanase may demonstrate specific hydrolysis of cellulose in addition to non-specific hydrolysis of xylan, xyloglucan, β-glucan and other structures (Henrissat and Davies, 1997).

Ecological coherence at high taxonomic rank has been identified for some GH families, such as GH48 (cellobiohydrolases, endo-β-1,4-glucanases, chitinases) and GH10 (xylanases, cellobiohydrolases) in the Firmicutes and Actinobacteria, with some horizontal gene transfer to Proteobacteria (Collins et al., 2005; Sukharnikov et al., 2012). Other families, such as GH5, demonstrate incredibly diverse substrate specificity and are distributed across many phyla (Collins et al., 2005). While GH families may show ecological coherence, enzyme *function* does not necessarily. For example, a comparative genomics study of 5123 microbial genomes encoding for putative cellulases and/or a putative β-glucosidases noted an interesting dichotomy in the distribution of these genes. Putative cellulases were present in 24% of the genomes, distributed across several phyla but not uniformly present within those phyla (Berlemont and Martiny, 2013). Putative β-glucosidases, on the other hand, were present within 56% of the genomes and were essentially uniform throughout the Actinobacteria and Proteobacteria. Berlemont and Martiny (2013) concluded that while a minority of diverse microorganisms could begin the process of catabolising cellulose, the majority of microorganisms (heavily represented by Actinobacteria and Proteobacteria) could only utilise its breakdown products. Similarly, another comparative genomics study noted a similar relationship with chitinase and β-N-acetylglucosaminidase, whereby a minority of specific microorganisms could begin the process of chitin catabolism while the capacity to utilise its breakdown products were widely distributed across the majority of microorganisms (Zimmerman et al., 2013). Microorganisms that could only opportunistically utilise cellobiose or N-acetylglucosamine were considered 'opportunists' or 'cheaters' as they compete for C and N made bioavailable by 'specialists'. Interestingly, competition for soluble C and N between opportunistic and specialist microorganisms has been considered as an essential control on C and energy turnover (Freilich et al., 2011; Kaiser et al., 2015). To be consistent with the terminology used in Section 3.1 to refer to broad categories of functional diversity, this would imply that cellulases and chitinases demonstrate narrow functional diversity as they are encoded by the genomes of a minority of specific microorganisms, whereas β-glucosidases and β-N-acetylglucosaminidases demonstrate broad functional diversity and are present within a greater majority of microorganisms.

The activity of C degrading enzymes can be explained by functional gene abundance, the taxonomic composition of the microbial community and the quantity of SOM *in situ* (Allison and Vitousek, 2005; Sinsabaugh et al., 2005; Trivedi et al., 2016). Total OC (%) plays a strong role in shaping the relative abundance of GH families *in situ*, as shown by greater richness of GH families involved in cellulose, hemicellulose, lignin and pectin degradation in relatively C rich organic soil layers compared to a greater relative abundance of phenol and protein degradation in C poor mineral soil layers (Cardenas et al., 2015; de Menezes et al., 2015; Uroz et al., 2013). Comparative analysis of a relatively C rich grassland soil showed preferential enrichment of GH families involved in cellobiose and amine degradation while a relatively C poor wheat cropping soil enriched for GH families involved in chitin, β-N-acetylglucosamine and glycoside degradation (Manoharan et al., 2015). Similarly, a comparison of conventional cropping *versus* low input management of a corn-soybean-winter wheat rotational cropping soil showed that where SOC (%) was significantly lower under conventional management, there was a loss in relative abundances of functional genes involved in the degradation of starch, hemicellulose, cellulose, aromatic C compounds and an endochitinase (Xue et al., 2012). In a comparison of conventional tillage *versus* reduced tillage cropping soil, tillage had no effect on the composition of GH families (de Vries et al., 2015). However, significantly higher activities of cellobiohydrolase and β-glucosidase occurred under reduced tillage, where TOC and N were greater (1.6% *versus* 1.1% and 0.2% *versus* 0.1% for C and N, respectively) after 13 years of tillage management (de Vries et al., 2015). Conversely, where TOC (%) does not change between management practices (conventional *versus* growth of N-fixing legumes during a fallow period) the activity of cellobiohydrolase and β-glucosidase does not change (Bossio et al., 2005). In these examples, GHs could be predominantly associated to the potentially copiotrophic phyla Proteobacteria, Bacteroides and Actinobacteria, reflecting their dominance in agricultural systems (Uroz et al., 2013; de Vries et al., 2015; Manoharan et al., 2015). Thus the composition of the microbial community, the relative abundance of functional genes and the activity of C degrading enzymes closely follow SOM quantity and, presumably, availability.

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

4.4. Nutrient uptake affinity

Finally, an important physiological distinction to make revolves around the affinity of nutrient uptake. In energy poor, oligotrophic environments, it is necessary to employ high affinity transporters that can function when substrate is present in low concentrations, whereas mechanisms of transport with a low affinity and high K_m appear to be preferable in energy rich environments. *In vitro* physiological assays indicate that certain species preferentially utilise active transport of nutrients at concentrations between 5 and 500 μg C L^{-1} while the growth of others is more dependent upon diffusion of nutrients at concentrations between 0.5 and 5 mg C L^{-1} (Kuznetsov et al., 1979). Culture-dependent assays measuring cellulose degradation by complex microbial communities frequently show a biphasic pattern, whereby an initial high rate of respiration is followed by a lag period, and then a second period of increased respiration follows (Hu and vanBruggen, 1997; Saito et al., 1990). This is suggestive of a transition from initial copiotrophic activity when nutrient concentrations are high to oligotrophic activity when nutrient concentrations become low. Type I ATP binding cassette (ABC) transporters are an essential mechanism which enable microorganisms to actively transport soluble compounds across membranes with high affinity (Higgins, 2001). They are diverse and highly specific, and the majority are adapted to the transport of a single compound. Interestingly, the ABC transporters include nutrient uptake systems and also export systems that secrete extracellular enzymes, EPS, toxins and waste metabolites (Young and Holland, 1999). The relative abundance of ABC transporters, particularly those involved in nutrient scavenging such as iron-acquisition, is higher in relatively C poor mineral soil layers than organic soil layers (Uroz et al., 2013).

In accordance with the species compared in Supplementary Fig. 1, the genomes of *B. mallei* and *B. pseudomallei* encode for between 77 and 105 ABC transporters (Harland et al., 2007), the genome of *Can*. S. usitatus Ellin6076 encodes for 159 ABC transporters (Ward et al., 2009) and *S. coelicolor* A3(2) encodes for 222 ABC transporters (Bentley et al., 2002). The larger number of ABC transporters are necessary for *Can*. S. usitatus Ellin6076 and *S. coelicolor* A3(2), as it is predicted from their genomes that they can both utilise a relatively greater number of different C substrates than *B. mallei and B. pseudomallei*. Furthermore, it is also predicted that these two species can secrete a wide variety of extracellular enzymes (with both broad and narrow functionality) and in the case of *S. coelicolor* A3(2), secrete a number of antimicrobial compounds (Bentley et al., 2002; Ward et al., 2009). A greater diversity of ABC transporters potentially equip *Can*. S. usitatus Ellin6076 and *S. coelicolor* A3(2) with the capacity to remain active in the energy poor bulk soil, while many *Burkholderia* spp. are likely dependent upon activity within the rhizosphere. Given the genetic differences in these organisms that contribute to preferential growth under different nutrient availability (Kuznetsov et al., 1979) and the biphasic pattern observed in cellulose degradation (Hu and vanBruggen, 1997; Saito et al., 1990) it is probable that land management practices which increase the bioavailability of C will contribute to favouring microorganisms dependent on diffusion for the majority of their C uptake. To the authors' knowledge, in depth analyses considering the affinity for microbial nutrient uptake under various agricultural management practices do not currently exist.

