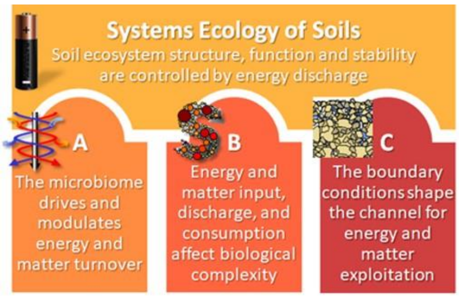


DFG Priority Programme

Deutsche Forschungsgemeinschaft

(SPP 2322) SoilSystems
Systems ecology of soils – energy discharge modulated by microbiome and boundary conditions

SoilSystems in a nutshell

Living microbes need energy delivered by oxidation or organic substrates coupled to reduction of electron acceptors. Soil Systems, their biodiversity and ecosystem services are underpinned by energy flows and storage in form of SOM, bio- and necromass that are subject to the laws of thermodynamics. Yet, energy-based descriptions are largely missing. For the first time, the DFG joint research program *SoilSystems* aims to integrate a thermodynamic description of the soil system in order to gain a systemic view on energy and matter fluxes and their interactions with living and non-living soil components. This will enable to elucidate dynamic biogeochemical processes, boundary constraints and performance limits, and to identify optimally approaches allowing to describe the complex energy-driven soil systems in much simpler terms. Advanced reliable prediction of soil system reactions, e.g. to human impact on global climate and land use will benefit from this research.

OBJECTIVES

Open questions

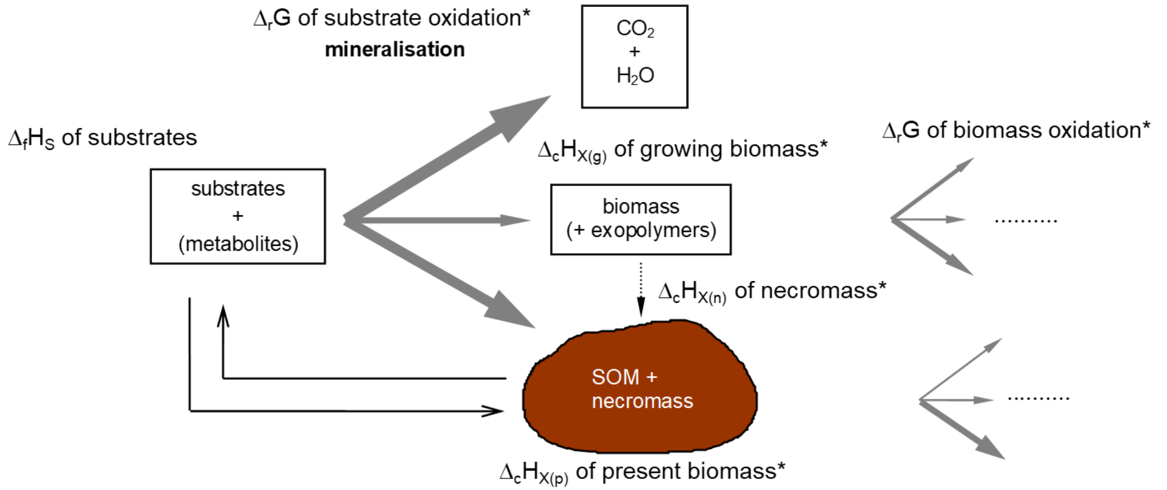
The following questions are addressed by the SoilSystems priority programme:

- How to identify the thermodynamic principles that link carbon and energy use efficiencies to microbial growth and activity dynamics in soil?
- Does the microbiome, its structural and functional diversity and interacting trophic levels on the turnover and storage of SOM control the energy flux?
- Do boundary conditions shape or even define the energy use channel in soil?
- Does a specific substrate and its energy content always result in similar microbial community composition and similar degradation performance in terms of kinetics?
- What causes the C-stabilization (‘entombing effect´) after conversion to microbial necromass in different soil types?

