

## REVIEW ARTICLE

# Biophysical processes supporting the diversity of microbial life in soil

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Tel: +41 44 633 6015; Fax: +41 44 633 1123; E-mail: [dani.or@env.ethz.ch](mailto:dani.or@env.ethz.ch)**One sentence summary:** Soil microorganisms live in complex pore spaces where nutrient heterogeneity and water dynamics play a fundamental role in shaping their ecology, diversity and functions at all scales.

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## ABSTRACT

Soil, the living terrestrial skin of the Earth, plays a central role in supporting life and is home to an unimaginable diversity of microorganisms. This review explores key drivers for microbial life in soils under different climates and land-use practices at scales ranging from soil pores to landscapes. We delineate special features of soil as a microbial habitat (focusing on bacteria) and the consequences for microbial communities. This review covers recent modeling advances that link soil physical processes with microbial life (termed biophysical processes). Readers are introduced to concepts governing water organization in soil pores and associated transport properties and microbial dispersion ranges often determined by the spatial organization of a highly dynamic soil aqueous phase. The narrow hydrological windows of wetting and aqueous phase connectedness are crucial for resource distribution and longer range transport of microorganisms. Feedbacks between microbial activity and their immediate environment are responsible for emergence and stabilization of soil structure—the scaffolding for soil ecological functioning. We synthesize insights from historical and contemporary studies to provide an outlook for the challenges and opportunities for developing a quantitative ecological framework to delineate and predict the microbial component of soil functioning.

**Keywords:** soil microbiology; microbial ecology; vadose zone; soil physics; microbial interactions; bacterial communities

## INTRODUCTION

Microorganisms have been named ‘stewards of the biosphere’ (Jansson and Fredrickson 2010), and perhaps nowhere else on the planet is this title more fitting than in soil. Globally, soil microbes are the drivers of key biogeochemical cycles involving carbon, nitrogen, phosphorus, iron and more. Their activity contributes to a wide variety of soil ecosystem functions, including the cycling of organic matter and nutrients, and the emergence of soil structure. These functions are tightly associated with essential ecosystem goods (e.g. food, fiber, wood) and services (regulating greenhouse gas emissions, sequestering carbon,

assuring water quality, mitigating erosion, attenuating pollutants, suppressing pathogens and promoting plant growth) (Brussaard 2012). Microbial activity is thus essential to a healthy and fertile soil. This is a crucial fact at a time where threats to soil quality and fertility are mounting at an alarming rate. The centrality of soil services to life on the planet prompted the Food and Agricultural Organization of the United Nations to declare 2015 the international year of soils (FAO 2015) in an effort to raise global awareness regarding soil’s role and the urgent need to preserve this thin layer of the terrestrial surface that teems with life (Wallander 2014).

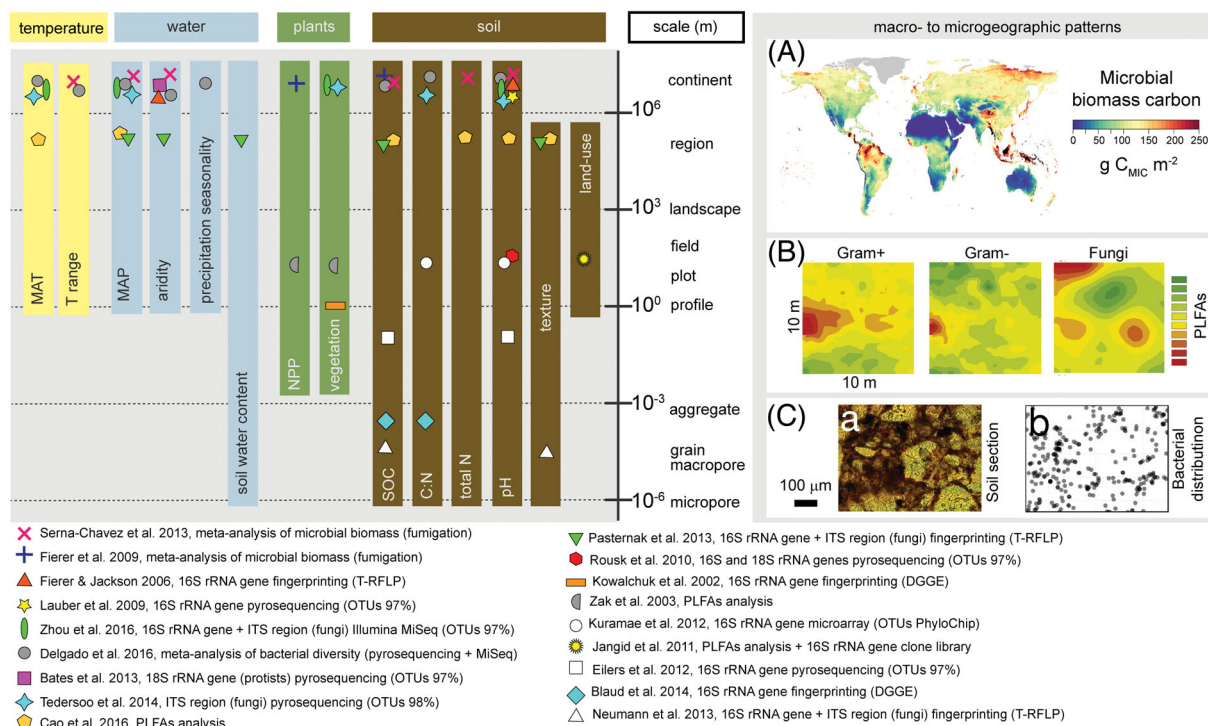
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Some portray soil as an unfavorable habitat for microbial life due to its harsh and fluctuating environmental conditions, yet evidence suggests that microorganisms thrive in soils (Stotzky 1997). One gram of surface soil may contain  $10^9$ – $10^{10}$  prokaryotic cells (bacteria and archaea),  $10^4$ – $10^7$  protists,  $\sim 100$  m of fungal hyphae and  $10^8$ – $10^9$  viruses (Srinivasiah et al. 2008; Bates et al. 2013; Bardgett and van der Putten 2014; Brady and Weil 2014). These values translate to prokaryotic biomass exceeding 5 tons per hectare in some soils, with fungal biomass ranging from 1 to 15 tons (Brady and Weil 2014). Soils also host tremendous genetic diversity: community DNA reassociation methods (Torsvik and Øvreås 2007) have shown that the total genomic diversity of bacterial communities from unperturbed pasture soils may exceed the diversity found in aquatic communities by three orders of magnitude, with the highest diversity estimates ranging from thousands to millions of distinct prokaryotic species (or OTUs, operational taxonomic units) per gram of soil (Torsvik and Øvreås 2002; Torsvik, Øvreås and Thingstad 2002; Gans, Wolinsky and Dunbar 2005; Schloss and Handelsman 2006; Roesch et al. 2007). Moreover, a few grams of soil contain hundreds of fungal and protistan species (Bates et al. 2013; Peay, Kennedy and Talbot 2016). Presently, the true extent of microbial diversity can only be estimated, not yet measured (Locey and Lennon 2016; Peay, Kennedy and Talbot 2016). Our limited knowledge of biodiversity and its links with specific ecosystem functions has motivated several soil metagenomics initiatives in the past few years (Nesme et al. 2016), notably the TerraGenome consortium in 2009 (Vogel et al. 2009), the Earth Microbiome Project in 2010 (Gilbert, Jansson and Knight 2014) and in 2014 the Brazilian and Chinese Microbiome Projects. In 2015, a group of researchers called for a unified international microbiome initiative (Alivisatos et al. 2015; Dubilier, McFall-Ngai and Zhao 2015). These large research campaigns have resulted in a wealth of genomic information, but it has also been suggested that harnessing the full potential of such data requires their integration into coherent ecological and theoretical frameworks that would enable systematic study of long-standing questions and test hypotheses and new theories (Prosser et al. 2007; Prosser 2015). An essential element for such frameworks is the nature of the soil habitat itself. The shallow part of the so-called critical zone (a domain extending from groundwater to plant canopies above) comprises unsaturated soil, a thin region that supports all terrestrial plants and is a product of the biological activity it hosts. A fundamental trait of soil functioning is its structure: the arrangement of particles of varying sizes, often glued by soil organic matter, that defines the complex pore spaces inhabiting microbial life, retaining water and nutrients and providing pathways for gas transport and cell dispersion (Crawford et al. 2005). Dynamic variations in water availability, both over space and time, affect the diffusion processes that shape microbial life in soil (Koch 1990). These variations, combined with a patchy distribution of organic resources, create unique environmental conditions for the development of microbial life. Overall, the immense degree of spatial and temporal heterogeneity found in soil makes it one of the most complex and dynamic compartments of the biosphere, harboring myriads of niches and promoting a vast array of microbial adaptations. As Patrick Lavelle nicely put it: 'Understanding these adaptations requires a holistic view of the nature of soils, linking physical, chemical, and biological processes and trying to understand what being a bacterium or a collembolan in this environment actually entails' (Lavelle 2012). Quantitative description and understanding of microbial life in soil is necessarily a cross-disciplinary endeavor that must integrate inputs from microbial