5. Conclusion

While agricultural systems can be quite varied in terms of climate and management, over time many factors in these systems tend to converge, such as losses in soil aggregation, insufficient replacement or oversupply of nutrients and changes in molecular composition of plant biomass input. Agricultural management practices that increase the bioavailability of C and energy consistently result in significant changes to the structure and function of the soil microbial community. As discussed in Section 2, the primary practices which increase C bioavailability are those that disrupt aggregate integrity, change aboveground plant biomass input (either by decreasing input and/or decreasing aboveground species diversity) and oversupply or insufficient replacement of N and P to the system. These practices may have secondary effects on the quality and quantity of bioavailable SOM, such as decreasing the molecular complexity of plant biomass input or reducing the stabilisation of SOM to soil particles by altering soil pH. Altering C bioavailability favours ecological groups of microorganisms with high growth rate, relatively poor CUE and which may favour broad functionality over narrow functionality. This is a consequence of a number of physiological factors, including reduced CUE and increased rate of ATP generation, transcriptional regulation of ribosome assembly and protein biosynthesis, and efficiency of nutrient uptake. Ultimately, the enrichment of these ecological groups in agricultural soils is likely to result in greater rates of SOC mineralisation relative to natural ecosystems.

A number of agricultural management practices to reduce C and energy bioavailability and improve SOC stocks have been developed, including no tillage, conversion from cropping to pasture, crop rotation, agroforestry and fertilisation with partially decomposed or composted OM. However, many of these studies do not consider the causative mechanisms for the improvements in SOC, which are driven at the cellular level by a dynamic microbial community. We consider the most effective means toward the restoration of stabilised, sequestered SOC stocks should be through targeted manipulation of the soil microbial community composition to favour functionally diverse, high CUE over functionally redundant, low CUE communities whilst maintaining agricultural productivity. As described above there is great potential for this, however a definitive role, if any, of various physiological properties on overall ecosystem properties and how management practices can influence both must be confirmed through future research. For example:

- The role of low-O_2 affinity cytochromes and low-affinity nutrient uptake systems in determining rates of SOC mineralisation, dependent on practices which affect physical soil aggregate integrity and/or increased redox potential and O_2 availability.
- The degree to which application of alternative e^- acceptors to O_2, such as nitrate, may favour low CUE copiotrophic heterotrophs that express low-affinity cytochromes, such as NAR.
- The response of metabolic pathways to various forms of N (organic such as urea and amino acids, or inorganic such as nitrate and ammonium) and various forms of C (such as organic acids, lipids, tannins) and whether fertilisation practices can be improved by redirecting matter and energy flow through specific metabolic pathways associated with high CUE.
- The degree to which single (and recurring) perturbation events in such anthropogenic systems affect microbial stress responses, and whether this has an effect on the CUE of the system.
- Quantification of how the diversity and relative complexity of input C and N chemical structures can enrich functionally diverse microbial communities capable of decomposing a wide range of chemical structures (hemicelluloses, lignin, chitin, phenolics, etc.) and how this may affect the CUE of the system.
- Determining a potential minimum threshold for aboveground plant species diversity (of specific species that preferentially allocate C and N to diverse chemical structures) and whether

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

this can improve CUE of the system through increases in the diversity of soil C and N chemical structures.
- To determine whether *in situ* inoculation of high CUE, functionally diverse microbial species of interest to soils of low energy and C bioavailability can improve system properties, such as CUE.

There is much scope for improving multi-disciplinary approaches between agronomy, soil microbiology and statistics, for example:

- Phylogenetic comparative methods to test the statistical validity of applying ecological frameworks to microbial functions, such as the copiotroph-oligotroph or competitor-stress tolerator-ruderal frameworks, should be considered as increasing numbers of annotated soil microbial genomes become more readily available.
- To address questions of species/function composition and H′, highly specific and semi-quantitative next generation sequencing, microarrays and proteomics techniques should be adopted in lieu of classically applied non-specific fingerprinting techniques, such as phospholipid fatty acid analysis and restriction fragment length polymorphism.
- To improve the statistical validity of modelling geochemical processes in relation to quantified broad/narrow functions, it will be necessary to consider what is occurring temporally across a number of the following scales: a) relative abundance of genes at the DNA level; b) differential expression at the RNA level; c) enzymatic activity and turnover rates at the protein level; and d) synergistic interactions between enzymatic reactions which carry out the geochemical process being measured.
- The relative importance of microbial ecology and functionality in explaining observed variability in geochemical processes, such as increases or decreases in SOC stocks, should be modelled appropriately in order to improve upon existing predictive methods.
- Both spatial and temporal scales should be considered within an ecosystem that exhibits high spatial heterogeneity and is influenced by seasonal variability.

Ideally, an improved multi-disciplinary approach will result in a greater understanding of the regulation of biogeochemical processes and subsequently lead to improvements in the sustainability of agricultural systems.

Acknowledgements

The authors wish to thank Marc Cirera for preparing the presented illustrations, and the Australian Commonwealth Department of Agriculture Farming and Futures Filling the Research Gap for funding.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.04.010.

