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INVITED REVIEW

The Prokaryotic Biology of Soil

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Abstract

Prokaryotes ('Bacteria' and 'Archaea') are the most dominant and diverse form of life in soil and are indispensable for soil ecology and Earth system processes. This review addresses and interrelates the breadth of microbial biology in the global context of soil biology primarily for a readership less familiar with (soil) microbiology. First, the basic properties of prokaryotes and their major differences to macro-organisms are introduced. Further, technologies to study soil microbiology such as high-throughput next-generation sequencing and associated computational challenges are addressed. A brief insight into the principles of microbial systematics and taxonomy is provided. Second, the complexity and activity of microbial communities and the principles of their assembly are discussed, with a focus on the spatial distance of a few µm which is the scale at which prokaryotes perceive their environment. The interactions of prokaryotes with plant roots and soil fauna such as earthworms are addressed. Further, the role, resistance and resilience of prokaryotic soil communities in the light of anthropogenic disturbances such as global warming, elevated CO_2 and massive nitrogen and phosphorous fertilization is discussed. Finally, current discussions triggered by the above-addressed complexity of microbes in soil on whether microbial ecology needs a theory that is different from that of macroecology are viewed.

Keywords spatial microbial ecology | nutrient cycling | high-throughput sequencing | OTU | ecological theory

1. Introduction

Soil is one of the most abundant, complex and valuable natural products of the Earth and can be viewed from different angles. Soil is the habitat for bacteria, fungi, plants and animals, resulting in an enormous biodiversity of belowground and aboveground soil. Soil organisms are major drivers of biogeochemical nutrient cycles (carbon, nitrogen, phosphorous: C, N, P), and hence are indispensable for life on Earth. Soils display a large diversity of soil types, ranging from dry and nutrient-poor sandy soils in the desert to well-moistured loamy soils in the tundra. Healthy soils provide important ecosystem services, e.g. growth of crops, and are of substantial monetary value (Lehman et al. 2015). For example, terrestrial biomes are estimated to have an ecosystem value for the provisioning service 'food' of ca. 2300 US$/ha/year (in 2007) (de Groot et al. 2012), which, however, appears to decline (Costanza et al. 2014). Although soil covers most of the Earth's land surface (which in itself is close to 30% of the Earth's surface), healthy and fertile soil can be regarded as a 'threatened species' (Kaiser 2004, Drohan & Farnham 2006, Lehman et al. 2015). Currently soil appears to degrade more rapidly than it is replenished (Quinton et al. 2010, Stockmann et al. 2014). Soil on a microscale (< 1 mm^3) is highly heterogeneous, providing numerous microhabitats per gram of soil. It is this spatial microheterogeneity that is a strong driver of community assembly and function of soil micro-organisms such as prokaryotes ('Bacteria' and 'Archaea') and fungi.

Prokaryotes are the unseen majority (Whitman et al. 1998). The Earth hosts $>10^{30}$ cells, of which approximately 2.5 x 10^{29} cells occur in soil (Whitman et al. 1998). A single gram of soil may harbour from 10^8 (bulk soil) up

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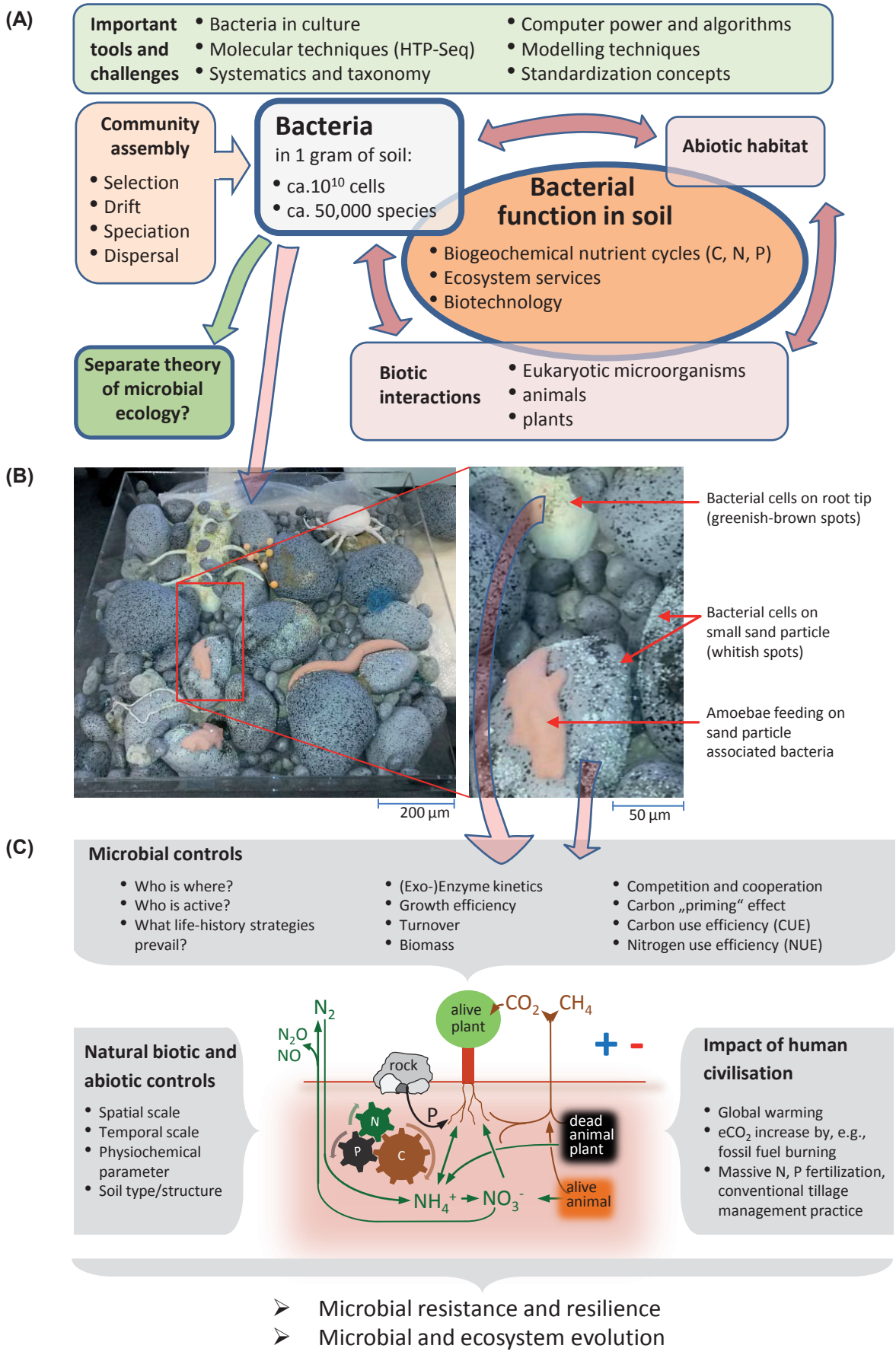
(A)
Important tools and challenges
• Bacteria in culture
• Molecular techniques (HTP-Seq)
• Systematics and taxonomy
• Computer power and algorithms
• Modelling techniques
• Standardization concepts
Community assembly
• Selection
• Drift
• Speciation
• Dispersal
Bacteria
in 1 gram of soil:
• ca.10^10 cells
• ca. 50,000 species
Abiotic habitat
Bacterial function in soil
• Biogeochemical nutrient cycles (C, N, P)
• Ecosystem services
• Biotechnology
Separate theory of microbial ecology?
Biotic interactions
• Eukaryotic microorganisms
• animals
• plants
(B)
Bacterial cells on root tip (greenish-brown spots)
Bacterial cells on small sand particle (whitish spots)
Amoebae feeding on sand particle associated bacteria
200 µm
50 µm
(C)
Microbial controls
• Who is where?
• Who is active?
• What life-history strategies prevail?
• (Exo-)Enzyme kinetics
• Growth efficiency
• Turnover
• Biomass
• Competition and cooperation
• Carbon „priming“ effect
• Carbon use efficiency (CUE)
• Nitrogen use efficiency (NUE)
Natural biotic and abiotic controls
• Spatial scale
• Temporal scale
• Physiochemical parameter
• Soil type/structure
N2
N2O
NO
alive plant
CO2
CH4
+ -
rock
P
N
P
C
dead animal plant
alive animal
NH4+
NO3-
Impact of human civilisation
• Global warming
• eCO2 increase by, e.g., fossil fuel burning
• Massive N, P fertilization, conventional tillage management practice
➢ Microbial resistance and resilience
➢ Microbial and ecosystem evolution

to 10^{11} (rhizosphere) prokaryotic cells (Torsvik et al. 1990, Portillo et al. 2013, Regan et al. 2014) and an estimated species diversity of 4 x 10^3 (Torsvik et al. 1990) to 8 x 10^6 species (Gans et al. 2005). Prokaryotes are central to the important ecological functions of soils (Prosser et al. 2007, Treseder et al. 2012).

The purpose of this review is to synthesize the current knowledge on prokaryotic biology in soil in a comprehensive breadth to a non-microbiologist readership (soil fungi will not be addressed). As a consequence of adopting this bird's-eye view, this review can only superficially scratch the surface of prokaryotic soil biology, which obviously comes at the expense of the details of individual topics. However, rather than addressing each topic with the depth it deserves and which I leave to other specialized reviews listed in the references, the focus of this review is to embed them in a more global context as summarized in Fig. 1. For a deeper insight into specific topics I point readers to the extensive reference list of the most recent and important (review) literature.