ecology, soil physics, environmental chemistry, agronomy and more.

Not only is microbial diversity unparalleled in soil environments, but it is also observed at all scales, from single grains to soil profiles, from landscapes to geographic regions. This wealth of diversity raises many questions (Prosser 2012; Shade 2016). What are the ecological and evolutionary mechanisms that foster microbial diversity? What dynamics govern the distribution of diversity over space and time? What are the links between microbial diversity and the emergent functions of soil ecosystems? Knowledge has not advanced yet to adequately address these daunting questions, partly because of the complexity of the intertwined deterministic and stochastic processes at play (Dumbrell et al. 2010; Stegen et al. 2012; Konopka, Lindemann and Fredrickson 2015). Yet, the identification of general underlying principles could provide a theoretical basis required for rudimentary processes quantification and a certain degree of prediction (Curtis and Sloan 2005). We argue that progress in addressing these ecological questions and advancing predictive capabilities requires development of quantitative models that integrate key biophysical and ecological processes at spatial and temporal scales relevant for microbial life in soil. This view, which was first formulated by Young and Crawford (2004), is now shared by a rapidly growing scientific community from a variety of fields that jointly work to advance the quantitative basis of soil microbial ecology. Along these lines, the primary objective of this review is to offer a qualitative and quantitative assessment of the biophysical—especially hydrological—characteristics that define microbial habitats in soil, and to discuss how these characteristics affect microbial diversity and activity. The present review follows the footsteps of studies that highlighted the crucial role of biophysics in soil microbial ecology (Young and Crawford 2004; Or et al. 2007; Young et al. 2008; Hinsinger et al. 2009), while pointing at the large body of research accumulated within the past decade. A more recent (and highly recommended) review by Vos et al. (2013) has addressed microscale factors influencing bacterial diversity in soil and the experimental methods currently available to explore microhabitats. While the present review shares the general scope covered by Vos et al., it emphasizes recent advances in modeling that link physical processes with the response of microbial populations in soil. The focus on modeling quantitative physical processes and hydrologically mediated mechanisms is thus complementary to the review of Vos et al., which elaborated more on technological and methodological advances. We discuss the soil habitat in general, with examples stemming from very distinct ecosystems (forest, desert, grassland, agricultural, etc.). We do not offer a detailed examination of the rhizosphere habitat, although we discuss it on several occasions (readers interested in this specific topic should consult the reviews of Hinsinger et al. 2009; Mendes, Garbeva and Raaijmakers 2013; Philippot et al. 2013 and York et al. 2016). Considering the complexity of the soil-microbe environment, a certain degree of simplification and focus is inevitable. Consequently, the review focuses primarily on bacteria, the most abundant cellular life forms in terrestrial habitats. Nevertheless, we discuss archaea, protists and fungi where appropriate and relevant. Viruses are important players in the soil ecosystem; however, consideration of their role in any detail is beyond the scope of the review. We begin with reviewing the distribution of soil microorganisms across space and time (i.e. their biogeography), and how such patterns pertain to physicochemical conditions. We then explore the physical nature of the soil as a microbial habitat with an emphasis on the aqueous phase architecture, and discuss aspects of soil microbiology specific to terrestrial environments.



**Figure 1.** Climate and biophysical factors influencing microbial geographic patterns from continent to pore scale. Each bar represents the expected range of spatial scales over which a factor can produce changes in microbial abundance or diversity. MAT: mean annual temperature; T range: annual or diurnal temperature range; MAP: mean annual precipitation; NPP: plant net primary production; SOC: soil organic carbon; C:N: carbon to nitrogen ratio; total N: total nitrogen. Symbols refer to a selection of specific studies demonstrating factor effects on abundance or diversity, with the symbol position indicating the approximate scale considered in the study. The references also indicate which type of method was used. Examples of microbial biogeographic patterns at various scales are shown. (A) Global distribution estimates of microbial biomass carbon ( $C_{MIC}$ ) per square meter of soil. Adapted from Serna-Chavez, Fierer and Bodegom (2013) with permission from John Wiley and Sons. [This image is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.] (B) Kriged maps of bacterial and fungal phospholipid fatty acids (PLFAs) biomarkers in a grassland soil at the meter scale. Adapted from Regan et al. (2014). (C) View of soil microhabitats in a soil thin section and corresponding observed bacterial distribution at the microscale, with darker shades indicating higher probability of bacterial presence. Adapted from Raynaud and Nunan (2014).