These questions are condensed to three working hypotheses of SoilSystems. The research requires coupling of experiments on detritus decomposition and SOM formation plus turnover facing two major challenges: (i) understanding the combination of soil organisms, their genetic potential, physiological status and interactions, type and access to resources, and the environmental boundaries and constraints recently termed as `soil metaphenome´ (Jansson and Hofmockel, 2018), and (ii) integrating thermodynamic concepts into soil science by linking theories of systems ecology to energy based approaches.

Hypotheses

SoilSystems developed three main hypotheses on the premises that soils are highly complex, open thermodynamic systems and that the soil ecosystem structure, function and stability are controlled by energy discharge and consumption. It may even be argued that soil microbial biomass as well as SOM can be understood as dissipative structures emerging from the energy and matter fluxes (Fig. 1).

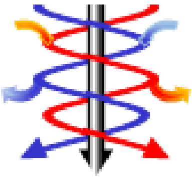


* *specified for different organism groups*

Fig. 1: Experimental concept for linking balances and fluxes of heat, enthalpies (H), Gibbs energies (G) of oxidation reactions, losses, efficiencies to matter turnover mass balances of C, H, O, N, (S, P). (Fig. modified from Kästner et al., 2014)

SoilSystems addresses the research questions by linking energy and matter fluxes to systems ecology (microbial ecology and diversity; connectedness to higher trophic, faunal levels) and the boundary conditions perspective focussing at first on organic matter (organic carbon) transformation in topsoils from agricultural sites, which are ideal objects for application of energy-based concepts to managed soil systems. Research will focus on the high diversity in the composition of carbon and energy sources connected to the development of microbial communities, their structures and maintenance, and finally necromass stabilisation. The energy and carbon use efficiency (EUE and CUE) as key-parameters linked to the energy use principles on all trophic levels vary with input of substrate matter and energy, whereby reports are inconsistent about the role of influencing factors such as substrates' energy content, stoichiometry, and molecular structure, as well as nutrients (Spohn et al., 2016; Takriti et al., 2018). Process based knowledge shall be achieved, whether the microbiome of a soil or its constituents and properties, especially the mineral matrix with their nutrient resources are determining the steady state amounts of biomass and SOM in a system with a given input of energy substrates. The analysis of the energy dissipation and matter fluxes, and the microbial ecology of the system will provide the data basis for the assessment of thermodynamic principles in soil ecology and will enable integrated modelling founded on ecosystem properties and processes. The following three hypotheses (A-C) give the general research objectives of SoilSystems.

Hypothesis A:



"The microbiome modulates ***energy dissipation*** *and matter turnover along various energy use channels."* The microbial carbon turnover activity ('carbon pump') is part of the energy-use-channel and the dominant \`contributor´ to SOM via carbon use and recycling and necromass stabilisation.

Research under this hypothesis will target microbes as energy, organic matter, and nutrient consumers, mass contributors, and \`shapers´ of the soil system within the overall frame set by the boundary conditions (see Hypothesis C). Focus will be laid on trophic networks within the microbiome, i.e. the linkage between microorganisms and fauna that are organized by spatial and temporal arrangement within the soil microhabitat architecture thereby modulating SOM turnover. Integrating soil food webs is thus important to understand and manage the processes of SOM regulation, which has not yet been systematically analysed based on a systems ecology view. Studies under this hypothesis will link the energy content and the input and stoichiometry of plant/detritus-derived substrates to the amount and type of degrader biomass formed as well as degradation kinetics under the respective boundary conditions of a given soil, which was not in the focus of previous research.

Projects shall employ thermodynamic theories of systems ecology on the levels of molecules, organisms, and habitats, resulting in extensive interdisciplinary research. Basic thermodynamic approaches that consider the sum of heat fluxes, enthalpies, and Gibbs reaction energy changes available for work will be analysed in relation to turnover and fractions of SOM. Modern ecological methods such as metabolic footprints, combining biomass and activity of biota as functional trait (Ferris, 2010b; Mulder and Maas, 2017) will be applied. Determined parameters can be used for quantitative thermodynamic predictions of biological growth and turnover (Heijnen, 2013).