Instead of the term 'prokaryotes' I will use for simplicity in most cases the more common terms 'bacteria/bacterial' or 'microbes/microbial', nevertheless pointing out that the contents apply equally to both large prokaryotic domains, the 'Bacteria' and 'Archaea'. (Note that taxa above the rank of class are not covered by the Rules of the Bacteriological Code (Lapage et al. 1992). Such names cannot be validly published and are therefore cited in quotes.) The review is structured into two main sections with each several subsections. First, given the overall complexity and importance of bacteria for soil biology, it is necessary to introduce some basic knowledge about bacteria. (1) What are bacteria? Why is it at all it worthwhile dealing with bacteria in soil? What would a world without soil bacteria look like? (2) How do we address them? What is the classification system of bacteria? (3) How can we study soil bacteria? We are not able to culture the majority of bacteria as living organisms, we only know of them from molecular studies. What molecular techniques are available and what are the associated computational challenges? (4) Where in the soil do bacteria live? A distance of 1 mm for a bacterium is comparable to a distance of 1 km for humans. From a numerical perspective, the occupation of 1 g of sterile soil is comparable to the occupation of the Earth's globe by humans (Prosser 2012). Thus, what characterizes and drives microbial cell numbers, diversity, activity and communication of bacteria at a level of 1 mm^3 or even below? Second, bacterial communities and their function will be addressed. (5) What drives the assembly of bacterial soil bacteria? Is there biogeography of soil bacteria, and if so, on which spatial scales? What is the effect of temporal changes? How do selection, random drift, the dispersal process or speciation affect community assembly? (6) How do bacteria interact with macrobiological organisms such as plants and animals? (7) What is the function of bacteria in the global nutrient cycling process with respect to C, N and P turnover? (8) To what extent are microbial (soil) communities resistant and resilient to disturbances such as climate change or massive fertilization? What consequences can a severe disturbance of a bacterial community structure and thus of nutrient cycling have for life on Earth? (9) Finally, I review recent discussions on whether micro- as well as macro-ecology can be described by similar theories.

None of the above-addressed topics can be viewed separately. For a holistic view on bacterial soil biology it is essential to understand them as being ultimately interlinked to each other (Fig. 1).

2. What are prokaryotes, and why are they important?

Prokaryotes were originally defined in a seminal paper as single-celled entities by their cellular structure, e.g. the lack of a nucleus, the division by fission and not by mitosis, and the special structure of the cell wall (Stanier & van Niel 1962). This is an important difference from animals or plants, since bacterial cells are independent entities that carry out their life processes typically independently of other cells (Madigan et al. 2010). In 1990, Carl Woese suggested splitting prokaryotes into two domains of life, the 'Bacteria' and the 'Archaea', with the consequence of grouping all other organisms into the third domain of life, the Eucarya (Balch et al. 1977, Woese & Fox

Figure 1. The complexity of microbial soil biology.

(**A**) Summarizing sketch on the numerical dimensions, community assembly, abiotic and biotic interactions and functions of bacteria in soil. Some important tools and challenges for addressing bacterial biology in soil are listed. The potential need for developing a separate theory for microbial ecology is addressed.

(**B**) The DSMZ has developed for educational and demonstrational purposes a three-dimensional model depicting the spatial microscale in soil from the point of view of how microbes perceive their environment. A 1×1×0.2 mm soil volume was upscaled 10^9-fold to a dimension of 100×100×20 cm. At this scale, the diameter of an earthworm would exceed 5 metres. The model shows root rhizosphere and bulk soil (sand, silt and clay particles) with (water-filled) soil pores of different sizes, soil fauna (amoebae, nematodes, mites) and different types of fungi and bacteria and their interactions. Typically, such a soil volume contains several million bacterial cells, of which only a small fraction is shown.

(**C**) Simplified sketch on nutrient cycling in soil. The parameters that may control the quantity and quality of the nutrient cycles have been grouped into three categories.

1977). Though there have been debates about the nature of prokaryotes and their role in the global classification of organisms (Woese et al. 1990, Mayr 1998, Woese 1998, Martin & Koonin 2006, Pace 2006), substantial knowledge about the enormous abundance and diversity of prokaryotes has now accumulated (Schleifer 2009, Whitman 2009, Woese 2013).

2.1. What makes prokaryotes special and important?

Bacteria differ further from multicellular eukaryotic macro-organisms by below described properties.

First, though seemingly trivial, a major difference lies in their body size, which has substantial consequences for the organism's physiology. The smaller a body, the larger the surface-to-volume ratio, the faster the rate of nutrient exchange between the cell body and its environment, the larger the amount of nutrients that can be mineralized per time unit, and the shorter the cell replication time resulting in large population sizes. For example, a 1 cm^3 cube has a surface area of 6 cm^2. The same volume consisting of small cubes of the 1 µm edge size of soil bacterial length results in 1 x 10^{12} cubes of a total surface area of 6 m^2, which is 10,000-fold the surface area of a single 1 cm^3 cube. In consequence, a bulk of multiple bacteria exert much higher nutrient turnover rates than a macro-organism of comparable cell numbers. In a thought experiment, a single bacterium with a cell mass of 10^{-12}g would yield at a generation time of 1 hour and under optimal nutrition within less than six days (132 cell replications) a mass of 6×10^{21} tons (ca. half of which is protein), which is the weight of the planet Earth. In contrast, a cow of 500 kg weight would yield under optimal nutrition in the same period only a few kg of protein (Fuchs 2014).

A second important difference lies in the levels of morphological and physiological heterogeneity. Animals and plants have radiated into very different and complex morphologies but are rather uniform in their metabolism. In contrast, bacteria have rather simple and limited morphologies such as cocci or rods. However, as bacterial cells carry out their life processes independently of other cells, they have evolved a far broader spectrum of metabolic diversity than animals or plants. For example, besides using light as energy for fixing carbon (like phototrophic plants) or using organic carbon sources as an energy source (like heteroorganotrophic animals), several bacteria can use H_2, H_2S or Fe^{2+} as an energy source. This ability is termed 'chemolithotrophy' and is exclusive for bacteria (Madigan et al. 2010). Moreover, extremophilic bacteria can thrive in far more extreme environments than plants and animals typically do. Bacteria can grow at temperatures ranging from -12 °C up to 122 °C, at pH ranges from -0.06 to 12, at pressure > 1000 atmospheres and at salinity concentrations up to 32% (Madigan et al. 2010). With respect to oxygen, bacteria cover the full spectrum from obligate anaerobic to obligate aerobic (Madigan et al. 2010). Some bacteria survive radioactive radiation in doses that are 1000fold larger than doses lethal to humans (Blasius et al 2008). In addition, bacteria have a degree of physiological plasticity that is unparalleled in the eukaryotic world (Shade et al. 2012). A classic example is *Rhodobacter sphaeroides*, which can grow anaerobically as a phototroph fixing CO_2 as a carbon source but also grows aerobically as a chemoheterotroph using organic carbon. Additionally, this bacterium can fix atmospheric N_2 when other nitrogen sources are scarce (Porter et al. 2008). Though far more could be added to exemplify the enormous metabolic and physiological heterogeneity of bacteria (Madigan et al. 2010), these examples should suffice to indicate that bacteria can live and proliferate in a much broader range of environmental conditions than macro-organisms can do. Despite the single-celled nature of bacteria there is increasing evidence that bacteria can communicate with each other and adopt multicellular lifestyles in which functional tasks are split between cells (Gary M. Dunny & Dworkin 2008, Overmann 2010, Claessen et al. 2014).

Finally, a third major difference is the peculiar parasexual behaviour of bacteria. Bacteria do not proliferate sexually but by binary fission. Nevertheless, bacteria can exchange genetic material by a process termed 'lateral/horizontal gene transfer' (Redfield 2001, Popa & Dagan 2011). In contrast to sexually replicating organisms, where the phylogenetic distance of mating organisms is rather low (typically within a species), bacteria are far more promiscuous. One would not expect distant eukaryotes such as primates and perennial grasses to transfer genes between each other; however, gene exchange among bacterial taxa at this and far larger phylogenetic distances is fairly common, and may have marked consequences (Rothman et al. 2014).

2.2. Of what relevance are bacteria for life on Earth?

What is the global relevance of bacteria for humans, or, more generally speaking, for life on Earth? Typically, bacteria are regarded as being something bad because they spoil food or cause diseases. However, from the approximately 12,600 bacterial species currently known to science, only ca. 5% are harmful for either plants or animals. To date, not even a single pathogenic species is known among the domain 'Archaea'. Although it is not necessarily true that eukaryotic life on Earth would cease

immediately upon loss of all bacteria, the consequences would be substantial. This issue has been addressed in a noteworthy perspective in *PLOS Biology* that is worthy of direct and cumulated quotations (Gilbert & Neufeld 2014): 'Microbes sustain life on this planet because of their myriad associations and biogeochemical processes. In a world without bacteria, most biogeochemical cycling would cease; human and animal waste would accumulate rapidly. Living food sources would be increasingly difficult to find. Most ruminant livestock would starve without microbial symbionts, and plants would rapidly deplete nitrogen, cease photosynthesis, and then die. We predict complete societal collapse only within a year or so, linked to catastrophic failure of the food supply chain. Although the quality of life on this planet would become incomprehensibly bad, life as an entity would endure.'

In addition to global ecological relevance, humans directly benefit from bacterial products. For example, recently a bacterium from soil was discovered that produces a highly promising new antibiotic that could provide a breakthrough in the therapy of infections (Ling et al. 2015). Some bacteria detoxify harmful gold (Au) ions and produce as waste pure gold nuggets (Johnston et al. 2013). Geochemical exploration for gold is becoming increasingly important to the mining industry. Recently, a whole-cell biosensor for the detection of gold was constructed on the basis of the bacterial *golTSB* genes from *Salmonella enterica* (Zammit et al. 2013).