References

Adu, J.K., Oades, J.M., 1978. Physical factors influencing decomposition of organic materials in soil aggregates. Soil Biology and Biochemistry 10, 109–115.
Alix, J.H., Nierhaus, K.H., 2003. DnaK-facilitated ribosome assembly in Escherichia coli revisited. RNA-a Publication of the RNA Society 9, 787–793.
Allen, D.E., Pringle, M.J., Bray, S., Hall, T.J., O'Reagain, P.O., Phelps, D., Cobon, D.H., Bloesch, P.M., Dalal, R.C., 2013. What determines soil organic carbon stocks in the grazing lands of north-eastern Australia? Soil Research 51, 695–706.
Allison, S.D., Martiny, J.B.H., 2008. Resistance, resilience, and redundancy in microbial communities. Proceedings of the National Academy of Sciences of the United States of America 105, 11512–11519.
Allison, S.D., Vitousek, P.M., 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. Soil Biology & Biochemistry 37, 937–944.
Amy, P.S., Morita, R.Y., 1983. Starvation-survival patterns of 16 freshly isolated open-ocean bacteria. Applied and Environmental Microbiology 45, 1109–1115.
Anderson, J.P.E., Domsch, K.H., 1980. Quantities of plant nutrients in the microbial biomass of selected soils. Soil Science 130 (4), 211–216.
Angers, D.A., Recous, S., Aita, C., 1997. Fate of carbon and nitrogen in water-stable aggregates during decomposition of $^{13}C^{15}N$-labelled wheat straw in situ. European Journal of Soil Science 48, 295–300.
Angly, F.E., Dennis, P.G., Skarshewski, A., Vanwonterghem, I., Hugenholtz, P., Tyson, G.W., 2014. CopyRighter: a rapid tool for improving the accuracy of microbial community profiles through lineage-specific gene copy number correction. Microbiome 2, 11.
Baani, M., Liesack, W., 2008. Two isozymes of particulate methane monooxygenase with different methane oxidation kinetics are found in Methylocystis sp. strain SC2. Proceeds of the National Academy of Science of the United States of America Journal 105 (29), 10203–10208.
Badgery, W.B., Simmons, A.T., Murphy, B.M., Rawson, A., Andersson, K.O., Lonergan, V.E., van de Ven, R., 2013. Relationship between environmental and land-use variables on soil carbon levels at the regional scale in central New South Wales, Australia. Soil Research 51, 645–656.
Baldock, J.A., Oades, J.M., Vassallo, A.M., Wilson, M.A., 1990. Solid state CP/MAS ^{13}C NMR analysis of particle size and density fractions of soil incubate with uniformly labelled ^{13}C-glucose. Australian Journal of Soil Research 28, 193–212.
Baldock, J.A., Masiello, C.A., Gelinas, Y., Hedges, J.I., 2004. Cycling and composition of organic matter in terrestrial and marine ecosystems. Marine Chemistry 92, 39–64.
Baldock, J.A., Oades, J.M., Nelson, P.N., Skene, T.M., Golchin, A., Clarke, P., 1997. Assessing the extent of decomposition of natural organic materials using solid-state C-13 NMR spectroscopy. Australian Journal of Soil Research 35, 1061–1083.
Baldock, J.A., Sanderman, J., Macdonald, L.M., Puccini, A., Hawke, B., Szarvas, S., McGowan, J., 2013. Quantifying the allocation of soil organic carbon to biologically significant fractions. Soil Research 51, 561–576.
Baldock, J.A., Skjemstad, J.O., 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. Organic Geochemistry 31, 697–710.
Balesdent, J., Wagner, G.H., Mariotti, A., 1988. Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. Soil Science of America Journal 52, 118–124.
Banu, N.A., Singh, B., Copeland, L., 2004. Soil microbial biomass and microbial biodiversity in some soils from New South Wales, Australia. Australian Journal of Soil Research 42, 777–782.
Barron, P.F., Wilson, M.A., Stephens, J.F., Cornell, B.A., Tate, K.R., 1980. Cross-polarization ^{13}C NMR spectroscopy of whole soils. Nature 286 (7), 585–587.
Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W.X., Coleman, D.C., Crossley, D.A., 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecological Monographs 62, 569–591.
Beijerinck, M., 1888. Die bacterien der Papilionaceen-Knöllchen. Botanische Zeitung 46, 725–735.
Beijerinck, M., 1895. Über *Spirillum desulfuricans* als Ursache von sulfat-reduktion. Zentralblatt für Bakteriologie, Parasitenkunde Infektionskrankheiten und Hygiene 1, 104–114.
Bejarano, M., Crosby, M.M., Parra, V., Etchevers, J.D., Campo, J., 2014. Precipitation regime and nitrogen addition effects on leaf litter decomposition in tropical dry forests. Biotropica 46, 415–424.
Bender, S.F., Wagg, C., van der Heijden, M.G.A., 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends in Ecology & Evolution 31, 440–452.
Bentley, S.D., Chater, K.F., Cerdeno-Tarraga, A.M., Challis, G.L., Thomson, N.R., James, K.D., Harris, D.E., Quail, M.A., Kieser, H., Harper, D., Bateman, A., Brown, S., Chandra, G., Chen, C.W., Collins, M., Cronin, A., Fraser, A., Goble, A., Hidalgo, J., Hornsby, T., Howarth, S., Huang, C.H., Kieser, T., Larke, L., Murphy, L., Oliver, K., O'Neil, S., Rabbinowitsch, E., Rajandream, M.A., Rutherford, K., Rutter, S., Seeger, K., Saunders, D., Sharp, S., Squares, R., Squares, S., Taylor, K., Warren, T., Wietzorrek, A., Woodward, J., Barrell, B.G., Parkhill, J., Hopwood, D.A., 2002. Complete genome sequence of the model actinomycete *Streptomyces coelicolor* A3(2). Nature 417, 141–147.
Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Reviews 5, 1–25.
Berlemont, R., Martiny, A.C., 2013. Phylogenetic distribution of potential cellulases in bacteria. Applied and Environmental Microbiology 79, 1545–1554.
Bertrand, J.C., Bonin, P., Caumette, P., Gattuso, J.P., Grégori, G., Guyoneaud, E., Le Roux, X., Matheron, R., Poly, F., 2011. Biogeochemical cycles. In: Environmental Microbiology: Fundamentals and Applications. Springer, New York, NY, USA.
Blagodatsky, S.A., Richter, O., 1998. Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity state of microorganisms. Soil Biology and Biochemistry 30, 1743–1755.
Blazewicz, S.J., Barnard, R.L., Daly, R.A., Firestone, M.K., 2013. Evaluating rRNA as an indicator of microbial activity in environmental communities: limitations and uses. ISME Journal 7, 2061–2068.