Certain biophysical processes that control microbial life in soil are examined in some detail. We conclude by identifying some significant challenges and outlooks in the field.

## THE MACROGEOGRAPHY AND MICROGEOGRAPHY OF SOIL MICROBES

Microbial biogeography is a rapidly expanding field that provides climatic and large-scale context to soil microbial life. We limit the review to a few important aspects of this large field, highlighting the variety of scales and processes at play (Fig. 1).

Microbial life is found in all terrestrial environments on Earth. By virtue of their adaptation and metabolic versatility, microorganisms function not only in temperate soils but also in the most forbidding hottest and coldest deserts (albeit at a lower abundance). Considering the vast diversity of soil microbial life, the difficulty of peering into the soil, and diverse biomes and niches, a definitive determination of global soil microbial distribution is not possible with any degree of accuracy. Instead, it is estimated based on data collected at smaller scales and using various modeling approaches to constrain the values and extrapolate (Fig. 1A). Recent estimates (Fierer et al. 2009; Serna-Chavez, Fierer and Bodegom 2013; Xu, Thornton and Post 2013) suggest that microbial biomass varies within and across biomes by up to three orders of magnitude primarily due to moisture availability and soil nutrients, but is only weakly related to to-

tal plant biomass. Across biomes, increased organic C availability and near-neutral pH are associated with increased microbial biomass regardless of climate conditions. The ratio of microbial carbon to organic carbon in the topsoil often ranges from 1% to 3% and is driven by climate and soil characteristics (Fierer et al. 2009; Serna-Chavez, Fierer and Bodegom 2013; Xu, Thornton and Post 2013). Microbial abundance is thus variable across earth terrestrial habitats, and although it shares similarities with the distribution of plant and animal biomass (for example, high abundance in the tropics), they also differ in important ways (notably with higher than expected microbial biomass in grassland and tundra soils).

Microbial diversity at continental scales was investigated during the past decade thanks to molecular fingerprinting and sequencing techniques. It is worth noting that findings strongly depend on the taxonomic or phylogenetic rank under study (Martiny et al. 2006; Philippot et al. 2010). While certain microbial phyla are found virtually in all soils across the globe (Ramette and Tiedje 2007; Van Elsas et al. 2007b), at the genus and species levels microorganisms are not randomly distributed on the planet (Martiny et al. 2006). Non-random distributions may reflect selective pressures of the environment or local historical contingencies (dispersal limitations). Although it has been assumed in the past that microorganisms are generally not dispersal limited ('everything is everywhere', Baas-Becking 1934; O'Malley 2007), mounting evidence suggests that dispersal limitations contribute to soil microbial diversity and promote

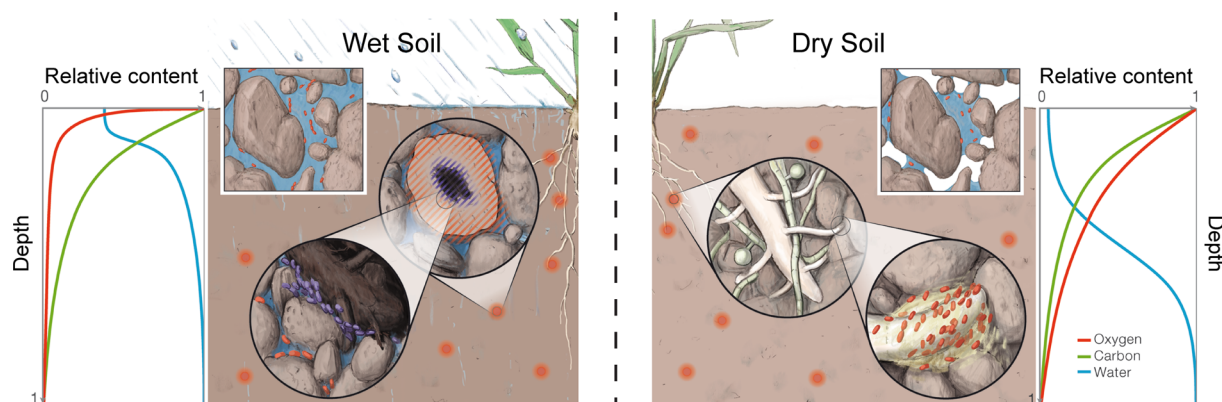
regional endemism (Cho and Tiedje 2000; Fulthorpe et al. 2008; Andam et al. 2016). The pioneering work of Fierer et al. (Fierer and Jackson 2006; Lauber et al. 2009) explored the diversity of bacterial communities in soils across South and North America and across different biomes. Their findings suggest that soil characteristics, in particular soil pH, are the best predictors of bacterial community composition at the continental scale, whereas variables such as latitude, mean annual temperature and potential evapotranspiration (which are good predictors of the distribution of plants and animals) are poorly related to bacterial diversity. Soil communities from different biomes but sharing relatively similar acidity conditions (for example, temperate and tropical forests) thus tend to cluster together in diversity analysis. These studies suggest that similarities between bacterial communities are controlled more by environmental factors than by geographic distances, at least at the continental scale and at a low taxonomic resolution (Fierer and Jackson 2006; Lauber et al. 2009; Chu et al. 2010). More recent studies at higher taxonomic resolution of bacterial diversity indicate that temperature may play a larger role than previously thought in shaping community composition (Garcia-Pichel et al. 2013; Zhou et al. 2016). Similar to plant and animal communities, bacterial communities are also generally comprised the same most dominant phyla in soil, e.g. *Acidobacteria*, *Actinobacteria*, *Proteobacteria*, *Bacteroidetes* and *Verrucomicrobia* (Janssen 2006; Fierer et al. 2009; Lauber et al. 2009; Chu et al. 2010; Fierer et al. 2012). We note, however, that many species (OTUs) are present in soil at very low abundance and constitute a so-called rare biosphere (Lynch and Neufeld 2015). The rare biosphere contributes to a large part of the total microbial diversity, and to the resilience of the community where some rare taxa can have a disproportionate effect on various ecosystem processes (Lynch and Neufeld 2015). Associations between specific soil bacterial communities and biomes are relatively weak, with the exception of desert soils which apparently harbor distinct communities, with notably high abundance of *Cyanobacteria* (Fierer et al. 2012). Archaeal to bacterial biomass ratio can vary across soil types but usually does not exceed 10% (Roesch et al. 2007). Fungal to bacterial biomass ratios vary significantly across biomes (with the lowest values found in desert and grassland soils, which are dominated by bacteria) (Fierer et al. 2009), and they correlate well with soil pH and C/N ratio (Fierer et al. 2009; Orgiazzi et al. 2016). In contrast to bacteria and archaea, the distribution of soil fungi and protists are less sensitive to soil pH and more influenced by climate and latitudinal gradients (Bates et al. 2013; Tedersoo et al. 2014; Peay, Kennedy and Talbot 2016). To sum up, the factors influencing biodiversity at the continental scale vary between microbial and macrobial communities, but differences are more marked for prokaryotes than for microbial eukaryotes.