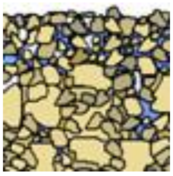
Hypothesis B:

"Energy and matter input, discharge, and consumption in the soil system affect ***biological complexity****"*, i.e. the structural and functional diversity, trophic networks and organization of the soil microbiome.

Research under this hypothesis will address microbial diversity and complexity in soils that are not random or accidental but a result of various factors. Also, the potential energy yield from substrates entering a (micro)habitat determines the functional diversity of soil biota involved in metabolic transformation. Yet, predictions on how microbial complexity and network structures are shaped by, and how this feeds-back on SOM composition and storage, are highly limited and require more systematic understanding of these factors in relation to microhabitat conditions (e.g. presence of electron acceptors, nutrients, activity of water). In line with the maximum power principle (Odum and Odum, 1981), we hypothesize that syntrophic microbial groups, entire communities or trophic networks able to exploit the highest amount of energy from a particular carbon source for growth and respiration will become dominant in comparison to less efficient competitors. The potential energetic yield from a compound presumably gives the link to functional diversity – in the sense that a function is redundantly provided by diverse communities. In case of redundancy energy yield would be apparently independent from community composition. This has implications for resilience research to be tested against disturbance and changes of boundary conditions (Ludwig et al., 2018). Integrating soil food web interactions will enable to understand and also manage processes of SOM regulation and energy cycling. This, however, still awaits systematic research (Fierer, 2017).

Projects shall address the question how the provided substrate with its energy content, the microbial community composition with their functional traits, and their faunal grazers are interlinked and whether trigger values and tipping points exist, beyond which community and/or pathways and fluxes are sustainably altered.

Hypothesis C:



*"The **boundary conditions** and mineral composition shape the channel for energy and matter use."* They constrain the non-equilibrium steady states of living and non-living organic matter in soil.

Research under this hypothesis will focus on the soil mineral composition (parent rock material, secondary minerals) and boundary conditions shaping the energy use channel in soil. Boundary conditions encompass (i) factors of soil formation, such as pedoclimate, (ii) nutrients, (iii) structures (e.g. aggregates) developed upon pedogenesis, and (iv) present physicochemical properties such as pH, redox potential and electron acceptor availability as well as water activity (Mikutta et al., 2009; Turner et al., 2017). These conditions are determinants of the energy channel that can be exploited by the microbiome. Linking functional traits of microbes to mineral composition and boundary conditions and properties of macro- and micro-aggregates (e.g. connectivity, tortuosity and heterogeneity of the 3D pore space) is needed to understand SOM turnover and energy use in the sphere of energy and matter consumption. The resulting composition and spatial arrangement of microhabitats along with the basic principle that self-organization is a feature also of soil systems need to be analysed (Addiscott, 2010; Prigogine and Stengers, 1984).

Studies will investigate the link of functional traits of microbes to SOM turnover and energy use at the scales of macro- and micro-aggregates. Research will give answers to the question in how far boundary conditions are shaping or even driving the energy use channel in soil.

Systems ecology and soil science

The soil system understanding is at its advent and thus needs novel perspectives. A new paradigm was opened with Systems Ecology, targeting an integrated understanding of the biological system in its abiotic environment emphasizing interconnections and organizational structures rather than individual, separated components (Aon et al., 2014; Evans et al., 2013). Changes in external factors (forcing functions) define a further aspect in soil systems research answering the resistance and resilience of the system related to disturbances (e.g. by changing temperatures, moisture status, redox potential, pH, and others) (Göransson et al., 2013; Moyano et al., 2012).

Systems ecology offers up-to-date approaches to unravel the linkages of biotic networks, organism-modulated energy and matter fluxes, related self-regulation processes in soil and abiotic ecosystem components and to identify general underlying principles. Systems ecology relies on both the individual organism and/or compound based community ecology (e.g. metabolic theory) and flux and mass-balance based ecosystem ecology (e.g. system theory) (Jørgensen et al., 2016; Loreau, 2010). Systems ecology approaches are suited to holistically assess matter and energy fluxes and balances and to predict emergent system properties such as SOM storage and turnover. Yet, such approaches were rarely applied to soils (Addiscott, 2010).