3. Bacterial systematics and taxonomy

Biological research is not possible without having a suitable system of addressing and naming organisms. Bacterial systematics and taxonomy is still a young and developing science (Oren & Garrity 2014). Whereas systematics can be described as the 'cradle of comparative biology', taxonomy can be clearly defined as encompassing characterization, classification and nomenclature (Tindall et al. 2007). In order to characterize a bacterium taxonomically it must be available as a living culture. Only this will allow the study of metabolic, phenotypic, physiological and molecular traits as listed recently (Tindall et al. 2010, Kämpfer & Glaeser 2013).

3.1. The pragmatic approach to bacterial species delimitation

The currently applied bacterial classification scheme at the level of the species hierarchy is an operational-based approach that depends rather on pragmatism than on a unifying theory (Kämpfer & Glaeser 2013). As bacteria multiply by binary fission and not by natural interbreeding the so-called biological species concept (Mayr 1942) for species delimitation is not applicable. Instead, a phenetic approach based on overall genomic and phenotypic similarity is adopted (Wayne et al. 1987, Stackebrandt et al. 2002). This highly successful approach allows the majority of cultivated prokaryotes to be affiliated into species categories. Genomic similarity is typically determined via DNA-DNA hybridization (DDH) in a molecular laboratory experiment (Wayne et al. 1987, Stackebrandt et al. 2002). Two bacterial strains that show less than ~70% similarity in DDH and can be clearly distinguished by diagnostic phenotypes (Tindall et al. 2010, Kämpfer & Glaeser 2013) are regarded as members of two different species. The 70% threshold value has been calibrated to match species borders that were previously determined on phenotypes only (Rosselló-Mora & Amann 2001). An average nucleotide identity of approximately 94% across shared genes corresponds roughly to the traditional 70% DDH threshold value of species delimitation (Konstantinidis & Tiedje 2005). As genome sequences become rapidly cheaper the DDH can be based alternatively on bioinformatic comparison of genome sequences (Meier-Kolthoff et al. 2013a). As a rule of thumb, DDH was agreed on to be mandatory if the 16S rRNA gene sequence similarity is larger than 97%, as below that threshold bacteria would not have a DNA-DNA similarity larger than 70% (Stackebrandt & Goebel 1994). However, recently the border of 16S rRNA gene similarity making DDH analysis mandatory was moved to 98.2–99 %, depending on the taxonomic group investigated (Meier-Kolthoff et al. 2013b). The extent to which microbial taxonomy needs to be revised in the light of high-quality and complete genome sequences is currently being discussed (Thompson et al. 2014, Rosselló-Móra & Amann 2015).

To introduce a new bacterial taxon to the scientific community, the effective publication of its properties and its distinctness from neighbouring taxa is the first step. There is wide agreement that the effective publication has been peer-reviewed, is in a form that is widely available, cannot be altered, and is intended to serve as a permanent record (Tindall et al. 2006). There is no official classification of prokaryotes, as this is a matter of scientific judgment and general agreement (Parte 2014). However, the valid publication of the name of the new taxon is strictly controlled and must meet the rules of the International Code of Nomenclature of Bacteria (Lapage et al. 1992). The correct name of a bacterial taxon is based on (a) valid publication, (b) legitimacy, and (c) priority of publication. Since 1 January 1980, the priority of bacterial

names has been based upon the APPROVED LISTS OF BACTERIAL NAMES (Skerman et al. 1980). Names that were not included in the APPROVED LISTS at that time lost standing in bacterial nomenclature. Valid publication of new names and new nomenclatural combinations can only be done by publication in the INTERNATIONAL JOURNAL OF SYSTEMATIC AND EVOLUTIONARY MICROCBIOLOGY (IJSEM, http://ijs.sgmjournals.org/), either as an original article or in the 'VALIDATION LISTS' regularly appearing in that journal. The VALIDATION LISTS constitute valid publications of new names and new combinations that were previously effectively published outside the IJSEM (Tindall et al. 2006). A manually curated and therefore monthly up-to-date and complete list of bacterial names with standing in nomenclature can be found at http://www.dsmz.de/de/support/bacterial-nomenclature-downloadseite.html. The prerequisite for the acceptance of a description of a new taxon in the IJSEM is the deposit and free availability of the designated type strain in two open collections (e.g. DSMZ, www.dsmz.de) that must be in two different countries. Further important online sources on bacterial taxonomy and nomenclature can be found at http://www.taxonomicoutline.org and www.namesforlife.com. Recently a detailed and well-designed workflow for taxonomic characterization, identification, classification and nomenclature of new bacterial isolates in pure culture has been suggested (Kämpfer & Glaeser 2013).

3.2. Challenges to the pragmatic approach to bacterial species delimitation

It has been criticized that the current approach to bacterial species delimitation is entirely driven by pragmatism but not by a theory-based understanding of what 'species' would be from an evolutionary perspective and how they come into being. As an alternative, the ecotype concept has been proposed in which bacteria are affiliated to the same species (i.e. ecotype) if they are facing the same set of ecological challenges resulting them being members of the same cohesive group (Cohan 2002, 2006, Cohan & Perry 2007, Koeppel et al. 2008). The ecotype concept, however, has been questioned because the extent to which it can be universally applied to all bacteria is unclear. It cannot be excluded that bacterial species may form as a result of, for example, random genetic drift, instead of selection pressure due to ecological constraints. Moreover, frequent lateral gene transfer may prevent the formation of genetically stable groups. Based on that, a discussion has emerged about the extent to which bacterial species, besides the formal affiliation to taxonomic and validly named groups, do in fact exist in nature (Doolittle & Papke 2006, Doolittle & Zhaxybayeva 2009).

3.3. Higher-rank taxa above the genus level

Based on 16S rRNA gene data, all prokaryotes are classified into the domains 'Archaea' or 'Bacteria', which are subdivided in a hierarchical manner into the lower non-overlapping ranks 'phylum', 'class', 'order', 'family', 'genus' and 'species', and all these ranks are sometimes (not consistently) subdivided into lower ranks using the suffix 'sub-', like, for example, 'suborder' or 'subspecies' (Brenner et al. 2005, Schleifer 2009, Kämpfer & Glaeser 2013). There are no robust rules for the circumscription of ranks above the genus, although these high taxonomic ranks describe the majority of the bacterial ecological diversity (Yarza et al. 2014). The entities that are known as taxa and their hierarchical classifications are ultimately artificial constructs and are somewhat subjective (Rosselló-Móra 2012, Yarza et al. 2014).

Prokaryotes are subdivided into 30 phyla (or divisions) in the domain 'Bacteria' and five phyla in the domain 'Archaea' (http://www.bacterio.net/-classifphyla.html). Ca. 90% of all described prokaryotic species belong to only four of the 30 bacterial phyla (Yarza et al. 2014), whereas the majority of phyla are hardly represented by living isolates. For example, the phylum 'Acidobacteria' may comprise up to 50% of all soil bacteria (Janssen 2006) but currently only ca. 30 species are described. The absence of living isolates to calibrate overall bacterial diversity resulted in pragmatic challenges to taxonomically characterize the bacterial diversity known only from culture-independent methods. To overcome this, Yarza and colleagues recently proposed a way to unite the classification of cultured and uncultured bacteria by the use of 16S rRNA gene sequences (Yarza et al. 2014).

4. How can we study soil microbiology?

The study of organismal biology typically requires the availability of the organism as a living entity. Only under this premise is the exploration of physiologic, ecologic and behavioural aspects of organisms possible in sufficient detail. The organismal study of macroscopic animals and plants has a long history, which is well documented by the work of Charles Darwin and Carl Linnaeus. In contrast, organismal work with bacteria has only been possible for the last 140 years.

4.1. Cultivation of bacteria and their accessibility to the scientific community

A major breakthrough in microbiology was the ability to isolate organisms in pure culture developed by Robert Koch (in 1873) and Joseph Lister (in 1873) (Overmann 2013). Since then, numerous sophisticated ways have been developed to culture bacteria (Overmann 2013), resulting in 12,604 effectively described and validly named species (as of January 2015; http://www.dsmz.de/bacterial-diversity/prokaryotic-nomenclature-up-to-date). Why are there so few bacterial species known to science (Fig. 1A)? Are there no more species, which would seem odd in the light of already ca. 6,000 earthworm species, let alone one million insect species? Apparently not, as it was found in 1985 that counts of bacterial cells obtained via cultivation are orders of magnitude lower than those directly observed via microscope, a phenomenon coined 'great plate-count anomaly' (Staley & Konopka 1985). It is estimated that it has been possible to cultivate only 0.001% to 0.1% of all bacterial species (Epstein 2013, Overmann 2013).

There may be two major reasons for this discrepancy. First, the not-yet cultured prokaryotes most probably exhibit a physiology that does not match the addressed cultivation methods (Overmann 2013). Though more than 1500 cultivation methods are known (http://www.dsmz.de/catalogues/catalogue-microorganisms/culture-technology/list-of-media-for-microorganisms.html), microbial science is still heavily struggling to identify novel appropriate cultivation conditions, which could be based on, for example, enrichment on solid steel or synthetic polymers (Gich et al. 2012, Overmann 2013). Second, many micro-organisms can enter the reversible state of dormancy, which is a bet-hedging strategy to overcome unfavourable environmental conditions (Jones & Lennon 2010). Dormant individuals become members of a seed bank, which has the potential to substantially shape the structure of microbial (soil) communities (Lennon & Jones 2011).