At regional scales, various factors contribute to the differentiation among ecosystem types, including precipitation, temperature, location, vegetation and soil characteristics (Cao et al. 2016). Microbial community structure can be influenced by elevation gradients in mountainous regions (Lipson 2007; King et al. 2010; Pellissier et al. 2014; Yashiro et al. 2016) as well as precipitation gradients in arid and semi-arid regions (Angel et al. 2010; Pasternak et al. 2013). However, and in stark contrast to plants and animals, prokaryotic diversity is not constrained by precipitation in arid ecosystems (Angel et al. 2010). At local (field) scale, pH gradients have been shown to influence microbial populations, although the effects are stronger for bacterial diversity than for fungal diversity (Rousk et al. 2010). The importance of above-ground vegetation types and patterns has also been documented (Marschner et al. 2001; Kowalchuk et al. 2002; Zak et al.

2003; Wardle et al. 2004; Kulmatiski and Beard 2011), but its effects appear at smaller scales (e.g. plant vicinity). Patchy distributions of microbial biomass and diversity can thus be observed at the meter scale (Fig. 1B), often in association with the location of an individual plant or plant populations (Ettema and Wardle 2002; Franklin and Mills 2003). Land-use and soil management are other important factors influencing soil microbial diversity at the profile and field scale. Agricultural soils, for example, host markedly different microbial community structures relative to uncultivated soils (Buckley and Schmidt 2001, 2003; Jangid et al. 2008; Wu et al. 2008; Fierer et al. 2013). Many management practices affect physicochemical conditions in soils: crop cultivation (changes in soil texture and nutrients content), tillage (disruption of aggregate structure and exposure of protected carbon), irrigation and drainage (changes in soil moisture) or addition of fertilizer (changes in nutrients content and C/N ratio). Overall microbial abundance is higher and diversity lower in arable soils compared to pasture soils (Torsvik, Øvreås and Thingstad 2002). Studies have documented the effects of specific cultivation practices on the structure of bacterial, archaeal or fungal communities, notably for N fertilization and liming (Kennedy et al. 2004; Jangid et al. 2008; Ramirez et al. 2010; Rousk et al. 2010; Keil et al. 2011). Overall, contrasting findings suggest that the relative importance of land-use and soil characteristics on microbial diversity varies across lands and microbial groups.

Soil microbial composition does not only change spatially but also temporally, and over time scales ranging from hours to millennia (Bardgett and van der Putten 2014; Orgiazzi et al. 2016). Soil environments are highly dynamic, as illustrated by the rapid changes induced by rainfall events (Fig. 2). For example, it has been shown that bacterial communities from grassland soils respond to rewetting (after seasonal draught) within hours to days, with significant changes in the relative abundance of ecologically important phyla (Cruz-Martínez et al. 2012; Placella, Brodie and Firestone 2012; Barnard, Osborne and Firestone 2013), and similar changes have been observed following rare wetting events in desert soil (Štoviček et al. 2017). Seasonal changes in climate and vegetation have detectable effects on the composition of bacterial and fungal communities (Schutter, Sandeno and Dick 2001; Buckley and Schmidt 2003; Schadt et al. 2003; Kennedy et al. 2006; Lauber et al. 2013; Regan et al. 2014). Microorganisms can respond rapidly to environmental fluctuations (rainfall), but, importantly, community composition does not change drastically or immediately in response to modified soil properties, land-use or vegetation. Instead, effects build over years (Buckley and Schmidt 2003; Kulmatiski and Beard 2011). For this reason, soil microbial communities can be described at the same time as very dynamic systems (relative abundances of taxa change over hours or days in response to stimuli) and as highly resilient systems (over long periods microbial communities resist better to perturbations than macrobial communities) (Cruz-Martínez et al. 2009; Barnard, Osborne and Firestone 2013; Williams et al. 2013).

Microbial presence and function vary with depth in the soil profile. The patterns are driven by strong vertical resource gradients and stratification of nutrients, water availability, oxygen, pH and temperature that give rise to distinct environments for microbial life (Fig. 2). A well-documented distribution pattern is the exponential decline in microbial (archaea, bacteria, fungi and protozoa) biomass, diversity and activity observed as function of soil depth, from the nutrient-rich, aerated topsoil to the nutrient-poor, water-saturated subsurface (Ekelund, Rønn and Christensen 2001; Blume et al. 2002; Zhou et al. 2002; Fierer, Schimel and Holden 2003; Lehman 2007; Hartmann et al.