Borisov, V.B., Gennis, R.B., Hemp, J., Verkhovsky, M.I., 2011. The cytochrome bd respiratory oxygen reductases. Biochimica Et Biophysica Acta-Bioenergetics 1807, 1398–1413.
Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. Soil Biology and Biochemistry 31, 1889–1891.
Bossio, D.A., Girvan, M.S., Verchot, L., Bullimore, J., Borelli, T., Albrecht, A., Scow, K.M., Ball, A.S., Pretty, J.N., Osborn, A.M., 2005. Soil microbial community response to land use change in an agricultural landscape of western Kenya. Microbial Ecology 49, 50–62.
Bremer, H., 1975. Parameters affecting rate of synthesis of ribosomes and RNA-polymerase in bacteria. Journal of Theoretical Biology 53, 115–124.
Brochier-Armanet, C., Talla, E., Gribaldo, S., 2009. The multiple evolutionary histories of dioxygen reductases: implications for the origin and evolution of aerobic respiration. Molecular Biology and Evolution 26, 285–297.
Cai, Y., Zheng, Y., Bodelier, P.L.E., Conrad, R., Jia, Z., 2016. Conventional methanotrophs are responsible for atmospheric methane oxidation in paddy soils. Nature Communications 7, 11728.
Caldon, C.E., March, P.E., 2003. Function of the universally conserved bacterial GTPases. Current Opinion in Microbiology 6, 135–139.
Calhoun, M.W., Oden, K.L., Gennis, R.B., Demattos, M.J.T., Neijssel, O.M., 1993. Energetic efficiency of *Escherichia coli* - effects of mutations in components of the aerobic respiratory-chain. Journal of Bacteriology 175, 3020–3025.
Campbell, C.A., Zentner, R.P., Liang, B.C., Roloff, G., Gregorich, E.C., Blomert, B., 2000. Organic C accumulation in soil over 30 years in semiarid southwestern Saskatchewan - effect of crop rotations and fertilizers. Canadian Journal of Soil Science 80, 179–192.
Cantarel, B.L., Coutinho, P.M., Rancurel, C., Bernard, T., Lombard, V., Henrissat, B., 2009. The Carbohydrate-Active EnZymes database (CAZy): an expert resource for Glycogenomics. Nucleic Acids Research 37, D233–D238.
Capaldi, R.A., 1990. Structure and assembly of cytochrome-C-oxidase. Archives of Biochemistry and Biophysics 280, 252–262.
Cardenas, E., Kranabetter, J.M., Hope, G., Maas, K.R., Hallam, S., Mohn, W.W., 2015. Forest harvesting reduces the soil metagenomic potential for biomass decomposition. ISME Journal 9, 2465–2476.
Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81, 2359–2365.
Carson, J.K., Gonzalez-Quiñones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B., 2010. Low pore connectivity increases bacterial diversity in soil. Applied and Environmental Microbiology 76 (12), 3936–3942.
Chain, P.S.G., Denef, V.J., Konstantinidis, K.T., Vergez, L.M., Agullo, L., Reyes, V.L., Hauser, L., Cordova, M., Gomez, L., Gonzalez, M., Land, M., Lao, V., Larimer, F., Lipuma, J.J., Mahenthiralingam, E., Malfatti, S.A., Marx, C.J., Parnell, J.J., Ramette, A., Richardson, P., Seeger, M., Smith, D., Spilker, T., Sul, W.J., Tsoi, T.V., Ulrich, L.E., Zhulin, I.B., Tiedje, J.M., 2006. *Burkholderia xenovorans* LB400 harbors a multi-replicon, 9.73-Mbp genome shaped for versatility. Proceedings of the National Academy of Sciences of the United States of America 103, 15280–15287.
Chapman, S.J., Gray, T.R.G., 1986. Importance of cryptic growth, yield factors and maintenance energy in models of microbial growth in soil. Soil Biology and Biochemistry 18 (1), 1–4.
Chenu, C., Plante, A.F., 2006. Clay-sized organo-mineral complexes in a cultivation chronosequence: revisiting the concept of the 'primary organo-mineral complex'. European Journal of Soil Science 57, 596–607.
Chotte, J.L., Ladd, L.N., Amato, M., 1998. Sites of microbial assimilation, and turnover of soluble and particulate ^{14}C-labelled substrates decomposing in a clay soil. Soil Biology and Biochemistry 30 (2), 205–218.
Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quere, C., Myneni, R.B., Piao, S., Thornton, P., 2013. Carbon and other biogeochemical cycles. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Coleman, K., Jenkinson, D., 1996. RothC-26.3-A Model for the Turnover of Carbon in Soil. Springer, New York, NY, USA.
Collins, T., Gerday, C., Feller, G., 2005. Xylanases, xylanase families and extremophilic xylanases. FEMS Microbiology Reviews 29, 3–23.
Conant, R.T., Paustian, K., Elliott, E.T., 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11, 343–355.
Constancias, F., Terrat, S., Saby, N.P.A., Horrigue, W., Villerd, J., Guillemin, J.P., Biju-Duval, L., Nowak, V., Dequiedt, S., Ranjard, L., Prevost-Boure, N.C., 2015. Mapping and determinism of soil microbial community distribution across an agricultural landscape. Microbiology Open 4, 505–517.
Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Global Change Biology 19, 988–995.
Craine, J.M., Morrow, C., Fierer, N., 2007. Microbial nitrogen limitation increases decomposition. Ecology 88, 2105–2113.
Cusack, D.F., Silver, W.L., Torn, M.S., McDowell, W.H., 2011. Effects of nitrogen additions on above- and belowground carbon dynamics in two tropical forests. Biogeochemistry 104, 203–225.
Cusack, D.F., Torn, M.S., McDowell, W.H., Silver, W.L., 2010. The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. Global Change Biology 16, 2555–2572.
Dalal, R.C., 1998. Soil microbial biomass - what do the numbers really mean? Australian Journal of Experimental Agriculture 38, 649–665.
Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7, 10541.
de Menezes, A.B., Prendergast-Miller, M.T., Poonpatana, P., Farrell, M., Bissett, A., Macdonald, L.M., Toscas, P., Richardson, A.E., Thrall, P.H., 2015. C/N ratio drives soil actinobacterial cellobiohydrolase gene diversity. Applied and Environmental Microbiology 81, 3016–3028.
de Vries, M., Scholer, A., Ertl, J., Xu, Z.F., Schloter, M., 2015. Metagenomic analyses reveal no differences in genes involved in cellulose degradation under different tillage treatments. FEMS Microbiology Ecology 91.
Diaz, S., Fargione, J., Stuart Chapin III, F., Tilman, D., 2006. Biodiversity loss threatens human well-being. PloS Biology 4 (8), e277.
Don, A., Schumacher, J., Freibauer, A., 2011. Impact of tropical land-use change on soil organic carbon stocks - a meta-analysis. Global Change Biology 17, 1658–1670.
Drinkwater, L.E., Wagoner, P., Sarrantonio, M., 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature 396, 262–265.
Dunfield, P.F., Yuryev, A., Senin, P., Smirnova, A.V., Stott, M.B., Hou, S.B., Ly, B., Saw, J.H., Zhou, Z.M., Ren, Y., Wang, J.M., Mountain, B.W., Crowe, M.A., Weatherby, T.M., Bodelier, P.L.E., Liesack, W., Feng, L., Wang, L., Alam, M., 2007. Methane oxidation by an extremely acidophilic bacterium of the phylum Verrucomicrobia. Nature 450, 879. U818.
Dungait, J.A., Hopkins, D.W., Gregory, A.S., Whitmore, A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. Global Change Biology 18, 1781–1796.
Edwards, A.P., Bremner, J.M., 1967. Microaggregates in soils. Journal of Soil Science 18, 64–73.
FAO, 2015. Chapter 5: drivers of global soil changes. In: Status of the World's Soil Resources (SWSR). Food and Agriculture Organization of the United Nations, Rome, Italy.
Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. Ecology 88, 1354–1364.
Fierer, N., Ladau, J., Clemente, J.C., Leff, J.W., Owens, S.M., Pollard, K.S., Knight, R., Gilbert, J.A., McCulley, R.L., 2013. Reconstructing the microbial diversity and function of pre-agricultural tallgrass prairie soils in the United States. Science 342, 621–624.
Fierer, N., Lauber, C.L., Ramirez, K.S., Zaneveld, J., Bradford, M.A., Knight, R., 2012. Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. ISME Journal 6, 1007–1017.
Finn, D., Page, K., Catton, K., Strounina, E., Kienzle, M., Robertson, F., Armstrong, R., Dalal, R., 2015. Effect of added nitrogen on plant litter decomposition depends on initial soil carbon and nitrogen stoichiometry. Soil Biology & Biochemistry 91, 160–168.
Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M., Pitchford, J.W., Programme, N.S.B., 2005. Biodiversity and ecosystem function in soil. Functional Ecology 19, 369–377.
Flemming, H.C., Wingender, J., 2010. The biofilm matrix. Nature Reviews Microbiology 8, 623–633.
Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Trautman Richers, B., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12, 22–33.
Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biological Reviews 63, 433–462.
Fogal, S., Beneventi, E., Cendron, L., Bergantino, E., 2015. Structural basis for double cofactor specificity in a new formate dehydrogenase from the acidobacterium *Granulicella mallensis* MP5ACTX8. Applied Microbiology and Biotechnology 99, 9541–9554.
Foster, R.C., 1988. Microenvironments of soil microorganisms. Biology and Fertility of Soils 6 (3), 189–203.
Freilich, S., Zarecki, R., Eilam, O., Segal, E.S., Henry, C.S., Kupiec, M., Gophna, U., Sharan, R., Ruppin, E., 2011. Competitive and cooperative metabolic interactions in bacterial communities. Nature Communications 2.
Frenk, S., Dag, A., Yermiyahu, U., Zipori, I., Hadar, Y., Minz, D., 2015. Seasonal effect and anthropogenic impact on the composition of the active bacterial community in Mediterranean orchard soil. FEMS Microbiology Ecology 91.
Frey, S.D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B.A., Crow, S., Goodale, C.L., Grandy, A.S., Finzi, A., Kramer, M.G., Lajtha, K., LeMoine, J., Martin, M., McDowell, W.H., Minocha, R., Sadowsky, J.J., Templer, P.H., Wickings, K., 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochemistry 121, 305–316.
Frey, S.D., Gupta, V.V.S.R., Elliot, E.T., Paustian, K., 2001. Protozoan grazing affects estimates of carbon utilization efficiency of the soil microbial community. Soil Biology and Biochemistry 33, 1759–1786.
Friedrich, T., Scheide, D., 2000. The respiratory complex I of bacteria, archaea and eukarya and its module common with membrane-bound multisubunit hydrogenases. FEBS Letters 479, 1–5.
Gebhart, D.L., Johnson, H.B., Mayeux, H.S., Polley, H.W., 1994. The CRP increases soil organic carbon. Journal of Soil and Water Conservation 49, 488–492.
Geisseler, D., Scow, K.M., 2014. Long-term effects of mineral fertilizers on soil