In contrast to taxonomical practice in zoology and botany, where type specimens are deposited in museums or herbaria as dead material, prokaryotic type specimens must be deposited as living material in bacterial strain collections or microbial Bioressource Centres (mBRC) such as the DSMZ (www.dsmz.de) (Kämpfer & Glaeser 2013). The World Data Centre for Microorganisms (WDCM, http://www.wdcm.org/databases.html) lists close to 600 collections of micro-organisms in nearly 70 countries. Currently, major efforts are being undertaken to ensure that precious cultivated prokaryotic diversity will be preserved by deposits in mBRCs (Stackebrandt 2010, 2011, Stackebrandt et al. 2014). The BacDive database (http://bacdive.dsmz.de/) lists metadata (name and taxonomic classification, morphology and physiology, culture and growth conditions, isolation, sampling and environmental information, application and interaction, molecular biology and strain availability) on more than 53,000 bacterial strains that are available as living cultures (Söhngen et al. 2013).

4.2. Cultivation-independent methods

The limited potential for bacterial cultivation (Overmann 2013) calls for methods that avoid cultivation to study the full diversity of bacteria in natural habitats. Based on the seminal work of Carl Woese, who discovered the 'Archaea' as a third domain of life (Balch et al. 1977, Woese & Fox 1977), the 16S rRNA gene turned out to be an excellent marker for studying the diversity of uncultured bacteria in their natural (soil) habitats. As in the beginning the determination of the DNA sequences was far too expensive for the analysis of numerous samples and bacteria, alternative molecular methods were developed. Denaturing and temperature gradient gel electrophoresis (DGGE and TGGE), single-strand confirmation polymorphism (SSCP), amplified ribosomal DNA restriction analysis (ARDRA) and terminal restriction fragment length polymorphism (T-RFLP) techniques characterize the sequence diversity of 16S rRNA gene PCR amplicons obtained from soil DNA without sequencing (Kirk et al. 2004). The PhyloChip, based on Affymetrix GeneChip microarray technology, categorizes with high reproducibility all known bacteria and archaeal Operational Taxonomic Units (OTU, typically defined at 97% 16S rRNA gene similarity) into over 50,000 taxa using 1,100,000 25-mer probes that target variations in the 16S rRNA gene (Hazen et al. 2010).

Much higher resolution is provided by so-called metagenomic projects (Daniel 2005). Next-generation high-throughput (HTP) sequencing methods enable sequencing of the entire genetic material in a habitat (Council 2007, Thomas et al. 2012) (Fig. 1A). The costs of sequencing have dropped substantially down to 1 million base pairs per one US dollar with dozens of millions of bp obtained per day in a single run per laboratory (Caporaso et al. 2012). Metatranscriptome studies target environmental RNA, hence the functional part of the environmental community (Moran et al. 2013). Despite the wealth of insights in prokaryotic biology of environmental samples from HTP analysis, metagenomics, even if it covers the entire genetic information available and not only the 16S rRNA gene sequence, does not necessarily allow deeper insight

into the genomics of prokaryotic individuals. However, technology has advanced so far that genome sequences of single cells can be obtained with reasonable coverage and quality (Rinke et al. 2013, Lasken & McLean 2014, Rinke et al. 2014).

Besides analysing the bacterial community composition itself it is also important to study the physicochemical structure of their soil habitats (O'Donnell et al. 2007). Several methods are available for non-destructive three-dimensional analysis of the soil environment on the µm scale, such as micro-computed tomography (µCT), nuclear magnetic resonance (NMR) and magnetic resonance imaging (MRI) (Vos et al. 2013). Predominantly destructive chemical analysis methods include micro-electrodes, electro-dispersive X-ray spectroscopy (EDS or EDX), infrared spectroscopy (IRS) and nano-secondary ion mass spectrometry (NanoSIMS) (Heister et al. 2012, Vos et al. 2013).

4.3. Computational challenges: software, databases, algorithms

Dozens to hundreds of millions of (16S rRNA gene) sequence reads obtained from hundreds of samples almost simultaneously result in substantial challenges for computational data processing and scientific analysis (Fig. 1A). The analytical tools for classifying 16S rRNA gene sequence reads to either known taxa or into OTUs to, for example, determine diversity estimates within and across microbial communities (alpha-, beta-, gamma-diversity) are under constant refinement (Schloss et al. 2009, Caporaso et al. 2010, Anderson et al. 2011, Fierer & Ladau 2012, Larsen et al. 2012, Haegeman et al. 2013, Matias Rodrigues & von Mering 2014, Schmidt et al. 2014b, a). 16S rRNA gene sequences are stored in appropriate publicly available data repositories such as SILVA (Quast et al. 2013), RDP (Cole et al. 2014) or Greengenes (DeSantis et al. 2006). CAMERA is a database and associated computational infrastructure that provides a single system for depositing, locating, analysing, visualizing and sharing data about microbial biology through an advanced Web-based analysis portal. CAMERA collects and links metadata relevant to environmental metagenome data sets with annotation in a semantically aware environment allowing users to write expressive semantic queries against the database (Sun et al. 2011). MG-RAST is a metagenomics analysis server that currently harbours more than 161,300 microbial metagenomes with more than 540 billion sequences and more than 66 Terrabases (Wilke et al. 2015). Another important albeit smaller metagenomics database and analysis tool is IMG/M (Markowitz et al. 2014). Kim and colleagues have summarized in an excellent overview the strategic procedure, the software tools and the respective large database repositories needed for successful analysis of bacterial metagenomic sequences for microbial ecology (Kim et al. 2013). Besides the initial processing of raw data, downstream analysis of the taxonomic or functional analysis of microbial communities consisting of tens of thousands of OTUs studied and potentially hundreds of soil sampling sites affords appropriate statistical tools. Buttigieg and Ramette provided a guide to statistical analysis in microbial ecology: GUSTA-ME, a community-focused, living review of multivariate data analyses, which is a dynamic, Web-based resource providing accessible descriptions of numerous multivariate techniques relevant to microbial ecologists (Buttigieg & Ramette 2014). The exponentially increasing raw data flood and the increasing complexity of microbial ecological research recently prompted the Genomic Standards Consortium (GSC) (Field et al. 2011) to call for a Genomics Software Institute (GSI) (Gilbert et al. 2012).

4.4. The need for standardization of methods

Different HTP sequencing technologies and strategies (Thomas et al. 2012) challenge the comparability of results across soil samples (Caporaso et al. 2012). Different additional laboratory methods and different sets of associated soil metadata further impede comparison (Fig. 1A). Consequently, the GSC proposed standards for describing genomic ('minimum information about a genome sequence', MIGS) and metagenomic ('minimum information about a metagenome sequence', MIMS) sequence data (Yilmaz et al. 2011). Additionally, standardized sets of measurements and observations describing particular habitats, e.g. soil, water, human-associated, plant-associated or laboratory, were proposed (MIMARKS) (Yilmaz et al. 2011).

5. The importance of scale for soil microbiology

Billions of bacterial cells of thousands of species typically occupy a single gram of soil, at a cell size of < 1.2 µm in diameter (Portillo et al. 2013, Regan et al. 2014). Bacteria can occupy a biomass of 300–3000 kg wet mass per ha (Sylvia et al. 2005). Nevertheless, the fraction of soil surface that is covered by soil prokaryotes is just about 10^{-6}% (Young & Crawford 2004). The soil volume occupied by micro-organisms is considerably less

than 1% (Schmidt et al. 2011). Based on hundreds of soil thin sections taken at different depths it was estimated that at 10^9 cells per gram of soil, the average number of neighbours surrounding a single cell was ca. 1040 at a distance of 50 µm and 120 cells (representing ca. 100 species) at a distance of 20 µm. For ca. 10^{10} cells per gram, the average number of neighbour cells is ca 5500 (at 50 µm distance) and ca. 550 cells (at 20 µm distance, representing ca. 280 species) (Raynaud & Nunan 2014).

Hence, bacterial life in soil needs to be addressed at a spatial scale of clearly below a single mm (Nunan et al. 2003). The reason lies in the enormous habitat heterogeneity that soil provides on a microscale level (Fig. 1B). Within shortest distances, aerobic and anaerobic as well as dry and water-saturated habitats can alternate. As bacteria are essentially aquatic organisms, they typically thrive in only those fragmented parts of the pore network that are filled with water or are covered by water films (Vos et al. 2013). The coarser and the patchier the soil is as a function of sand, silt or clay proportions, the more highly fragmented is the water phase due to differences in matric potential, hence the more isolated microhabitats are present, which in turn mostly increases bacterial diversity (Carson et al. 2010, Chau et al. 2011, Ruamps et al. 2011, Vos et al. 2013). Hence, bacteria in soils tend to have a 'patchy' distribution and to form micro-colonies on microscales (Grundmann 2004). Bacterial community composition differs also between micro- and macroaggregates (Mummey et al. 2006). In sum, there is microbial biogeography on the soil pore scale. The potential for active dispersal of prokaryotic cells across partially hydrated soil in the range of a few mm within, for example, 48 hours is limited (Wong & Griffin 1976). One way for bacteria to cross aerated microhabitats could be by gliding on water films on fungal hyphae ('hyphal highways'; Fig. 1B) (Kohlmeier et al. 2005, Warmink & van Elsas 2009, Nazir et al. 2010).