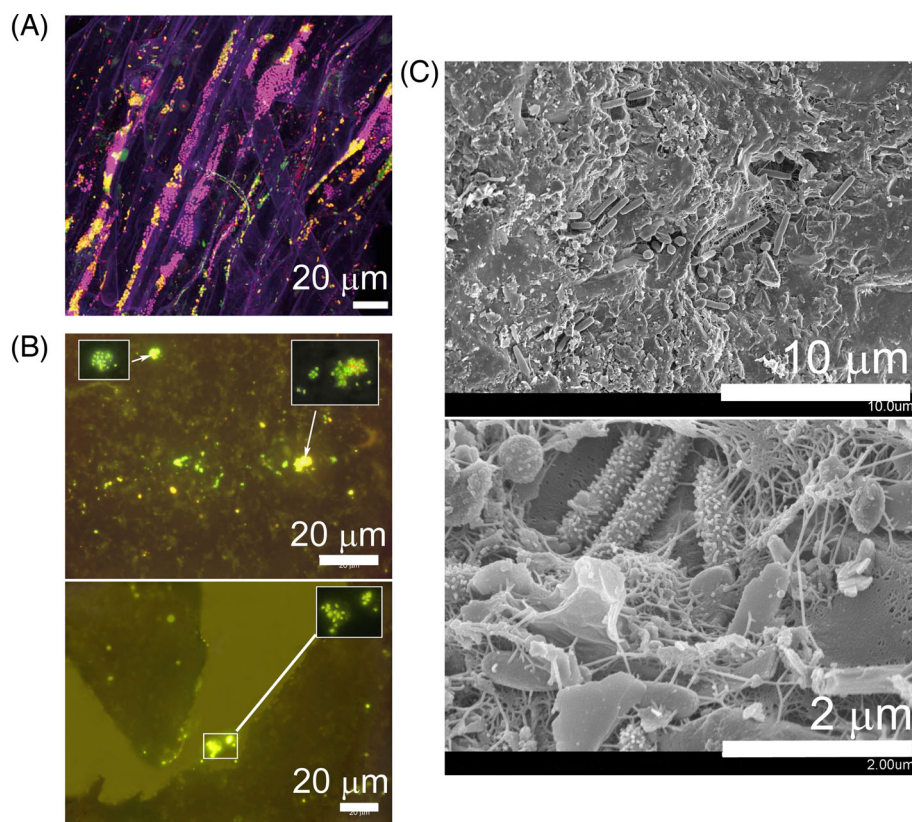
**Figure 2.** Microbial hotspots and hydration conditions in soil. Conceptual illustration shows hotspots of microbial activity (orange dots), with on the left anaerobic (purple) and aerobic (red) bacterial populations inside an aggregate, and on the right bacteria colonizing a root hair tip. Squares show water and air configuration in the pore space at the microscale under wet conditions following rainfall or irrigation (left), or under dry conditions after water drainage and evaporation (right). Graphs show macroscopic profiles of oxygen, carbon and water content over soil depth. Oxygen concentration is highest at the soil surface and water saturation maximal when it reaches the water table. Oxygen and water profile change under wet or dry conditions, while carbon profile is unchanged.

2009; Eilers et al. 2012). Generally, microbial communities deep in the soil are dominated by prokaryotes and are one to two orders of magnitude less numerous than at the topsoil. Strikingly, communities that are spatially close (within the same soil profile) but separated by only 10–20 cm in depth can be more different from one another than from communities thousands of kilometers away (Eilers et al. 2012). Evidence links the vertical distribution of soil microorganisms with soil organic carbon availability (Blume et al. 2002; Fierer, Schimel and Holden 2003; Eilers et al. 2012), often provided by plant root exudates or decaying plant residues. The availability of soil organic C to microorganisms is (i) heterogeneous in space and time and (ii) dependent on its chemical form (e.g. dissolved or particulate organic C). Consequently, microbial abundance and activity are often associated with so-called hotspots in soils (Bundt et al. 2001; Kuzyakov and Blagodatskaya 2015) (Fig. 2). For example, hotspots are typically found close to plant roots (rhizosphere) or associated with decaying plant material, and unsurprisingly many studies have shown that bacterial communities in the rhizosphere differ from those in the bulk soil (e.g. Marilley et al. 1998; Smalla et al. 2001; Uroz et al. 2010), often exhibiting reduced diversity and enrichment in specific taxa (Mendes, Garbeva and Raaijmakers 2013; Philippot et al. 2013).

Several biotic and abiotic processes act to redistribute organic C within the soil profile: roots extension, transport by fungal hyphae (further discussed in the next section), bioturbation by soil macrofauna (e.g. earthworms, ants, termites) and transport by water flow in soil pores (Lavelle 2012). At the scale of plant roots and macrofauna (centimeters to millimeters), soil is best described as a highly complex assemblage of pore spaces (more or less water saturated) and soil aggregates (Tisdall and Oades 1982; Six et al. 2004; Orgiazzi et al. 2016). These aggregates consist of mineral particles and organic substances tightly bound together, and they are often considered as the basic and functional units of terrestrial environments (Standing and Killham 2007). Soil aggregates vary widely in size (from micrometers to centimeters) and composition (relative abundance of sand, silt or clay particles; sources of organic matter; oxygen gradients), and they typically show a nested organization, with smaller (micro)aggregates lumped into larger ones (macroaggregates) (Tisdall and Oades 1982; Six et al. 2004). Importantly, soil biota is the main driver of aggregate formation (Totsche et al. 2010): polymeric substances secreted by bacteria and fungi act

as a glue that agglomerate inorganic particles and organic material (a process that can also take place in the earthworm's gut), while fungal hyphae and plant roots contribute to holding aggregates together. The variety of aggregate size, pore spaces and chemical gradients thus results in highly diversified microhabitats (or niches) for soil microbes (Young and Ritz 2000; Standing and Killham 2007; Vos et al. 2013; Gupta and Germida 2015). Researchers have found evidence for microbial non-random distribution at the soil pore scale (Ruamps, Nunan and Chenu 2011; Kravchenko et al. 2014), based on aggregate size (Ranjard and Richaume 2001; Sessitsch et al. 2001; Mummey et al. 2006), or associated to specific organic material (Blaud et al. 2014) or to specific particle-size fractions (Neumann et al. 2013). Large pores are dominated by aerobic bacteria and fungi, while micropores can contain both aerobic and anaerobic microbes (in the anoxic interior of aggregates), notably denitrifiers and methanogens (Tiedje et al. 1984; Ranjard and Richaume 2001; Ebrahimi and Or 2015; Gupta and Germida 2015). Overall, prokaryotes are more abundant and more diverse in smaller aggregates, as fungal hyphae and protists are excluded by the pore sizes and hence cannot compete with or graze on bacteria and archaea.