Systems ecology is based on (1) hierarchy, (2) thermodynamics, (3) networks, and (4) biogeochemistry (Jørgensen, 2012). Jørgensen et al. (2016) stated that these approaches, each with its own strengths, weaknesses, and perspectives, have often been developed in parallel and further progress arises with their continued integration. They outlined the four approaches:

1. Hierarchy theory—the understanding of the hierarchical structure of ecosystems with its vertical hierarchies and also control hierarchies, forming an interface to the cybernetic processes of the systems (Nielsen, 2015).
2. Thermodynamics—the understanding of the use, need, and transfer of energy by ecosystems, with irreversible, dissipative processes working along imposed gradients (Aoki, 2012). They may serve as indicators of functional state or be subjected to optimization by adaptive and selective processes (Nielsen and Jorgensen, 2013).
3. Network theory—the understanding of the functions and advantages of ecological networks allowing for identification and quantification of interdependence along complex, indirect pathways (Borrett et al., 2014; Patten, 2016).
4. Biogeochemistry—the understanding of the biogeochemical processes in ecosystems with focus on the cycling of matter and of particular (quantitative important) elements such as C and N, respectively (Morowitz and Smith, 2007).

Expedient thermodynamics-based modelling approaches exist, but they need to be related to soil functioning. For example, systems ecology offers up-to-date approaches to unravel the linkages of biotic networks, organism-modulated energy and matter fluxes, related self-regulation processes in soil and abiotic ecosystem components and to identify general underlying principles. Systems ecology relies on both the individual organism and/or compound based community ecology (e.g. metabolic theory) and flux and mass-balance based ecosystem ecology (e.g. system theory) (Jørgensen et al., 2016; Loreau, 2010). Systems ecology approaches are suited to holistically assess matter and energy fluxes and balances and to predict emergent system properties such as SOM storage and turnover. Yet, such approaches were rarely applied to soils (Addiscott, 2010).

- The metabolic theory is organism-based, works bottom-up in order to quantify fluxes and stores of energy and materials within organisms and to predict structural and functional characteristics at multiple levels of organization from individual organisms to ecosystems.
- Systems theory is ecosystem-based, works top-down and quantifies fluxes and stores of energy or materials among functional compartments in order to derive emergent whole-ecosystem properties, i.e. average residence times of carbon and other molecules (Jørgensen et al., 2016).

Researching this experimentally is enabled by top-down approaches, exploiting the new options and novel techniques in life sciences for investigating the `science of the system´ by making use of meta-omics methods (metagenomics, metaproteomics, meta-metabolomics). In complementary bottom-up approaches specific fluxes of organisms, components and energy can be investigated with high spatial and temporal resolution, which approach is boosted by the novel options for low invasive high-resolution methods of visualization and analysis of microscale spatial heterogeneity and to obtain high density data.

The relevance of the combined matter and energy fluxes is reflected in the ecosystem theory with its propositions acc. to Jørgensen (2012):

1. Ecosystems are open systems and require an input of free energy (receiving from environment in which they are embedded).
2. Ecosystems on one hand conserve and on the other hand recycle matter and (most of the) energy.
3. All ecosystem processes are irreversible, produce entropy and consume free energy.
4. If an ecosystem receives more free energy than needed to maintain its functions, the surplus will be applied to move the system further away from thermodynamic equilibrium.
5. As a consequence, ecosystems have emergent system properties.
6. Ecosystems apply three growth forms, i.e. growth of (i) biomass, (ii) network, (iii) information.
7. The carbon based life on Earth, has a characteristic basic biochemistry which all organisms share.
8. Ecosystems are hierarchically organized, forming a complex interactive, self-organizing ecological network.
9. Ecosystems have a high diversity in all levels of the hierarchy.
10. Ecosystems have a buffer capacity toward changes.