Bacteria apparently do not entirely passively react towards the three-dimensional structure of soil on the microscale. There is evidence that the soil-microbe system is self-organizing as a consequence of the feedback between microbial activity and particle aggregation (Young et al. 2008, Crawford et al. 2011). However, a theory linking microbial population dynamics to biodiversity and function in terms of the soil microenvironment is more or less absent (Young & Crawford 2004).

5.1. Social interaction of bacteria in soil biofilms

Bacteria are social organisms that can express highly social lifestyles, despite the fact that we are used to treating bacteria in the laboratory as single-celled and basically solitary organisms (West et al. 2006, Foster 2011, Pepper 2014). Bacteria can communicate via 'quorum sensing'; they can 'count' their cell density in an environment with the help of small excreted autoinducer molecules, which accumulate in a cell density-dependent manner (Nadell et al. 2008). Upon reaching the quorum, bacteria can exert respective physiological responses.

At the solid-liquid interface within water-filled soil pores or in thin water films covering sand or silt soil particles bacteria build so-called biofilms (Burmølle et al. 2012) in which they can reside as complex communities displaying taxonomic (Hall-Stoodley et al. 2004) and physiological (Stewart & Franklin 2008) heterogeneity. Cooperation, competition and communication are closely intertwined in microbial biofilms (Nadell et al. 2008, Cornforth & Foster 2013). In these biofilms, typically surrounded by an extracellular polymeric substance matrix (EPS), bacteria gain several advantages such as protection from protozoan predation, desiccation and exposure to antibacterial substances, but also optimized acquisition of nutrients. In sum, the ecological success of biofilms is based on their resilience in the light of numerous challenges (Nadell et al. 2009). Some soil bacteria cannot or only weakly form a biofilm when occurring as single species but are known to form a large multi-species biofilm when they cooperate in a community (Ren et al. 2015).

Myxobacteria are best known for social development of multicellular, spore-bearing fruiting bodies in response to starvation (Kraemer & Velicer 2011). Cells of the predatory soil bacterium *Myxococcus xanthus* swarm in a coordinated manner through soil habitats in cohesive groups and kill and lyse prey cells of other microbial species with secreted antibiotics and lytic enzymes (Kraemer & Velicer 2011). These swarms show pronounced social variation within many natural fruiting bodies, which suggests that within-group conflict most probably plays a major role in myxobacterial social evolution.

6. Global patterns in bacterial soil diversity (community assembly)

Current theory in community ecology suggests that communities are assembled by only four distinct kinds of processes: selection, drift, speciation and dispersal (Vellend 2010). These processes are close analogues to the four processes acting in population genetics: selection, drift, mutation and recombination (Vellend 2010). Recently, this theoretical framework, which stems from

macro-organismal ecology, was adapted to the assembly of microbial communities (Nemergut et al. 2013).

6.1. Selection

In a global comparison of diverse terrestrial and aquatic habitats at different temperatures, salinity rather than extremes of temperature, pH or other physical and chemical factors determines the structure of microbial communities (Lozupone & Knight 2007). Bacterial communities from cold and dry desert soils (Alpine, Arctic and Antarctic soils) differ substantially from soils of moderate climate or even tropical climate (desert, semi-arid, mangrove or rainforest soils), indicating sensitivity to lack of water availability and extremes of temperature and short-term large temperature ranges (Macrae et al. 2013, Rhodes et al. 2013). Within a set of 98 soil samples from rather moderate climates in North and South America, bacterial diversity was found to be unrelated to site temperature, latitude, geographic distance and other variables that often shape animal and plant diversity, but appeared to be largely shaped by the soil pH value, with bacterial diversity decreasing in more acidic soils (Fierer & Jackson 2006). Using a set of 11 pairs of soils from a natural forest and adjacent grassland, ranging from Hawaii to Northern Alaska, it was demonstrated that the soil bacterial community strongly responded to deforestation (Crowther et al. 2014). Within the same soil types, there are substantial differences between microbial communities in direct proximity to the plant roots as compared to the bulk soil typically just a few millimetres apart (Mendes et al. 2013, Minz et al. 2013, Philippot et al. 2013a). These studies exemplify some of the soil abiotic parameters that exert selective pressure in soil bacterial communities on different ecological and spatial scales.

6.2. Global dispersal of soil bacteria

Despite the limited potential of bacteria for active dispersal in soil (Wong & Griffin 1976), wind-borne soil bacteria can passively easily cross continents within a few days (Kellogg & Griffin 2006, Griffin 2007). The African dust system carries Saharan dust in the summer to the Caribbean and USA and in the winter to the South American Amazon rainforest. The Asian dust system exports dust primarily across the Pacific to the west coast of North America. Occasionally, both dust systems can reach Europe (Kellogg & Griffin 2006). The amount of dust transported is not trivial, since most of the clay soil on carbonate Caribbean islands is derived from African dust (Muhs et al. 1990). Given the fact that soil bacteria can be transported, associated with soil particles, via wind thousands of kilometres within a few days, the question arises as to whether there is also a soil microbial biogeography on a large scale of hundreds to thousands of kilometres. It is now well established that biogeographic patterns such as distance-decay or taxa-area relationships exist in some bacteria (Horner-Devine et al. 2004, Martiny et al. 2006, Nemergut et al. 2011, Hanson et al. 2012), as identified for some eukaryotes. However, there are aspects of biogeography that may be unique to micro-organisms. For example, Martiny and colleagues conclude that the 'rates of processes underlying biogeography probably vary more widely for microorganisms of a given size than for macroorganisms of a given size'. The authors hypothesize that 'body size does not constrain a microorganism's dispersal rate, population size and range size, whereas it does somewhat constrain those of larger organisms' (Martiny et al. 2006). Nevertheless, the processes that govern biogeography in micro-organisms are only partially understood and are difficult to infer from biogeographic patterns only (Hanson et al. 2012).

6.3. Drift

Drift is the mechanism leading to community size and composition changes due to chance events only. Studies that address the influence of drift in (microbial) communities are still rather scarce. The effect of genetic drift in the divergence of populations has been studied with *Myxococcus xanthus* (Vos & Velicer 2008) by using a distance-decay approach (Hanson et al. 2012). Soil populations were consistently differentiated on scales exceeding 10^2–10^3 km, and isolation by distance, which is the divergence of populations by genetic drift due to limited dispersal, rather than local adaptation (i.e. selection) was found to be responsible (Vos & Velicer 2008). Stegen and colleagues developed an elegant mathematical framework to disentangle for the first time on a quantitative basis the effects of selection, dispersal limitation, drift and homogenizing dispersal. In an experimental work in horizontally and vertically spaced aquifer (not soil) sampling sites they estimated that drift accounted for ca. 25% of turnover in bacterial community composition (Stegen et al. 2012, Stegen et al. 2013). Freedman & Zak studied soil samples that were deglaciated at different time points and hence represent a long-term chronosequence of ca. 4000 years. Disentangling temporal from environmental factors, the authors identified ca. 35–57 % of the soil bacterial community structure to be due to dispersal limitation and drift (Freedman & Zak 2015).

6.4. Speciation

Though microbial taxonomists are blessed by a well-working pragmatic and functional species definition (Stackebrandt et al. 2002), there is no widely accepted concept of species for prokaryotes (Gevers et al. 2005). Yet, the ecotype concept (Cohan 2002, 2006, Cohan & Perry 2007, Koeppel et al. 2008) states that ecological populations of micro-organisms can be operationally defined and are recognized as groups of coexisting individuals that are highly clustered on the genotypic and phenotypic levels (Cordero & Polz 2014), and hence may lead to speciation due to different lineages occupying different ecological niches. The conditions and borders for incipient sympatric speciation of bacteria into different ecological niches have been modelled recently (Friedman et al. 2013). It is well accepted that two valid bacterial species may have the same 16S rRNA gene sequence (Fox et al. 1992). Thus, speciation events cannot be detected by HTS approaches that target a fragment of the 16S rRNA gene only and that are currently standard in microbial diversity analyses. Studying speciation of soil bacteria based on ecological diversification requires bacteria to be obtained as living organisms and enables speciation to be proved via the phenotype (Mayr 1997) that the bacterial putative ecotypes are indeed adapted to different environmental constraints. This affords a well-planned factorial design for obtaining the soil samples, as it is currently not possible to both sample microbial cells and determine the habitat characteristics on the spatial microscale of a few µm. It also affords a sufficiently large number of bacterial isolates, as passive dispersal may transport bacterial cells to habitats to which they are not adapted but where selective pressure is not stringent enough to immediately eradicate the migrant cell. Below I present an example of ecological speciation within a group of bacteria that belong to a single species as based on the above-discussed pragmatic species delimitation practice.