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

microorganisms - a review. Soil Biology & Biochemistry 75, 54–63.
Girvan, M.S., Campbell, C.D., Killham, K., Prosser, J.I., Glover, L.A., 2005. Bacterial diversity promotes community stability and functional resilience after perturbation. Environmental Microbiology 7, 301–313.
Gleixner, G., 2013. Soil organic matter dynamics: a biological perspective derived from the use of compound-specific isotopes studies. Ecological Research 28, 683–695.
Golchin, A., Oades, J.M., Skjemstad, J.O., Clarke, P., 1994. Soil structure and carbon cycling. Australian Journal of Soil Research 32, 1043–1068.
Goldfarb, K.C., Karaoz, U., Hanson, C.A., Santee, C.A., Bradford, M.A., Treseder, K.K., Wallenstein, M.D., Brodie, E.L., 2011. Differential growth responses of soil bacterial taxa to carbon substrates of varying chemical recalcitrance. Frontiers in Microbiology 2.
Grandy, A.S., Neff, J.C., 2008. Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. Science of The Total Environment 404, 297–307.
Grandy, A.S., Salam, D.S., Wickings, K., McDaniel, M.D., Culman, S.W., Snapp, S.S., 2013. Soil respiration and litter decomposition responses to nitrogen fertilization rate in no-till corn systems. Agriculture Ecosystems & Environment 179, 35–40.
Griffiths, B.S., Ritz, K., Bardgett, R.D., Cook, R., Christensen, S., Ekelund, F., Sorensen, S.J., Baath, E., Bloem, J., de Ruiter, P.C., Dolfing, J., Nicolardot, B., 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: an examination of the biodiversity-ecosystem function relationship. Oikos 90, 279–294.
Grime, J., Pierce, S., 2012. The Evolutionary Strategies that Shape Ecosystems. Wiley-Blackwell, Hoboken, NJ, USA.
Gupta, V.V.S.R., Germida, J.J., 2015. Soil aggregation: influence on microbial biomass and implications for biological processes. Soil Biology and Biochemistry 80, A3–A9.
Haney, R.L., Franzluebbers, A.J., Hons, F.M., Hossner, L.R., Zuberer, D.A., 2001. Molar concentration of K2SO4 and soil pH affect estimation of extractable C with chloroform fumigation-extraction. Soil Biology and Biochemistry 33, 1501–1507.
Harland, D.N., Dassa, E., Titball, R.W., Brown, K.A., Atkins, H.S., 2007. ATP-binding cassette systems in *Burkholderia pseudomallei* and *Burkholderia mallei*. BMC Genomics 8, 83.
Harold, F.M., 1972. Conservation and transformation of energy by bacterial membranes. Bacteriological Reviews 36, 172.
Hartmann, A., Rothballer, M., Schmid, M., 2008. Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant and Soil 312, 7–14.
Hartmann, M., Frey, B., Mayer, J., Mader, P., Widmer, F., 2015. Distinct soil microbial diversity under long-term organic and conventional farming. ISME Journal 9, 1177–1194.
Hassink, J., 1997. The capacity of soils to preserve organic C and N by their association with clay and silt particles. Plant and Soil 191, 77–87.
Haynes, R.J., 1999. Labile organic matter fractions and aggregate stability under short-term, grass-based leys. Soil Biology and Biochemistry 31, 1821–1830.
Hecker, M., Volker, U., 2001. General stress response of *Bacillus subtilis* and other bacteria. Advances in Microbial Physiology 44, 35–91.
Helmann, J.D., Chamberlin, M.J., 1988. Structure and function of bacterial sigma factors. Annual Review of Biochemistry 57, 839–872.
Henrissat, B., Davies, G., 1997. Structural and sequence-based classification of glycoside hydrolases. Current Opinion in Structural Biology 7, 637–644.
Higgins, C.F., 2001. ABC transporters: physiology, structure and mechanism - an overview. Research in Microbiology 152, 205–210.
Ho, A., Kerckhof, F.M., Luke, C., Reim, A., Krause, S., Boon, N., Bodelier, P.L., 2013. Conceptualizing functional traits and ecological characteristics of methane-oxidizing bacteria as life strategies. Environmental Microbiology Reports 5, 335–345.
Hobbie, S.E., 2005. Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems 8, 644–656.
Hu, S., vanBruggen, A.H.C., 1997. Microbial dynamics associated with multiphasic decomposition of C-14-labeled cellulose in soil. Microbial Ecology 33, 134–143.
Hungate, R.E., 1966. The Rumen and its Microbes. Academic Press Inc., New York, NY, USA.
Hutchinson, J.J., Campbell, C.A., Desjardins, R.L., 2007. Some perspectives on carbon sequestration in agriculture. Agricultural and Forest Meteorology 142, 288–302.
Jardine, P.M., Weber, N.L., McCarthy, J.F., 1989. Mechanisms of dissolved organic carbon adsorption on soil. Soil Science Society of America Journal 53, 1378–1385.
Jenkinson, D.S., 1990. The turnover of organic carbon and nitrogen in soil. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 329, 361–368.
Jenkinson, D.S., Rayner, J.H., 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Science 123 (5), 298–305.
Jimenez-Bueno, N.G., Valenzuela-Encinas, C., Marsch, R., Ortiz-Gutierrez, D., Verhulst, N., Govaerts, B., Dendooven, L., Navarro-Noya, Y.E., 2016. Bacterial indicator taxa in soils under different long-term agricultural management. Journal of Applied Microbiology 120, 921–933.
Johnston, A.E., 1975. The Woburn market garden experiment, 1942-69. Effects of the treatments on soil pH, soil carbon, nitrogen, phosphorous and potassium. Rothamstead Experimental Research Station Reports 1974, 103–131. Part 2.
Jordan, A., Zavala, L.M., Gil, J., 2010. Effects of mulching on soil physical properties and runoff under semi-arid conditions in Southern Spain. Catena 81, 77–85.
Kaiser, C., Franklin, O., Richter, A., Dieckmann, U., 2015. Social dynamics within decomposer communities lead to nitrogen retention and organic matter build-up in soils. Nature Communications 6.
Kao, W.C., Kleinschroth, T., Nitschke, W., Baymann, F., Neehaul, Y., Hellwig, P., Richers, S., Vonck, J., Bott, M., Hunte, C., 2016. The obligate respiratory supercomplex from Actinobacteria. BBA-Bioenergetics 10, 1705–1714.
Kemmitt, S.J., Lanyon, C.V., Waite, I.S., Wen, Q., Addiscott, T.M., Bird, N.R.A., O'Donnell, A.G., Brookes, P.C., 2008. Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass - a new perspective. Soil Biology & Biochemistry 40, 61–73.
Khan, S.A., Mulvaney, R.L., Ellsworth, T.R., Boast, C.W., 2007. The myth of nitrogen fertilization for soil carbon sequestration. Journal of Environmental Quality 36, 1821–1832.
Killham, K., Amato, M., Ladd, J.N., 1993. Effect of substrate location in soil and soil pore-water regime on carbon turnover. Soil Biology and Biochemistry 25 (1), 57–62.
Kirkby, C.A., Richardson, A.E., Wade, L.J., Batten, G.D., Blanchard, C., Kirkegaard, J.A., 2013. Carbon-nutrient stoichiometry to increase soil carbon sequestration. Soil Biology and Biochemistry 60, 77–86.
Klappenbach, J.A., Dunbar, J.M., Schmidt, T.M., 2000. RRNA operon copy number reflects ecological strategies of bacteria. Applied and Environmental Microbiology 66, 1328–1333.
Kogel-Knabner, I., 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biology and Biochemistry 34, 139–162.
Kogel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., Leinweber, P., 2008. Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde 171, 61–82.
Koumandou, V.L., Kossida, S., 2014. Evolution of the F0F1 ATP synthase complex in light of the patchy distribution of different bioenergetic pathways across prokaryotes. Plos Computational Biology 10.
Koumandou, V.L., Kossida, S., 2015. Evolution of b-type cytochromes in prokaryotes. Febs Journal 282, 123, 123.
Kramer, M.G., Sanderman, J., Chadwick, O.A., Chorover, J., Vitousek, P.M., 2012. Long-term carbon storage through retention of dissolved aromatic acids by reactive particles in soil. Global Change Biology 18, 2594–2605.
Kuznetsov, S.I., Dubinina, G.A., Lapteva, N.A., 1979. Biology of oligotrophic bacteria. Annual Review of Microbiology 33, 377–387.
Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. Soil Biology and Biochemistry 42, 1363–1371.
Kuzyakov, Y., Blagodatskaya, E., 2015. Microbial hotspots and hot moments in soil: concept & review. Soil Biology and Biochemistry 83, 184–199.
Lal, R., 2014. Soil conservation and ecosystem services. Int. Soil Water Conserv. Res. 2 (3), 36–47.
Lal, R., 2008. Carbon sequestration. Philosophical Transactions of the Royal Society B-Biological Sciences 363, 815–830.
Lankiewicz, T.S., Cottrell, M.T., Kirchman, D.L., 2016. Growth rates and rRNA content of four marine bacteria in pure cultures and in the Delaware estuary. ISME Journal 10, 823–832.
Lee, Z.M., Schmidt, T.M., 2014. Bacterial growth efficiency varies in soils under different land management practices. Soil Biology and Biochemistry 69, 282–290.
Loranger-Merciris, G., Barthes, L., Gastine, A., Leadley, P., 2006. Rapid effects of plant species diversity and identity on soil microbial communities in experimental grassland ecosystems. Soil Biology and Biochemistry 38, 2336–2343.
Lorenz, K., Lal, R., 2014. Soil organic carbon sequestration in agroforestry systems. A review. Agronomy for Sustainable Development 34, 443–454.
Manzoni, S., Porporato, A., 2009. Soil carbon and nitrogen mineralization: theory and models across scales. Soil Biology and Biochemistry 41, 1355–1379.
Manzoni, S., Taylor, P., Richter, A., Porporato, A., Ågren, G.I., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytologist 196, 79–91.
Manoharan, L., Kushwaha, S.K., Hedlund, K., Ahrén, D., 2015. Captured metagenomics: large-scale targeting of genes based on 'sequence capture' reveals functional diversity in soils. DNA Research. http://dx.doi.org/10.1093/dnares/dsv026.
Markowitz, V.M., Chen, I.M.A., Palaniappan, K., Chu, K., Szeto, E., Grechkin, Y., Ratner, A., Jacob, B., Huang, J.H., Williams, P., Huntemann, M., Anderson, I., Mavromatis, K., Ivanova, N.N., Kyrpides, N.C., 2012. IMG: the integrated microbial genomes database and comparative analysis system. Nucleic Acids Research 40, D115–D122.
Mathers, N.J., Jalota, R.K., Dalal, R.C., Boyd, S.E., 2007. C-13-NMR analysis of decomposing litter and fine roots in the semi-arid Mulga Lands of southern Queensland. Soil Biology & Biochemistry 39, 993–1006.
Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277, 504–509.
Matzner, E., Borken, W., 2008. Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. European Journal of Soil Science 59, 274–284.
McDaniel, M.D., Grandy, A.S., Tiemann, L.K., Weintraub, M.N., 2014. Crop rotation complexity regulates the decomposition of high and low quality residues. Soil