Despite the high microbial density found in soil relative to other habitats, it is surprising to learn that microbial biomass colonizes <<1% of the accessible soil surfaces (Hissett and Gray 1976; Young et al. 2008). Considering limitations on self-dispersion in unsaturated soils (to be discussed shortly), it is safe to conclude that soils are not uniformly occupied by microbes, but rather harbor a non-random, patchy distribution of colonized microsites (Grundmann and Debouzie 2000; Nunan et al. 2003; Raynaud and Nunan 2014) (see Fig. 1C). This high heterogeneity observed at the microscale suggests that researchers often sample soils and assess microbial abundance and diversity at scales ( $\geq \text{cm}^3$ ) that are not directly relevant for microbial interactions and processes (Dechesne, Pallud and Grundmann 2007). A few studies have examined soil bacterial diversity or activity at the millimeter scale and below (Grundmann and Debouzie 2000; Pallud et al. 2004; Gonod, Martin-Laurent and Chenu 2006; Stefanic and Mandic-Mulec 2009; Monard et al. 2012; Bailey et al. 2013; Dechesne et al. 2014; Kim et al. 2015; Pinheiro et al. 2015). They confirm the patchy distribution of bacteria and show that communities distinct in activity can be spatially isolated across small scales in soil (Kerr et al. 2002). Recently,



**Figure 3.** Bacteria colonizing pores and soil surfaces. (A) Fluorescence microscopy images of bacteria in the lettuce rhizosphere (phylogenetic groups were labeled by fluorescent in situ hybridization and shown with different colors); image adapted from Cardinale (2014). (B) Fluorescence microscopy images of bacteria (labeled by fluorescent in situ hybridization) in a sandy soil; images adapted from Eickhorst and Tippkötter (2008) with permission from Elsevier. [This image is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.] (C) Scanning electron microscopy images of bacterial cells attached to solid sand surfaces by EPS (seen as a filamentous mesh). Photo credit: Lewis Lab at Northeastern University. Image created by Anthony D'Onofrio, William H. Fowle, Eric J. Stewart and Kim Lewis.

Michelland et al. (2016) studied bacterial communities from two soils, and observed high bacterial diversity in soil samples as small as 20 mg, thus confirming that vast microbial diversity is present at all scales. Developments in microbiogeography and microbiogeochemistry (Hemkemeyer et al. 2015; Pronk et al. 2017), as well as in resolving soil microstructures (Kravchenko et al. 2014; Hapca et al. 2015), are encouraging, and further research might shed light on how community distribution at the microscale impact biogeochemical functions at larger scales.

### SOIL AS MICROBIAL HABITAT

The ecological heterogeneity of soil resulting from the interplay of spatiotemporal, physical, chemical and nutritional variables delineates spheres of influence that may separate bacteria with respect to location, physiology or phylogeny (Dion 2008) (Fig. 3). The soil biogeochemical environment is inherently heterogeneous and patchy, and the aqueous phase essential for microbial life is highly dynamic and fragmented (Koch 1990; Fenchel 2002; Young and Crawford 2004). Soil hydration status and pore-space characteristics greatly influence microbial motility and ranges of dispersion within the highly patchy environment (Barton and Ford 1997; Fenchel 2002; O'Donnell et al. 2007; Or et al. 2007; Tecon and Or 2016). Limitations to motility are particularly important for diffusion-dominated fields varying at submillimetric scales (Dechesne et al. 2010; Wang and Or 2010; Tecon and Or 2016), a characteristic of unsaturated soil in most geographic

regions. Heterogeneity and spatial and temporal microhabitat fragmentation are often cited as key factors promoting the immense microbial diversity found in soil (Zhou et al. 2002; Curtis and Sloan 2005; Dion 2008). Spatiotemporal segregation of microhabitats understandably influences evolutionary and ecological processes that shape microbial species distribution: speciation, selection (for example, via competition or cooperation), dispersal, horizontal gene transfer and random drift (effects of chance on species relative abundances) (Hanson et al. 2012; Kraemer et al. 2016). However, details of the dynamics and interplay of mechanisms that sustain such diversity require further clarification.

Bacterial cells inhabit highly heterogeneous pore spaces and soil grains surfaces where hydration conditions and nutrients diffusive fluxes constantly fluctuate. These traits of the unsaturated soil with patchy resource distributions, fragmented and flickering aqueous networks, and limited transport rates and dispersion ranges play critical roles in microbial distribution, diversity and function (Nunan et al. 2001; Fenchel 2002; Young and Crawford 2004). Attempts to link microbial distributions with nutrient spatial patterns yield limited insights into the spatial extent and function of microbial life in unsaturated soil (Fierer and Lennon 2011; Raynaud and Nunan 2014). In other words, the availability of nutrients at a given location does not ensure presence of competent bacteria, partially due to the relatively sparse cell coverage of soil surfaces (Chenu and Stotzky 2002; Raynaud and Nunan 2014), the relatively small fraction of active bacteria

at any given time (Blagodatskaya and Kuzyakov 2013) and the crucial role of the aqueous phase in connecting livable spaces and permitting diffusion of nutrients to cells (Wang and Or 2010).

The dynamic nature of soil processes and rapid changes in microbial community function obscures potential links between measured diversity and ecological functioning of soil microbes. Different microbial groups are active at different times punctuated by temporal discontinuities of their functional niches (Torsvik, Sørheim and Goksøyr 1996). The question of how much of genetic diversity estimates is directly linked and shaped by present ecological conditions versus how much of it is shaped by population and interspecies interactions over time remains a central challenge for modern microbial ecology (Curtis and Sloan 2005; Prosser et al. 2007). What makes soil such a successful habitat for microbial life and what characteristics of the soil microenvironments promote and sustain the incredible microbial diversity found in soil are reviewed next.

### The complexity of physical pore spaces and surfaces

The soil is a medium with high specific surface area with values ranging between  $10^{-1}$  and  $10^2$   $\text{m}^2 \text{g}^{-1}$  (sandy to clayey soils). Consequently, despite high bacterial abundance in soil, relatively large stretches of soil surfaces are devoid of bacterial cells (Young et al. 2008; Schmidt and Eickhorst 2014). A simple estimate considering a soil with moderate specific surface area of  $10^1$   $\text{m}^2 \text{g}^{-1}$ , bacterial density of  $10^{10}$  cells  $\text{g}^{-1}$  and 1000 cells per 'colony' that are uniformly distributed over the surface (Raynaud and Nunan 2014) would yield average spacing between adjacent colonies of 500  $\mu\text{m}$  in radius. Even a uniform coverage of the  $10^{10}$  cells  $\text{g}^{-1}$  with 1  $\mu\text{m}$  in size over the soil surface would result in only 0.1% surface coverage (within the range of values estimated by Chenu and Stotzky 2002). Spatial isolation arises from the complexity of the soil pore network; even if two microbial microcolonies are separated by a very small (Euclidian) distance, they may often not interact if located in unconnected pores or if the physical pathways are too small for passage of cells (as discussed later). Bacterial cells have been shown to be completely entrapped in closed pores (Foster 1988). Depending on soil type, it is estimated that between 15% and 50% of the soil porosity is inaccessible to bacterial cells due to pore throats smaller than 0.2  $\mu\text{m}$  (Chenu and Stotzky 2002), thus contributing to bacterial spatial isolation in soils. The large separation distances and sparse presence are important for understanding interactions among microbial communities inhabiting soil surfaces, especially considering the commonly fragmented aqueous phase that restricts ranges of cell dispersion (Wieland, Neumann and Backhaus 2001; Mills 2003; Ebrahimi and Or 2014) as will be elaborated shortly. Finally, an often overlooked factor in soil microbial ecology that masks direct links between nutrient and bacterial spatial distribution is the exceedingly small fraction of active bacteria at any given time. Recent estimates suggest that only a few % of the total microbial biomass found in a soil are active while most exist in dormant or inactive forms (Blagodatskaya and Kuzyakov 2013).