The 'Evolution Canyon' ('EC') system in Israel is a suitable sampling place for speciation studies in natural environments (Nevo 2001, Nevo 2012). 'EC' I at Nahal Oren in the Carmel Mountains close to Haifa is an east-west-orientated canyon. The south-facing slope (SFS) is constantly irradiated by sun, which makes it hotter and drier, savannah-like (i.e. 'African'-like), whereas the shady 'European' north-facing slope (NFS) is a mesic, lush forest. The slopes are separated by just 50–400 metres. Thus, geographic separation cannot account for any slope-specific intraspecies differences. The canyon system is an approximately 3–5-million-year-old and tectonically uplifting canyon, until now quite undisturbed by humans. Thus, sufficient time is given to potentially develop slope-specific intraspecies divergence. 'EC' II, which is located 40 km from 'EC' I in the Upper Galilee Mountains, is of a similar SFS and NFS slope structure and serves therefore as a suitable control site for the effect of passive bacterial dispersal. Despite having the same macroclimate (overall seasonal temperature, rainfall, etc.), the SFS and NFS have a substantially different microclimatic temperature and drought stress, which allows natural selective abiotic pressures to be identified and their effect in nature to be studied. For more than 20 years the adaptation and speciation of macro-organisms has been explored in the 'EC' system, with *Drosophila* flies and wild barley being two of the most prominent model organisms. The cyanobacterium *Nostoc linckia* and the fungi *Sordaria fimicola*, *Penicillium lanosum* and *Aspergillus niger* are other model organisms (Nevo 2012). Close to 1000 strains of the bacterial species *Bacillus simplex* have been sampled from both canyon systems, of which ca. 130 representative strains from all four slopes have been studied with respect to genotype and phenotype in closer detail. These strains belong to a single named species according to the above-described pragmatic species definition (Sikorski & Nevo 2005). Using two different population genetic algorithms, Ecotype Simulation and AdaptML (Hunt et al. 2008, Koeppel et al. 2008), to analyse DNA sequences from housekeeping genes, phylogenetic clusters were suggested as putative ecotypes. Indeed, the bacteria representing these clusters showed strong preferences for either the SFS or NFS slope, suggesting adaptation to the overall macroclimatic conditions shaping the soils on these slopes (Sikorski & Nevo 2005, Koeppel et al. 2008). Though there was an obvious effect of passive dispersal across the 40 km (both SFS slopes and accordingly both NFS slopes of 'EC' I and II, respectively, harbour almost the same *B. simplex* bacteria, whereas within a canyon the NFS and SFS *B. simplex* bacteria were quite different), these putative ecotypes may represent incipient speciation events due to abiotic ecological constraints. However, residence in ecologically different habitats may not be sufficient to claim adaptation due to selective pressure but needs support from respective phenotypes. Indeed, the *B. simplex* bacteria from the hotter SFS slopes perform physiologically better at high temperature than the strains from the colder NFS slopes (Sikorski & Nevo 2007, Sikorski et al. 2008a), but were not distinguishable with respect to the ecologically neutral trait of utilization of different carbohydrates as energy sources (Sikorski et al. 2008b). Similar results have been obtained for the *B. subtilis-B. licheniformis* clade in soils from a similarly east-west-running canyon in Death Valley, USA (Connor et al. 2010, Kopac et al. 2014).

7. Interaction of soil bacteria with soil macroorganisms

7.1. Soil bacteria in the rhizosphere

Plants get, via the roots, into direct contact with soil bacteria (Fig. 1B). Due to the nature of plant physiology, the rhizosphere surrounding the roots is rich in a large variety of different carbon sources originating from rhizodeposits and root exudates (Dennis et al. 2010). Bacteria from the bulk soil are attracted by those carbon sources into the rhizosphere. The rhizosphere microbiome is referred to as the collective communities of root-associated micro-organisms (Mendes et al. 2013). As a consequence, the microbial community of the rhizosphere differs both quantitatively and qualitatively from that outside these small zones and is affected by a complex interaction between soil type, plant species and diversity, and cultivar type, but also climate and agricultural and fertilization practice (Weinert et al. 2011, Berendsen et al. 2012, Bouffaud et al. 2012, Philippot et al. 2013a, Ai et al. 2015). Thus, the rhizosphere is defined by its function rather than its spatial dimension (Minz et al. 2013). The rhizosphere microbiome itself affects root health and development, hence the plant's fitness (Garbeva et al. 2004, Van Der Heijden et al. 2008, Lugtenberg & Kamilova 2009, Minz et al. 2013, Ahemad & Kibret 2014, Panke-Buisse et al. 2014). The interaction between the rhizosphere microbiome and its plants has probably significantly influenced the evolution of its plant hosts (Zilber-Rosenberg & Rosenberg 2008). However, part of the rhizosphere microbiome can be pathogenic for plants and also for humans (Berg et al. 2013, Mendes et al. 2013), whereas another fraction can trigger food contamination (Teplitski et al. 2011). It has been suggested that a 'core microbiome' or 'minimal microbiome' that is effective against soil-borne pathogens in different agro-ecosystems should be designed and applied (Mendes et al. 2013).

7.2. Soil bacteria and soil fauna

A substantial fraction of the soil biology is represented by the soil fauna (micro-, meso-, mega- and macrofauna). The extent and quality of this part of biological diversity is surely best known to the readers of *Soil Organisms*. Some of the soil fauna feeds on bacteria as a source of nutrients (Fig. 1B). However, not all of the ingested bacteria are mineralized; in a large number of cases the host and the gut microbiota cooperate by forming a 'mutualistic digestive system' (Drake & Horn 2007). The degradation of the complex organic matter during its passage through the gut is enhanced by the exoenzymes produced by the gut microbes. This increases the capacity of the host, e.g. earthworms and termites, to assimilate nutrients (Drake & Horn 2007, Wüst et al. 2011, Brune 2014). Hence, soil fauna such as earthworms modify the microbial communities through digestion, stimulation and dispersion in casts (Nechitaylo et al. 2010, Gómez-Brandón et al. 2011, Gómez-Brandón et al. 2012, Andriuzzi et al. 2013, Lemtiri et al. 2014). Earthworms and soil bacteria also cooperate outside the earthworms' gut in mineralizing soil organic matter (SOM), which has been nicely described in an analogy: 'To help digest this SOM, these earthworms have developed a mutualistic relationship with the soil microbiota, based on the 'Sleeping Beauty paradox'. The basis of this paradox is that soil microbial communities (the 'Sleeping Beauties') have the ability to digest almost any organic substrate yet are dormant most of the time, because they need assimilable carbon (food resources) but have a limited ability to move throughout the soil in order to reach these resources. Earthworms (the 'Prince Charming') secrete mucus ('the Kiss' = resources), move within the soil and provide the suitable temperature, moisture and organic resources within their guts for microbes to be activated' (Brown et al. 2000). This activation of the soil bacteria by an extra contribution of assimilable C, which can derive from soil fauna activity or from plant root exudates or rhizodeposits, is called a 'priming effect' (Kuzyakov 2002, 2010).

8. The importance of soil bacteria for biogeochemical nutrient cycling

Currently, the stability of Earth's environment is at risk. It has been estimated that three out of nine interlinked planetary boundaries (Earth-system processes) have been overstepped, with potentially disastrous consequences for humanity (Rockstrom et al. 2009). These are the rate of biodiversity loss (extinction), climate change and the nitrogen cycle (part of a boundary with the phosphorous cycle). To date it is not yet clear whether and to what extent bacteria are affected by extinction (Allison & Martiny 2008, Shade et al. 2012, Griffiths & Philippot 2013); however, climate change (Zhou et al. 2012, Frey et al. 2013, Hagerty et al. 2014) and the nitrogen cycle (Philippot et al. 2013b, Farrell et al. 2014, Mooshammer et al. 2014, Pansu et al. 2014) are strongly linked and partially driven by soil bacterial diversity and activity. The purpose of this chapter is to highlight the central role of soil bacteria in biogeochemical nutrient cycling in the light of global climate change.

8.1. Functions of soil bacteria in nutrient cycling

Carbon, nitrogen,and phosphorous are central chemical elements for all living beings. A lack of C, N and P in soils results in a decrease in plant productivity and hence a decreasing global food supply. Earth's prokaryotes store about the same amount of C and about the 10-fold amount of N and P as all plants, indicating a substantial relevance of bacteria to C, N and P nutrient cycling (Whitman et al. 1998). Here I briefly summarize mainly the soil part of the C, N and P nutrient cycles and the roles of bacteria in these (Figure 1C).

Carbon represents the molecular backbone of all organic molecules. All soil organisms leave behind posthumously dead organic material (which is part of the SOM) with molecular structures of a wide range of complexity (Kögel-Knabner 2002). The ecological contribution of micro-organisms such as fungi and bacteria is to demineralize the organic carbon into single-carbon molecules and to return it to the atmosphere mainly as carbon dioxide (CO_2) and to a far lesser extent as methane (CH_4) (IPCC 2007, Trivedi et al. 2013). Atmospheric CO_2 is then again fixed into organic carbon via photosynthesis by plants but also by many bacteria such as cyanobacteria and purple sulfur bacteria. Release of CO_2 into the atmosphere by bacteria is an ecologically important and necessary process, as all atmospheric CO_2 could be otherwise fixed by photosynthesis within 10–20 years (Fuchs 2014), which would then cease primary plant production. On the other hand, CO_2 is regarded as a greenhouse gas contributing to global climate warming. Quantitative and qualitative details of the participation of bacteria in the (soil) carbon cycle are presented elsewhere (Schimel & Schaeffer 2012, Zhou et al. 2012, Ibrahim et al. 2013, Wieder et al. 2013, Fernández-Martínez et al. 2014, van Groenigen et al. 2014).

The majority of the global nitrogen is in a gaseous N_2 form constituting 78% of the atmosphere. Plants require nitrogen sources for growth; however, plants cannot take up N_2 and N is often limited in soil. Some soil bacterial groups such as the root-colonizing rhizobacteria are capable of fixing gaseous N_2 to ammonium (NH_4^+) to the benefit of plant growth (Vacheron et al 2013). This ability is unique to bacteria and further demonstrates the ecological importance of soil bacteria. NH_4^+ is also the result of demineralization of proteins from dead organic material. In well aerated soils the relatively immobile NH_4^+ is oxidized by bacteria to the highly mobile nitrate (NO_3^-) in a process termed 'nitrification'. Plants can take up both NH_4^+ and NO_3^- as a source of nitrogen. Under anaerobic conditions in soil, the nitrate can be converted to atmospheric N_2, N_2O, NO_2^- or NO gases by a process termed 'denitrification', which additionally to nitrification can result in a substantial loss of nitrogen from soil (Houlton & Bai 2009, Fang et al. 2015). Further losses of N from soil are leaching of NO_3^- (both NO_3^- and soil particles are negatively charged, which prevents adsorption of NO_3^- to soil) and volatilization of ammonia (NH_3). Quantitative and qualitative details of the participation of bacteria in the (soil) nitrogen cycle are presented elsewhere (Gruber & Galloway 2008, Vlaeminck et al. 2010, Wang et al. 2010, Goll et al. 2012, Philippot et al. 2013b, Mooshammer et al. 2014).