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

Biology and Biochemistry 78, 243–254.
McLauchlan, K.K., 2006. Effects of soil texture on soil carbon and nitrogen dynamics after cessation of agriculture. Geoderma 136, 289–299.
Mendes, L.W., Tsai, S.M., Navarrete, A.A., de Hollander, M., van Veen, J.A., Kuramae, E.E., 2015. Soil-borne microbiome: linking diversity to function. Microbial Ecology 70, 255–265.
Meyer, D.J., Jones, C.W., 1973. Distribution of cytochromes in bacteria - relationship to general physiology. International Journal of Systematic Bacteriology 23, 459–467.
Mitchell, P., 1961. Coupling of phosphorylation to electron and hydrogen transfer by a chemi-osmotic type of mechanism. Nature 191, 144–148.
Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. Ecological Monographs 76, 151–174.
Morita, R.Y., 1993. Bioavailability of energy and the starvation state. In: Starvation in Bacteria. Springer, New York, NY, USA.
Morris, R.L., Schmidt, T.M., 2013. Shallow breathing: bacterial life at low oxygen. Nature Reviews: Microbiology 11, 205–212.
Mouginot, C., Kawamura, R., Matulich, K.L., Berlemont, R., Allison, S.D., Amend, A.S., Martiny, A.C., 2014. Elemental stoichiometry of fungi and bacteria strains from grassland leaf litter. Soil Biology and Biochemistry 76, 278–285.
Muller, A.K., Westergaard, K., Christensen, S., Sorensen, S.J., 2002. The diversity and function of soil microbial communities exposed to different disturbances. Microbial Ecology 44, 49–58.
Mulumba, L.N., Lal, R., 2008. Mulching effects on selected soil physical properties. Soil & Tillage Research 98, 106–111.
Navarrete, A.A., Venturini, A.M., Meyer, K.M., Klein, A.M., Tiedje, J.M., Bohannan, B.J.M., Nusslein, K., Tsai, S.M., Rodrigues, J.L.M., 2015. Differential response of Acidobacteria subgroups to forest-to-pasture conversion and their biogeographic patterns in the western brazilian Amazon. Frontiers in Microbiology 6, 1443.
Neufeld, J.D., Vohra, J., Dumont, M.G., Lueders, T., Manefield, M., Friedrich, M.W., Murrell, J.C., 2007. DNA stable-isotope probing. Nature Protocols 2, 860–866.
Noor, M.R., Soulimane, T., 2013. Structure of caa(3) cytochrome c oxidase - a nature-made enzyme-substrate complex. Biological Chemistry 394, 579–591.
Odum, E.P., 1968. Energy flow in ecosystems - a historical review. American Zoologist 8, 11–18.
Park, H.J., Kim, D., 2015. Isolation and characterization of humic substances-degrading bacteria from the subarctic Alaska grasslands. Journal of Basic Microbiology 55, 54–61.
Peoples, M.B., Baldock, J.A., 2001. Nitrogen dynamics of pastures: nitrogen fixation inputs, the impact of legumes on soil nitrogen fertility, and the contributions of fixed nitrogen to Australian farming systems. Australian Journal of Experimental Agriculture 41, 327–346.
Philippot, L., Andersson, S.G.E., Battin, T.J., Prosser, J.I., Schimel, J.P., Whitman, W.B., Hallin, S., 2010. The ecological coherence of high bacterial taxonomic ranks. Nature Reviews Microbiology 8, 523–529.
Pimentel, D., Stachow, U., Takacs, D.A., Brubaker, H.W., Dumas, A.R., Meaney, J.J., O'Neil, J.A.S., Onsi, D.E., Corzilius, D.B., 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42, 5.
Pimentel, D., 2000. Soil erosion and the threat to food security and the environment. Ecosystem Health 6, 221–226.
Pineiro, G., Paruelo, J.M., Oesterheld, M., Jobbagy, E.G., 2010. Pathways of grazing effects on soil organic carbon and nitrogen. Rangeland Ecology & Management 63, 109–119.
Potter, L.C., Millington, P., Griffiths, L., Thomas, G.H., Cole, J.A., 1999. Competition between Escherichia coli strains expressing either a periplasmid or a membrane-bound nitrate reductase: does Nap confer a selective advantage during nitrate-limited growth? Biochemical Journal 344, 77–84.
Powlson, D.S., Whitmore, A.P., Goulding, K.W.T., 2011. Soil carbon sequestration to mitigate climate change: a critical re-examination to identify the true and the false. European Journal of Soil Science 62, 42–55.
Prosser, J.I., 2012. Ecosystem processes and interactions in a morass of diversity. FEMS Microbiology Ecology 81, 507–519.
Prosser, J.I., Bohannan, B.J.M., Curtis, T.P., Ellis, R.J., Firestone, M.K., Freckleton, R.P., Green, J.L., Green, L.E., Killham, K., Lennon, J.J., Osborn, A.M., Solan, M., van der Gast, C.J., Young, J.P.W., 2007. Essay - the role of ecological theory in microbial ecology. Nature Reviews Microbiology 5, 384–392.
Prosser, J.I., Nicol, G.W., 2012. Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. Trends in Microbiology 20, 523–531.
Prove, B.G., Loch, R.J., Foley, J.L., Anderson, V.J., Younger, D.R., 1990. Improvements in aggregation and infiltration characteristics of a krasnozem under maize with direct drill and stubble retention. Australian Journal of Soil Research 28, 577–590.
Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. Soil & Tillage Research 43, 131–167.
Richardson, D.J., 2000. Bacterial respiration: a flexible process for a changing environment. Microbiology 146, 551–571.
Robertson, F., Armstrong, R., Partington, D., Perris, R., Oliver, I., Aumann, C., Crawford, D., Rees, D., 2015. Effect of cropping practices on soil organic carbon: evidence from long-term field experiments in Victoria, Australia. Soil Research 53, 636–646.