COMMON EXPERIMENTAL PLATFORM

Projects shall address at least two of the **SoilSystems hypotheses**. Experiments generally focus on defined **soils**, **substrates** and **incubation conditions** (see further information). At least one of the hypotheses has to be investigated using the common experimental platform. Studies should aim for integrated research on matter and energy flux related to ecology in individual or joint projects.

Soils

A set of soil materials was preselected in order to gain data that are highly coherent and exchangeable between groups. Soils are from well-documented long-term fertilization field experiments. Different sites were selected in order to cover different soil properties, ranging from poorly aggregated sandy soils with low pH and organic carbon (OC) content to well-structured, silt loam soils (providing substantially more microhabitats) with higher pH and OC content. Arable soils were selected, since they are less imprinted by plant cover compared to grassland and forest soils with permanent vegetation and presumably are most sensitive soils with regard to C storage. Arable Cambisol, Retisol and Luvisols are characterized by intensive OC turnover and CO_2 release, and are highly representative for arable soils in temperate regions.

We selected the plots ‘unfertilized’ (‘control’) and ‘organically fertilized’ (with addition of farmyard manure and in certain treatments of mineral fertilizers) in order to have pairs of soils with different SOM content and nutrient status but otherwise largely similar composition and properties. The microbial communities of unfertilized soils will be more dominated by fungi while fertilized soils will be more dominated by bacteria (fungal vs. bacterial energy use channel).

At least one soil (Tab. 1) has to be included in individual projects. Studies using more than one soil also take further soils from the preselected set that covers three 'texture types' and combinations of 'texture types' and 'fertilizer variations', respectively.

Participants of SoilSystems may include additional soil samples from other plots (e.g. with other fertilization management) or sites with different soil composition and properties (e.g. Mollisols). Overall, soils (soil substrates) for investigation should meet the following requirements (such as those proposed in Tab. 1):

- Topsoil from arable soils,
- with different mineral components/content and/or different SOM,
- from long-term field experiments with good data recording on soil use and properties,
- soils with different fertilization history and nutrient content but without one-sided nutrient limitation (e.g. single nutrient enrichment/depletion trial),
- enthalpies and major element composition of SOM contents should be provided.

Tab.1: Topsoil substrates proposed for use in individual studies.

Tex-ture	**Site**	**Trial established** (year)	**Soil group** (Bodentyp)	**Fertilizer treatment**	**Soil properties**	**pH** [b]	**OC** [b] (%)
Sand	Thyrow, Humboldt-Universität Berlin, Germany	1937	Haplic Retisol (Fahlerde)	a) unfertilized b) farmyard manure	aggregation weak, uFC [a] low	4.4	0.3
Sandy Loam	ZOFE, Agroscope, Zurich Reckenholz, Switzerland	1949	Haplic Luvisol (Parabraunerde)	a) unfertilized b) farmyard manure	aggregation moderate, uFC moderate	6.5	0.9
	Dikopshof, Universität Bonn, Germany	1940	Haplic Cambisol (Braunerde)	a) unfertilized b) farmyard manure	aggregation moderate, uFC moderate	6.4	1.2
Silt Loam	QualiAgro, INRA, Orgeval, France	1998	Haplic Luvisol (Parabraunerde)	a) unfertilized b) farmyard manure	aggregation moderate – strong, uFC moderate – high	7.1	1.1

[a] uFC = usable field capacity

[b] data of unfertilized soil plots

Substrates

Soils will be amended with selected substrates of known energy and elemental composition (Tab. 2), which is the basis for the turnover balancing, in selected concentrations. The substrates represent detritus (litter, necromass) and biopolymers (model substrates) of different origin and degradability. Substrates were further selected to represent compounds that require exoenzymatic transformation. Two or more of these substrates, should be used in individual projects. The overall idea of using model substrates is to compare the effect of molecular complexity and element composition vs. energetic properties on turnover of matter and energy. Isotope labelling (^{13}C, ^{14}C) of the proposed substrates is foreseen in order to ensure mass balancing and following metabolic pathways and spatial distribution in soil.