#### The solid phase

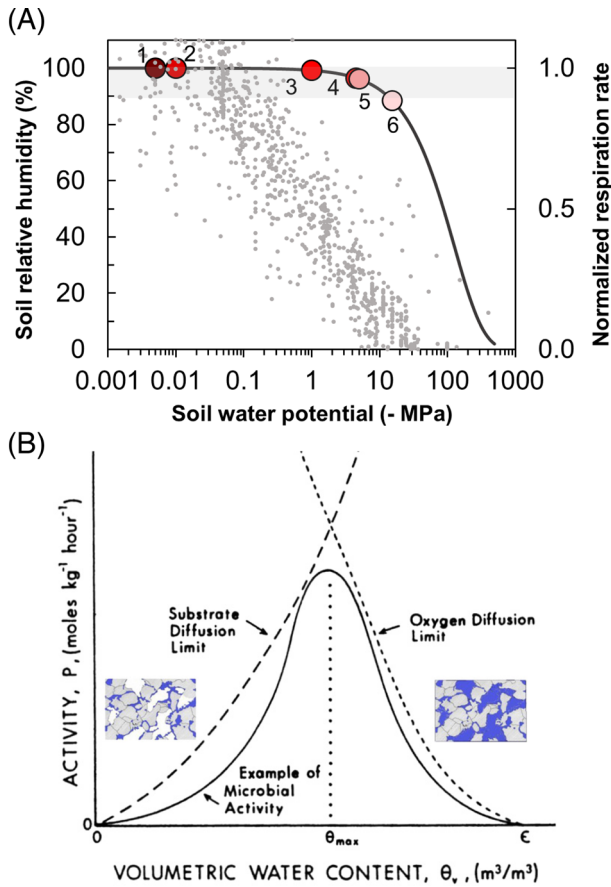
The properties and architecture of the soil solid phase are important factors in the formation of microbial habitats and shape the ecological functioning of soil (Chenu and Stotzky 2002; Nunan et al. 2003; Young and Crawford 2004). The soil solid-phase spatial organization determines the soil structure, an important (and difficult to quantify) trait for plant growth and soil productivity that drives many agricultural soil management

operations (cultivation, tillage). Central to the concept of soil structure is the emergence of biologically promoted soil aggregates with 3D architecture of pores, carbon sources and transport processes. This 3D architecture gives rise to important 'hotspots' for biological activity (Tiedje et al. 1984; Ebrahimi and Or 2015) critical for several biogeochemical cycles in soil (Kuzyakov and Blagodatskaya 2015), for carbon protection (Six, Elliott and Paustian 2000; Kravchenko et al. 2014) and important greenhouse gas emissions from soil. Studies have shown that the placement of soil organic matter in different aggregate fractions (Six and Paustian 2014) or details of how organic carbon is organized within aggregates (Kravchenko et al. 2014) is of critical importance to the internal self-organization of microbial communities (Ebrahimi and Or 2016), the rates of carbon utilization and to the functioning of such communities as revealed by interruption of such organization using glucose profusion studies (Chenu, Hassink and Bloem 2001; Gupta and Germida 2015). Even at smaller scales of the individual soil grain surface, the structure and roughness of such a surface at the micrometric scale plays an important role in bacterial cell adhesion (Mills 2003) (Fig. 3). Roughness shapes local diffusion fields upon which surface-attached microcolonies rely (Long and Or 2007; Wang and Or 2010), and it has been shown to affect cell motion within aqueous films held in surface roughness (Dechesne et al. 2010; Tecon and Or 2016).

### The soil aqueous phase

Active soil microorganisms require an aquatic environment for their life function (filamentous fungi being an exception that we discuss below). In most soils, this critical environment is fragmented and in a constant state of change (Fig. 2). Episodes of rainfall or irrigation infiltrate water into the soil thus temporarily increasing its water content. These wetting events are followed by internal drainage, evaporation and plant water uptake that deplete water stored in soil pores. For most climatic and geographic regions, soil remains unsaturated for most of the time. The water remaining in soil to support microbial activity is often retained by capillary forces in corners and crevices between soil grains or adsorbed as thin liquid films on rough soil surfaces (Tuller, Or and Dudley 1999). The results of such solid-liquid interactions affect the energy state of soil water and are manifested in the shape of the aqueous phase and its structure. Both aspects (energy state and structure) are of great importance for microbial life in unsaturated soil (Figs 4 and 5). The energy state of soil water is formally defined by the concept of soil water potential with various components (matric, osmotic, gravitational and pressure) expressed in terms of energy per volume of water (pressure, Pa) or energy per mass of water (termed chemical potential,  $\text{J kg}^{-1}$ ) (Hillel 2003). In unsaturated soil, the primary component of soil water potential is the matric potential (resulting from capillary and surface interactions). The matric potential assumes negative values reflecting the lowering of potential energy in water held in soil relative to free water in a reference state. The drier the soil, the more negative the matric potential value (the maximal value of soil matric potential is zero, which indicates complete saturation). The main effect of the soil water potential (matric potential in particular) is on the architecture of the aqueous phase jointly shaped by the size and geometry of soil pore spaces, surface properties and by the prevailing soil water potential (Or and Tuller 1999; Hillel 2003).