Rocca, J.D., Hall, E.K., Lennon, J.T., Evans, S.E., Waldrop, M.P., Cotner, J.B., Nemergut, D.R., Graham, E.B., Wallenstein, M.D., 2015. Relationships between protein-encoding gene abundance and corresponding process are commonly assumed yet rarely observed. ISME Journal 9, 1693–1699.
Rousk, J., Baath, E., 2011. Growth of saprotrophic fungi and bacteria in soil. Fems Microbiology Ecology 78, 17–30.
Russell, J.B., Rychlik, J.L., 2001. Factors that alter rumen microbial ecology. Science 292, 1119–1122.
Sala, O.E., Staurt Chapin III, F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.
Saito, M., Wada, H., Takai, Y., 1990. Development of a microbial community on cellulose buried in waterlogged soil. Biology and Fertility of Soils 9, 301–305.
Sandhya, V., Ali, S.Z., 2015. The production of exopolysaccharide by Pseudomonas putida GAP-P45 under various abiotic stress conditions and its role in soil aggregation. Microbiology 84, 512–519.
Sauer, U., Eikmanns, B.J., 2005. The PEP-pyruvate-oxaloacetate node as the switch point for carbon flux distribution in bacteria. FEMS Microbiology Reviews 29, 765–794.
Schimel, J.P., Schaeffer, S.M., 2012. Microbial control over carbon cycling in soil. Frontiers in Microbiology 3, 348.
Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.
Segal, G., Ron, E.Z., 1996. Regulation and organization of the groE and dnaK operons in Eubacteria. FEMS Microbiology Letters 138, 1–10.
Semenov, A.M., 1991. Physiological bases of oligotrophy of microorganisms and the concept of microbial community. Microbial Ecology 22, 239–247.
Shen, S.M., Pruden, G., Jenkinson, D.S., 1984. Mineralization and immobilization of nitrogen in fumigated soil and the measurement of microbial biomass nitrogen. Soil Biology and Biochemistry 13, 493–498.
Singh, B.P., Cowie, A.L., Smernik, R.J., 2012. Biochar carbon stability in a clayey soil as a function of feedstock and pyrolysis temperature. Environmental Science & Technology 46, 11770–11778.
Sinsabaugh, R.L., Carreiro, M.M., Repert, D.A., 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. Biogeochemistry 60, 1–24.
Sinsabaugh, R.L., Gallo, M.E., Lauber, C., Waldrop, M.P., Zak, D.R., 2005. Extracellular enzyme activities and soil organic matter dynamics for northern hardwood forests receiving simulated nitrogen deposition. Biogeochemistry 75, 201–215.
Sinsabaugh, R.L., Manzoni, S., Moorhead, D.L., Richter, A., 2013. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. Ecology Letters 16, 930–939.
Sinsabaugh, R.L., Turner, B.L., Talbot, J.M., Waring, B.G., Powers, J.S., Kuske, C.R., Moorhead, D.L., Follstad Shah, J.J., 2016. Stoichiometry of microbial carbon use efficiency in soils. Ecological Monographs 86 (2), 172–189.
Six, J., Elliott, E.T., Paustian, K., 2000a. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. Soil Biology & Biochemistry 32, 2099–2103.
Six, J., Paustian, K., Elliott, E.T., Combrink, C., 2000b. Soil structure and organic matter I. Distribution of aggregate-size classes and aggregate-associated carbon. Soil Science Society of America Journal 64, 681–689.
Skjemstad, J.O., Feuvre, R.P.L., Prebble, R.E., 1990. Turnover of soil organic matter under pasture as determined by 13C natural abundance. Australian Journal of Soil Research 28, 267–276.
Skjemstad, J.O., Spouncer, L.R., Cowie, B., Swift, R.S., 2004. Calibration of the Rothamsted organic carbon turnover model (RothC ver. 23.3), using measurable soil organic carbon pools. Australian Journal of Soil Research 42, 79–88.
Skujins, J., Burns, R.G., 1976. Extracellular enzymes in soil. CRC Critical Reviews in Microbiology 4, 383–421.
Smith, P., House, J.I., Bustamante, M., Sobocka, J., Harper, R., Pan, G.X., West, P.C., Clark, J.M., Adhya, T., Rumpel, C., Paustian, K., Kuikman, P., Cotrufo, M.F., Elliott, J.A., McDowell, R., Griffiths, R.I., Asakawa, S., Bondeau, A., Jain, A.K., Meersmans, J., Pugh, T.A.M., 2016. Global change pressures on soils from land use and management. Global Change Biology 22, 1008–1028.
Sollins, P., Homann, P.S., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74, 65–105.
Soo, R.M., Skennerton, C.T., Sekiguchi, Y., Imelfort, M., Paech, S.J., Dennis, P.G., Steen, J.A., Parks, D.H., Tyson, G.W., Hugenholtz, P., 2014. An expanded genomic representation of the phylum Cyanobacteria. Genome Biology and Evolution 6 (5), 1031–1045.
Sousa, P.M.F., Silva, S.T.N., Hood, B.L., Charro, N., Carita, J.N., Vaz, F., Penque, D., Conrads, T.P., Melo, A.M.P., 2011. Supramolecular organizations in the aerobic respiratory chain of *Escherichia coli*. Biochimie 93, 418–425.
Souza, R.C., Cantao, M.E., Vasconcelos, A.T.R., Nogueira, M.A., Hungria, M., 2013. Soil metagenomics reveals differences under conventional and no-tillage with crop rotation or succession. Applied Soil Ecology 72, 49–61.
Souza, R.C., Mendes, I.C., Reis-Junior, F.B., Carvalho, F.M., Nogueira, M.A., Vasconcelos, A.T.R., Vicente, V.A., Hungria, M., 2016. Shifts in taxonomic and functional microbial diversity with agriculture: how fragile is the Brazilian Cerrado? BMC Microbiology 16, 42.
Sukharnikov, L.O., Alahuhta, M., Brunecky, R., Upadhyay, A., Himmel, M.E., Lunin, V.V., Zhulin, I.B., 2012. Sequence, structure, and evolution of cellulases in glycoside hydrolase family 48. Journal of Biological Chemistry 287, 41068–41077.