In contrast to nitrogen, phosphorous is reasonably abundant in soils at 1.2 g per kg on average (Hinsinger et al. 2011). Weathering of rocks during soil formation is the only natural source of P, leading to a decrease in total P content over time (Yang & Post 2011). To some extent, soil bacteria participate in rock weathering (Cockell & Herrera 2008, Uroz et al. 2009, Lepleux et al. 2013). In contrast to C and N, which can be in different chemical stages during biological cycling, P is bioavailable for plants or bacteria only as inorganic soluble orthophosphate. However, only a minority (0.1%) of soil P is bioavailable for plants (Sharma et al. 2013) because the majority is either in organic form (e.g. incorporated in biomass, associated with SOM) or in inorganic insoluble form, e.g. adsorbed to soil minerals. Bacteria have developed several strategies to convert P either directly or indirectly into a bioavailable form (Sharma et al. 2013, Ahemad & Kibret 2014, Liu et al. 2015).

It is becoming increasingly clear that although the three cycles are different, they are ultimately interlinked with each other (Fig. 1C). Often C, N and P are combined in the same organic molecules (Nash et al. 2014) and the cycling of one nutrient can be driven by the microbial need of another (Spohn & Kuzyakov 2013a). Also, both plants and bacteria compete for N and P sources in soil. For a comprehensive understanding of nutrient cycling it is therefore necessary to view them in combination (Wang et al. 2010, Goll et al. 2012, Fernández-Martínez et al. 2014, Lin et al. 2014, White et al. 2014).

8.2. Controls of the biogeochemical nutrient cycles

The stability, dynamics and stoichiometry of biogeochemical nutrient cycles are affected by a wide range of parameters that can be grouped into three major categories. Several of these parameters have already been introduced above, but are discussed here in a joint context (Fig. 1C).

8.2.1. Microbial controls

The qualitative and quantitative combination of several parameters related to bacterial biology, as addressed below, strongly determines the stoichiometry of nutrient cycling and hence ecological consequences (Fig. 1C). Which bacteria are present in the soil (Nemergut et al. 2011, Nemergut et al. 2013, Rhodes et al. 2013), and which numerical and taxonomical fraction is physiologically active (Jones & Lennon 2010, Lennon & Jones 2011, Blagodatskaya & Kuzyakov 2013)? Which life history strategies (r- vs. k-) are represented in what fractions of the active bacteria (Fierer et al. 2007)? These questions are central to the fate-controlling step of allocation: what do microbes do with the nutrient they can access? How do they allocate them (Schimel & Schaeffer 2012)?

Furthermore, among the active bacteria, what are the rates of enzyme kinetics, growth efficiency, turnover and biomass production? These parameters affect the rate at which SOM is processed. The kinetics and endurance of exoenzymes that are responsible for the breakdown of polymeric carbon sources may determine the growth efficiency of bacteria (i.e. the doubling rate) and hence the total biomass of bacteria (Hagerty et al. 2014). Microbial turnover is determined by microbial cell production and cell death. Dead cells can join the pool of soil organic carbon (SOC) or be metabolized by living microbes (Hagerty et al. 2014). Soil microbes compete with each other (Cornforth & Foster 2013) but also cooperate (Nadell et al. 2009, Burmølle et al. 2012, Claessen et al. 2014, Ren et al. 2015). Bacteria further differ in their carbon (CUE) and nitrogen (NUE) use efficiency. CUE is the efficiency by which bacteria convert organic C taken up into biomass C (e.g. growth) whereas the remaining C is typically respired (Allison 2014). NUE describes the partitioning of organic N taken up between growth and the release of inorganic N to the environment (i.e. N mineralization) (Mooshammer et al. 2014). The carbon 'priming' effect characterizes the increase in microbial activity due to the addition of fresh biomass (Kuzyakov 2002, 2010).

8.2.2. Natural biotic and abiotic controls

The above-addressed microbial parameters (in sum: microbial activity) are embedded in the abiotic and biotic characteristics of the habitat (Fig. 1C). The spatial and temporal scales influence microbial activity (Fierer & Ladau 2012). Spatial heterogeneity on the microscale is determined by, for example, soil type and structure, soil fauna density and activity, and intensity of root penetration and density, which itself is in part determined by the above-ground plant community. The scales of spatial variation within a local soil sample can vary from a range of several mm (diameter of the drilosphere) down to a few µm (Ruamps et al. 2011), which has at all spatial levels consequences for nutrient cycling (Brown et al. 2000, Andriuzzi et al. 2013, Ruamps et al. 2013, Spohn & Kuzyakov 2013b, Dallinger & Horn 2014). Spatial distance on the microscale determines the accessibility of SOM to bacteria (Schimel & Schaeffer 2012). If the SOM is too distant from the bacterial cells then accessibility, but not the catabolic process rate, is the limiting step. The microscale spatial heterogeneity in soil not only determines spatial distribution and community diversity but also the activity of soil bacteria. It has therefore been suggested to introduce the concepts of microbial hot spots and hot moments, which are characterized by a process rate of microbial activity that can be increased by several orders of magnitude compared to surrounding soil at very close distance (Kuzyakov & Blagodatskaya 2015). The rhizosphere affects biogeochemical cycling differently than does the prokaryotic community in the bulk soil. For example, active roots consume oxygen and thereby increase the anaerobic volume of the soil. This, in turn, along with the carbon-rich rhizosphere of active roots, increases the bacterial denitrification rate and thus promotes loss of nitrogen from soil (Henry et al. 2008, Philippot et al. 2013a). However, as loss of N from soil is detrimental for plants, some plants have evolved the ability to a priori prevent the bacteria-driven conversion of the relatively immobile NH_4^+ to the highly mobile NO_3^- by delivering nitrification inhibitors by the roots to soil-nitrifier sites (Subbarao et al. 2009).

The temporal scale may relate to hourly, circadian, seasonal, decadal or even longer cycles (Ibrahim et al. 2013, Regan et al. 2014). For example, on a circadian scale, photosynthesis drives, with a certain lag period, the amount of root exudates released to the rhizosphere. Periods of reduced photosynthesis may represent a period of substrate limitation for soil bacteria (Kuzyakov & Gavrichkova 2010). Similarly, on a seasonal scale, changes in root biomass and root-specific activity should be considered (Kuzyakov & Gavrichkova 2010). Another temporal effect can be observed for 'priming' via earthworms. Fresh and few-days-old casts lead to an increased microbial activity and mineralization processes over a few years. However, as casts age and with longer timescales (years to decades) of earthworm colonization of new sites, the stimulatory effects are reduced and static effects begin to predominate, promoting C and N conservation and a regulation of microbial activity (Brown et al. 2000). However, also independent of interactions with plants or soil fauna, seasonal differences, for example a winter and a summer N cycle, have been observed (Schmidt et al. 2007).

On the local scale, physicochemical and edaphic parameters such as soil type, structure, moisture, pH, temperature and aeration affect rates and directions of nutrient cycling. On a global scale, the macroclimate (hot and cold deserts, moderate climate, Alpine and Arctic soils) additionally strongly shapes the bacterial community structure and activity (Wilhelm et al. 2011, Macrae et al. 2013, Rhodes et al. 2013, Kim et al. 2014, Koyama et al. 2014, Deng et al. 2015, Neiderberger et al. 2015).

8.2.3. The impact of human civilization

The global ecology is currently challenged by the Anthropocene (Rockstrom et al. 2009, Corlett 2015). To what extent is bacterial soil ecology affected by human influence such as global warming, elevated CO_2 through massive fossil fuel burning, or by the massive agriculture characterized by heavy entry of inorganic N and P fertilizers and conventional tillage management practice (Fig. 1C)?

8.2.3.1. Global warming

There appears to be some agreement on the prediction that global warming will result in a positive feedback loop for carbon cycling (Heimann & Reichstein 2008), despite some controversy (Davidson & Janssens 2006). The warmer the climate, the larger the bacterial activity and respiration, the higher the CO_2 release from soil to atmosphere. Indeed, short-term experiments have shown that soil microbial respiration increases exponentially with temperature (Karhu et al. 2014). It is, however, not clear if this observation can be generalized, as others have observed in long-term field experiments an attenuation of CO_2 loss upon prolonged warming (Luo et al. 2001). One explanation for this decay could be the loss of readily decomposable C sources. Indeed, the temperature-dependent soil microbial efficiency for CO_2 production by respiration also appears to depend on the type of available C substrate (Frey et al. 2013). Depending on the soil characteristics, soil respiration can either be attenuated or even further enhanced during global warming. Enhancing responses were generally more common in soils with high C content, high C:N ratios and low pH values, suggesting that sensitivity to temperature may differ between the microbiologically driven parts of the C-cycle and N-cycle processes (Karhu et al. 2014). Other authors discussed the impact and feedback loops of warming-induced changes in the plant community structure and physiology on the changes of the soil microbial efficiency for carbon respiration (Zhou et al. 2012). It is still to some extent unclear which bacterial properties account for changes in microbial C respiration due to global warming. Whereas some authors do not see an impact of microbial biomass change (Karhu et al. 2014), others suggest that a decline in biomass, and also in degradative enzymes, weakens the positive feedback loop of global warming and the carbon cycle (Allison et al. 2010). Specifically, reduced carbon use efficiency (CUE) limits the biomass of bacterial decomposers and mitigates the loss of soil carbon (Allison et al. 2010). The effect of global warming may be even larger on methane (CH_4) than on CO_2 release to the atmosphere. Methane has 25 times more the global warming potential than CO_2 over a 100-year time frame, and due to microbial activities, wetlands are the single largest natural CH_4 source with about a third of total global emissions (Bridgham et al. 2013). Due to global warming, the fraction of methane due to soil (wetland) bacterial activity is estimated to increase strongly (Mackelprang et al. 2011, Klupfel et al. 2014).