Tab.2: Substrates and selected mixtures thereof for metabolic turnover testing.

Detritus		**Model substrates**		
Plant litter (Maize)	Biogas digestate from plant litter (Maize)	Starch $(C_6H_{10}O_5)_n$	Cellulose $(C_6H_{10}O_5)_n$	Starch-cellulose mixture 50:50
[a] -15.3 kJ g^{-1}	-15.0 kJ g^{-1}	-14.7 kJ g^{-1}	-16.3 kJ g^{-1}	
Fungal necromass [b] $(C_{10}H_{17}O_{4,4}N_1)$	Bacterial necromass [b] $(C_{10}H_{16}O_4N_2)$	Chitin $(C_8H_{13}NO_5)_n$	Peptidoglycane (Murein) $(C_{19}H_{37}N_3O_{14})_n$	Chitin-murein mixture 50:50
-21.5 kJ g^{-1}	-19.8 kJ g^{-1}	-18.8 kJ g^{-1}		

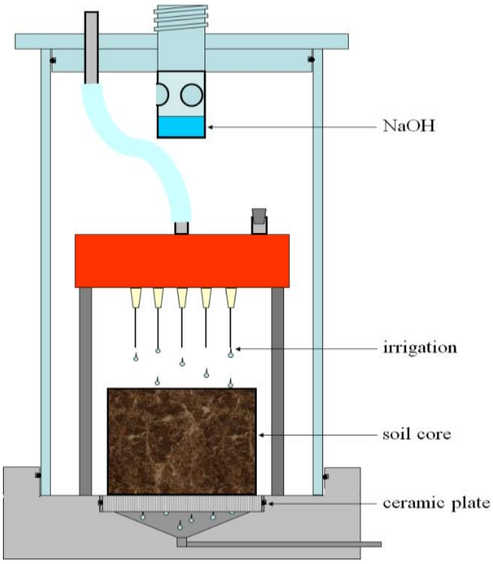
[a] Combustion enthalpies; own data, and for fungal and bacterial necromass derived from Popovic (2019).

[b] Labelled cell wall fragments.

Incubation system

Experiments are preferably conducted in microcosm systems enabling adjustable water tension and full control of ingoing/outgoing compounds and boundary conditions in order to gain mass and energy balances including CO_2 fluxes. For examples see, e.g. Poll et al. (2010), Richter et al. (2019) Calorimetric measurements can be performed in heat-protected systems with sensitive temperature measurements (megacalorimeters/cement calorimeters) or bomb / cement calorimeters (Maskow, 2013). This can be combined with techniques such as barometric process separation (Ingwersen et al., 1999; Ingwersen et al., 2008) or using alternatively a diffusion chamber-based approach (Bollmann et al., 2007). Incubation systems should have the following features:

- Closed systems with defined soil-volume to headspace ratios and the option to detect changes in heat production.
- Complete coverage of C balance (solids, liquids, gas) and options for determination of matter and energy distributions to various products (fluxes).
- Control/adjustment of boundary conditions. Standard conditions: soil moisture at 60% of water holding capacity, temperature (20 °C), O2 saturation (>10%), bulk density 1.2 g/cm³.
- Enable time-resolved (kinetics) and/or spatially highly resolved sampling.



Example for a possible incubation system. Microcosm according to Poll et al. (2010).

Variation of boundary conditions such as temperature, moisture, redox potential and resulting reactions can be used as an experimental approach. Respective details have to be defined by individual projects.

Soil fauna

Microbial grazers shall be investigated in combination with microorganisms (in single or joint projects) in order to study trophic interactions and fluxes in (simple) food webs. In order to keep an experimental focus and manageable complexity for ecosystem modelling this research is focused to the following groups: ***Protozoa and nematodes as major bacterial grazers, and Collembola as dominant soil fungivores***. Limiting experiments on trophic networks to two trophic levels will increase manageability of experiments and facilitate assignment of processes to specific taxa. The interaction strength, i.e. strong versus weak C flow, across trophic connections thereby determines network stability as well as C dynamics (Neutel et al., 2002; Neutel et al., 2007) and can be reliably detected by use of stable isotope labels.