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010

Tabatabai, M.A., 1994. Soil enzymes. Part 2. Microbiological and Biochemical Properties Book Series no. 5. In: Methods of Soil Analysis. Soil Science Society of America, Madison, WI, USA.

Thiet, R.K., Frey, S.D., Six, J., 2006. Do growth yield efficiencies differ between soil microbial communities differing in fungal:bacterial ratios? Reality check and methodological issues. Soil Biology and Biochemistry 38, 837–844.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Tisdall, J.M., Oades, J.M., 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33, 141–163.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173.

Trivedi, P., Delgado-Baquerizo, M., Trivedi, C., Hu, H., Anderson, I.C., Jeffries, T.C., Zhou, J., Singh, B.K., 2016. Microbial regulation of the soil carbon cycle: evidence from gene-enzyme relationships. The ISME Journal 10, 2593–2604.

Uksa, M., Schloter, M., Endesfelder, D., Kublik, S., Engel, M., Kautz, T., Kopke, U., Fischer, D., 2015. Prokaryotes in subsoil-evidence for a strong spatial separation of different phyla by analysing Co-occurrence networks. Frontiers in Microbiology 6, 1269.

Uroz, S., Ioannidis, P., Lengelle, J., Cébron, A., Morin, E., Buée, M., Martin, F., 2013. Functional assays and metagenomic analyses reveals differences between the microbial communities inhabiting the soil horizons of a Norway spruce plantation. PLoS One 8 (2), e55929. http://dx.doi.org/10.1371/journal.pone.0055929.

van Elsas, J.D., van Overbeek, L.S., 1993. Bacterial responses to soil stimuli. In: Starvation in Bacteria. Springer, New York, NY, USA.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass carbon. Soil Biology and Biochemistry 19, 703–707.

Vitousek, P.M., Naylor, R., Crews, T., David, M.B., Drinkwater, L.E., Holland, E., Johnes, P.J., Katzenberger, J., Martinelli, L.A., Matson, P.A., Nziguheba, G., Ojima, D., Palm, C.A., Robertson, G.P., Sanchez, P.A., Townsend, A.R., Zhang, F.S., 2009. Nutrient imbalances in agricultural development. Science 324, 1519–1520.

von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: relevance to functional pools and to stabilization mechanisms. Soil Biology and Biochemistry 39, 2183–2207.

Vorob'eva, L.I., 2004. Stressors, stress reactions, and survival of bacteria: a review. Applied Biochemistry and Microbiology 40, 217–224.

Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the United States of America Journal 111 (14), 5266–5270.

Wallenstein, M.D., Weintraub, M.N., 2008. Emerging tools for measuring and modeling the in situ activity of soil extracellular enzymes. Soil Biology and Biochemistry 40, 2098–2106.

Wang, W.J., Baldock, J.A., Dalal, R.C., Moody, P.W., 2004. Decomposition dynamics of plant materials in relation to nitrogen availability and biochemistry determined by NMR and wet-chemical analysis. Soil Biology and Biochemistry 36, 2045–2058.

Ward, N.L., Challacombe, J.F., Janssen, P.H., Henrissat, B., Coutinho, P.M., Wu, M., Xie, G., Haft, D.H., Sait, M., Badger, J., Barabote, R.D., Bradley, B., Brettin, T.S., Brinkac, L.M., Bruce, D., Creasy, T., Daugherty, S.C., Davidsen, T.M., Deboy, R.T., Detter, J.C., Dodson, R.J., Durkin, A.S., Ganapathy, A., Gwinn-Giglio, M., Han, C.S., Khouri, H., Kiss, H., Kothari, S.P., Madupu, R., Nelson, K.E., Nelson, W.C., Paulsen, I., Penn, K., Ren, Q.H., Rosovitz, M.J., Selengut, J.D., Shrivastava, S., Sullivan, S.A., Tapia, R., Thompson, L.S., Watkins, K.L., Yang, Q., Yu, C.H., Zafar, N., Zhou, L.W., Kuske, C.R., 2009. Three genomes from the phylum Acidobacteria provide insight into the lifestyles of these microorganisms in soils. Applied and Environmental Microbiology 75, 2046–2056.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews of the Cambridge Philosophical Society 67, 321–358.

Wertz, S., Degrange, V., Prosser, J.I., Poly, F., Commeaux, C., Guillaumaud, N., Le Roux, X., 2007. Decline of soil microbial diversity does not influence the resistance and resilience of key soil microbial functional groups following a model disturbance. Environmental Microbiology 9, 2211–2219.

Wessen, E., Hallin, S., Philippot, L., 2010. Differential responses of bacterial and archaeal groups at high taxonomical ranks to soil management. Soil Biology and Biochemistry 42, 1759–1765.

West, T.O., Post, W.M., 2002. Soil organic carbon sequestration rates by tillage and crop rotation: a global data analysis. Soil Science Society of America Journal 66, 1930–1946.

Whiteley, A.S., Thomson, B., Lueders, T., Manefield, M., 2007. RNA stable-isotope probing. Nature Protocols 2, 838–844.

Winogradsky, S., 1887. Über schwefelbakterien. Botanische Zeitung 45, 489–600.

Winogradsky, S., 1890. Sur les organismes de la nitrification. Comptes-Rendus de l'Academie des Sciences, Paris 60, 1013–1016.

Wood, S.A., Almaraz, M., Bradford, M.A., McGuire, K.L., Naeem, S., Neill, C., Palm, C.A., Tully, K.L., Zhou, J., 2015. Farm management, not soil microbial diversity, controls nutrient loss from smallholder tropical agriculture. Frontiers in Microbiology 6, 90.

Xue, K., Wu, L., Deng, Y., He, Z., Nostrand, J.V., Robertson, P.G., Schmidt, T.M., Zhou, J., 2012. Functional gene differences in soil microbial communities from conventional, low-input, and organic farmlands. Applied and Environmental Microbiology 79, 1284–1292.

Young, J., Holland, I.B., 1999. ABC transporters: bacterial exporters-revisited five years on. Biochimica Et Biophysica Acta-Biomembranes 1461, 177–200.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84, 2042–2050.

Zech, W., Guggenberger, G., Schulten, H.R., 1994. Budegts and chemistry of dissolved organic carbon in forest soils - effects of anthropogenic soil acidification. Science of The Total Environment 152, 49–62.

Zechmeister-Boltenstern, S., Keiblinger, K.M., Mooshammer, M., Penuelas, J., Richter, A., Sardans, J., Wanek, W., 2015. The application of ecological stoichiometry to plant-microbial-soil organic matter transformations. Ecological Monographs 85, 133–155.

Zhu, C.S., Delmont, T.O., Vogel, T.M., Bromberg, Y., 2015. Functional basis of microorganism classification. PLoS Computational Biology 11.

Zimmerman, A.E., Martiny, A.C., Allison, S.D., 2013. Microdiversity of extracellular enzyme genes among sequenced prokaryotic genomes. ISME Journal 7, 1187–1199.

Please cite this article in press as: Finn, D., et al., Microbial energy and matter transformation in agricultural soils, Soil Biology & Biochemistry (2017), http://dx.doi.org/10.1016/j.soilbio.2017.04.010