8.2.3.2. Elevated concentrations of carbon dioxide (eCO_2)

Emissions of CO_2 from fossil fuel combustion and cement manufacture are responsible for more than 75% of the increase in atmospheric CO_2 concentration since pre-industrial times (Denman et al. 2007). The remainder of the increase comes from land use changes dominated by deforestation (and associated biomass burning) with contributions from changing agricultural practices. All these increases are caused by human activity (Denman et al. 2007). How does elevated CO_2 (eCO_2) affect bacterial carbon cycling in soil? Is there a positive (soil C loss) or a negative (C sequestration) feedback of eCO_2 (He et al. 2010)?

The effects of eCO_2 on soil bacteria appear to be mainly indirect through increased plant biomass and changed rhizosphere deposits and root exudation. It was found that bacterial biomass increases and community composition changes strongly (He et al. 2010); evidence for a general positive feedback loop of eCO_2 to carbon cycling was found in several instances (Carney et al. 2007, Nie et al. 2013, He et al. 2014). In part, the abundance of genes involved in autotrophic CO_2 fixation and also N_2 fixation increased, suggesting the stimulation of C and N cycles by eCO_2 (He et al. 2014). Interestingly, the increase in soil C turnover with rising eCO_2, which exerts a priming effect on the soil bacteria, leads to lower equilibrium soil C stocks than expected from the rise in soil C input alone, indicating that faster decomposition is a general mechanism limiting C accumulation in soil (van Groenigen et al. 2014).

8.2.3.3. Negative effects of high N and P fertilization and conventional tillage management practices.

The heavy load of inorganic N and P fertilizers is a major source of environmental pollution and poses a serious challenge to (soil) ecology (Foley et al. 2005, Gruber & Galloway 2008, Rockstrom et al. 2009, Sharma et al. 2013). Soil bacterial conversion of fertilizer N by denitrification is a major source of the strong increase in nitrous oxide (N_2O), a potent greenhouse gas (Giles et al. 2012, Harter et al. 2014). But also the soil microbial community is directly and potentially negatively affected as N fertilization, irrespective of which type, was found to inhibit soil bacterial respiration (CO_2 production) by up to 60% over a period of up to 45 days (Ramirez et al. 2010). It has also been observed that increased (conventional) tillage management practices can strongly change soil microbial community structure and biomass compared to reduced or no-tillage practices (Aslam et al. 2013, van Kessel et al. 2013, Carbonetto et al. 2014, Ghimire et al. 2014).

In order to overcome the negative effects of inorganic N and P fertilization on both the global ecosystem and, in part also, the soil bacterial flora, recently a variety of alternative N and P fertilizers (e.g. biochar, organic P) have been proposed that are ecologically favourable and also sustain and stimulate the soil bacterial flora (Harter et al. 2014, Nash et al. 2014, Liu et al. 2015).

8.3. Modelling approaches

The ecologically important and complex process of interlinking C, N and P cycles has prompted researchers to investigate modelling approaches. In the last 80 years, more than 200 mathematical biogeochemical models of different levels of complexity have been developed to describe biogeochemical processes in soils, spanning spatial scales from a few mm to thousands of km and temporal scales from hours to centuries (Manzoni & Porporato 2009). Soil biogeochemical models describe a system including SOM constituents (both passive substrates and active biological decomposers), interacting with inorganic compounds and environmental variables, and subject to external inputs and outputs (Wang et al. 2007, Manzoni & Porporato 2009, Pansu et al. 2010, Wang et al. 2010, Faybishenko & Molz 2013, Ibrahim et al. 2013, Sinsabaugh et al. 2013, Pansu et al. 2014, White et al. 2014). However, most of these models do not explicitly take into account the mechanistic role of micro-organisms. The MOMOS model (Modeling Organic Transformations by Microorganisms of Soils) is one of the few models that explicitly put bacteria into the focus. It is based on the functional ecology of soil microbial biomass, which increases by enzymatic assimilation of labile and stable vegetal necromass and labile and stable humus and decreases by microbial respiration and mortality (Pansu et al. 2010, Ibrahim et al. 2013). All MOMOS parameters depend on soil moisture content and temperature. In an experimental application MOMOS enabled adequate prediction of total and microbial carbon dynamics during the decomposition of a standard plant material in six extremely contrasting tropical environments (Ibrahim et al. 2013). Climate, together with basic soil properties such as texture and pH, was the main driver of soil respiration and organic matter dynamics when a large range of conditions was considered. Another very recent carbon-cycle model focusing on soil microbes is PECCAD (PEsticide degradation Coupled to CArbon turnover in the Detritusphere) (Ingwersen et al. 2008, Pagel et al. 2014). This model distinguishes different microbial groups (bacteria, fungi, and specific pesticide degraders), different carbon sources (readily available high quality C, less easily decomposable low quality C, and pesticide carbon either in solution or in sorbed phases). Growth of the different microbial groups based on the consumption of the different carbon pools is based on Monod growth kinetics. This model is highly suited to study regulation mechanisms of accelerated pesticide degradation (in the context of priming effects) in the detritusphere (Ingwersen et al. 2008, Pagel et al. 2014).

9. Resistance and resilience of microbial communities to disturbance

Stability of microbial soil composition and function is important for global ecosystem functioning; however, stability is often challenged by natural as well as human-driven disturbances. Upon disturbance, a community can face three fates. If the community stays the same, it is regarded as being resistant. If, after being altered upon disturbance, it returns to the original composition it is regarded as being resilient. Functional redundancy characterizes a community composition that is persistently altered but performs like the original community (Allison & Martiny 2008). The stability of a soil bacterial community, characterized by resistance and resilience, is influenced by ecosystem drivers such as trophic structure, metacommunity properties, time/space heterogeneity, disturbance regime, and resources and temperature, which influences biological attributes on three levels, the individual, the population and the

community. Biological attributes contributing positively to stability are (i) stress tolerance, plasticity and dormant states at the level of individuals, (ii) stochastic gene expression, growth rate, adaptability and dispersal rate at the level of populations, and finally (iii) alpha-diversity, microbial interactions (networks) and turnover rates at the level of communities (Shade et al. 2012). Overall, the composition of most microbial groups, not only in soils, is sensitive and not immediately resilient to disturbance, regardless of the taxonomic breadth of the group or the type of disturbance (Allison & Martiny 2008, Griffiths et al. 2008, Shade et al. 2012, van Elsas et al. 2012, Griffiths & Philippot 2013, López-Lozano et al. 2013).

The disturbance of the microbial community can have drastic consequences. A single horizontal gene transfer event between two very distant prokaryotes, a bacterial *Clostridium* and an archaeal *Methanosarcina*, coincided with massive Siberian volcanism leading to a peak in nickel concentration. As a result, without going into the causal details described elsewhere (Rothman et al. 2014), this enabled a massive expansion of the methane-producing *Methanosarcina*, resulting in a substantial disturbance of the CO_2 carbon cycle and a depletion of O_2 oxygen to the benefit of methane increase leading to a strong greenhouse effect. These events coincided with the end-Permian extinction ca. 252 million years ago that marks one of the greatest taxonomic extinction losses ever observed worldwide and puts the microbe *Methanosarcina* as being responsible for this. These results indicate the exquisite sensitivity of the Earth's system to the disturbance and subsequent evolutionary change of microbial life (Rothman et al. 2014).

10. Theory of microbial ecology in soil

Macroecology examines the relationship between organisms and their environment on large spatial (and temporal) scales. Typically, macroecology explains the large-scale patterns of abundance, distribution and diversity in terms of species-area, distance-decay and productivity-diversity relationships (Keith et al. 2012, Soininen 2012). Macroecology has benefited from, and has also driven, concepts such as diversity-stability theory, resource-ratio theory and metabolic scaling theory (Beck et al. 2012, Soininen 2012).

Macroecology and macroecological theory was originally developed for macro-organisms. Currently, microbial ecology lacks theoretical concepts, and there is an active debate over whether macroecological theory and concepts can be adopted one-to-one to micro-organisms or if the peculiarities of bacteria such as those addressed in this review (e.g. the enormous cell number and density, high taxonomic diversity and heterogeneity of bacterial community composition on special scales ranging from a few µm to thousands of km) afford the development of ecological theory specifically for bacteria (Prosser et al. 2007, Barberan et al. 2014).

The time is ripe for including theory in microbial (soil) ecology since the technical advancements in microbiology put microbial ecology in a unique position in the larger field of ecology. From a single (soil) sample it is possible to determine a community's biodiversity, gene expression and metabolite production, providing insight into system-level stability. This provides microbial ecologists with the opportunity to address global principles in a manner that is not easily available in the broader field of ecology (Shade et al. 2012).

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