Techniques and options for modelling

Soilsystems will build SoilSystems will build on recent developments in methods that are ideally suited for integrated experimental work on the soil system. This asks for techniques such as:

1. dynamic balances of enthalpy and Gibbs energy during oxidation combined with matter fluxes and modelling (e.g. nano- to megacalorimetry, DSC, thermogravimetry),
2. biomarker analysis (e.g. proteins, aminosugars, membrane compounds and lipids), and improved quantitative stable isotope probing (SIP) techniques for the determination of compound turnover and metabolic pathways,
3. DNA, RNA and protein based (meta-)omics systems biology approaches for assessment of microbial communities including correlation analyses,
4. chemical high resolution analyses for metabolome identification and transformation pathway mapping (e.g. LC-QTOF-MS, FT-ICR-MS, Py-GC-MS),
5. high spatial resolution 3D imaging for soil structure analysis and chemical mapping for visualization of compound fluxes and spatial arrangements like XRT, NanoSIMS, XPS, and (H)SEM.

In order to assess the physiology of microorganisms and for ecological modelling, **determination of energy contents and fluxes** can be performed in different ways, for example by:

1. balancing turnover of isotope (stable/radioactive) labelled C-compounds including heat and CO2 in defined batch setups (Pausch et al., 2016a, 2016b);
2. (nano- and micro)calorimetric analysis of heat production rate from biotic activity (Barros et al., 2007) and/or megacalorimetric determination of total heat balance of micro- to mesocosms (Maskow, 2013);
3. measuring rates of oxygen uptake that are suited to estimate heat production (‘indirect calorimetry’) and, when related to CO2 evolution, provide a real-time measure for biomass related yield coefficients (Hansen et al., 2004; Maskow, 2013);
4. determination of enthalpies, and theoretical Gibbs energy or the nominal oxidation state of carbon (NOSC) in SOM or major constituents and selected key compounds as well as in developing biomass and remaining necromass (LaRowe and Amend, 2016; Sinsabaugh et al., 2016; Trapp et al., 2018);
5. information from ecological stoichiometry on (multiple) resource utilization and carbon use efficiency (CUE) (Geyer et al., 2019; Manzoni et al., 2018; Sinsabaugh et al., 2016; Zechmeister-Boltenstern et al., 2015) and from audit of small molecules (Addiscott, 1995).

Besides numerous expedient SOM models, various thermodynamics and flux related modelling approaches can serve to integrate thermodynamic principles into soil systems theory. Models may be based on, e.g.

1. throughflow analysis such as the Thermodynamics-based Metabolic Flux Analysis (TMFA; Henry et al., 2007), Thermodynamic Feasibility Analysis (TFA; Maskow and Paufler, 2015; Vojinović and Von Stockar, 2009), Flux-Force relations (Beard and Qian, 2007; Noor et al., 2013) and the Ecological Network Analysis (ENA; Matamba et al., 2009);
2. Dynamic Energy Budget (DEB) models such as the Metabolic Theory (Aoki, 2012; Kooijman et al., 2008; Schramski et al., 2015);
3. individual-based modelling allowing to capture emergent behaviour of microbial decomposer communities (Kaiser et al., 2015);
4. ecological network analysis to reveal inter-connection between microbiome diversity and function (Bascompte, 2007);
5. thermodynamic organizing principles, such as Maximum Entropy Production (MEP, e.g. Ozawa et al., 2003), Maximum Power (Odum and Pinkerton, 1955), Minimum Energy Expenditure (Rodriguez-Iturbe et al., 1992) and Minimum Dissipation (West et al., 1999);
6. modelling the potential growth yield of microbes feeding on organic compounds (Microbial Turnover to Biomass, MTB; (Brock et al., 2017; Trapp et al., 2018).

Such approaches can be complemented and refined for their application to SOM turnover.

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