Given a value of soil matric potential, we may readily predict the thickness of aqueous films adsorbed by van der Waals forces on soil surfaces using a simple algebraic expression (Iwamatsu

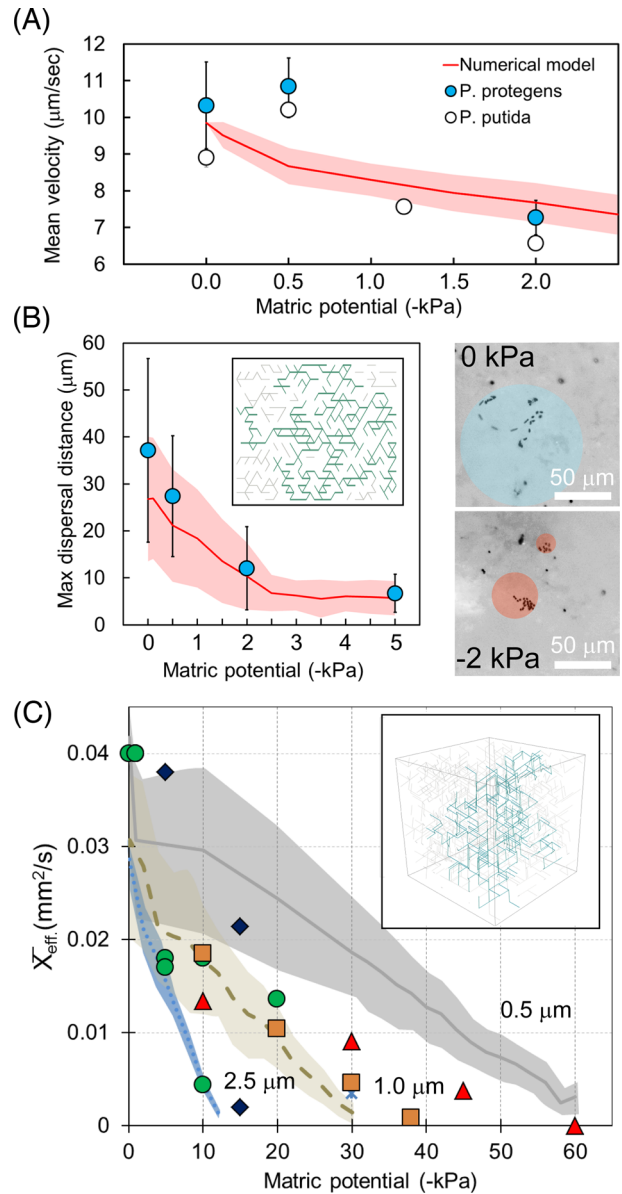


**Figure 4.** Impact of soil water on microbial activity. (A) Theoretical soil relative humidity (solid line) and microbial respiration rates measured in various soils (gray dots) as function of soil water potential. Respiration rate is normalized to its value at field capacity ( $-0.03$  MPa), and is from Manzoni and Katul (2014). Observed limits for microbial dispersion and respiration are as follows. (1) Flagellar motility of *Phytophthora* zoospores ceases at  $-5$  kPa (Griffin 1981). (2) Flagellar motility of *Pseudomonas* ceases around  $-10$  kPa (Dechesne et al. 2010; Tecon and Or 2016). (3) Microbial respiration in intact soil cores ceases at  $-1$  MPa (Manzoni and Katul 2014). (4) Mycorrhizal fungi growth and dispersal is still observed at  $\sim -4$ – $5$  MPa (dispersion limit is probably lower than this value) (Allen 2007). (5) Bacterial respiration ceases around  $-5$  MPa (Wilson and Griffin 1975). (6) Microbial respiration in disturbed soils ceases around  $-15$  MPa (Manzoni and Katul 2014). Almost all microbial activity takes place between 90% and 100% soil relative humidity (shaded area). Data on respiration rates in soil courtesy of Stefano Manzoni. (B) Conceptual view of the effects of soil water content on macroscopic microbial activity from unsaturated to fully saturated conditions. Dotted lines represent upper limits imposed by gaseous or substrate diffusion rates. From Or et al. (2007), with permission from Elsevier. [This image is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.]

and Horii 1996; Tuller, Or and Dudley 1999):

$$l(\psi) = \sqrt[3]{\frac{A_{svl}}{6\pi\psi}} \quad (1)$$

where  $l(\psi)$  is matric potential-dependent aqueous film thickness [m],  $A_{svl}$  is a surface parameter called the Hamaker constant (summarizing interactions between solid surface and gas through a liquid film,  $\sim -6 \times 10^{-20}$  J for water on silicate surfaces),  $\pi$  is the mathematical constant and  $\psi$  is the matric water potential [Pa]. For matric potential values in the range of  $-5$  to  $-30$  kPa (representing relatively wet conditions near the so-called



**Figure 5.** Role of matric potential in controlling bacterial dispersal. (A) Bacterial swimming velocity measured from experiments (symbols) or simulated (line) as function of water matric potential. Mean velocities are calculated from individual trajectories of *P. protegens* (blue dots) or *P. putida* (white dots) swimming on porous surface models with similar roughness. Error bars represent standard error of the mean. *Pseudomonas putida* results adapted from Dechesne et al. (2010). Simulation and *P. protegens* results adapted from Tecon and Or (2016). (B) Bacterial dispersal on a 2D hydrated porous surface. Results of maximal dispersal distance calculated from simulations (line) on a rough surface model and measured in experiments (dots, average values calculated from individual trajectories of *P. protegens* bacteria) are shown as function of matric potential. Bars and shaded areas represent standard deviations. Micrographs show exemplary dispersion radii (colored circles) from single cell trajectories at contrasting matric potentials. Adapted from Tecon and Or (2016). (C) Bacterial dispersal in a 3D hydrated porous network. Results show bacterial dispersion coefficient (mm<sup>2</sup> s<sup>-1</sup>) calculated from simulations (lines, considering three bacterial cell sizes: 0.5, 1.0 and 2.5  $\mu m$ ) in unsaturated porous network model and compared with experimental data from literature (symbols, see the text for references). Shaded areas represent standard deviations. Adapted from Ebrahimi and Or (2014) with permission from John Wiley and Sons. [This image is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.]



'field capacity'), the thickness of aqueous films on most smooth mineral surfaces is in the range of 10 to 20 nm, too thin to support immersion of typical microbial cells ( $\sim 0.5$  to  $2 \mu\text{m}$ ) or flagellated motion. Actual aqueous films on most natural rough surfaces are at least an order of magnitude thicker than predicted by Equation 1 for low matric potential values due to capillary condensation within surface roughness elements (Or and Tuller 2000; Tuller and Or 2005; Wang and Or 2010; Tecon and Or 2016), and due to presence of other surface forces that contribute to aqueous surface films (e.g. electrostatic interactions). Although such adsorbed thin films restrict cell motion, they may permit diffusion nutrient fluxes to microbial colonies even under dryer (or frozen) conditions as demonstrated by Rivkina *et al.* (2000).

As the soil gradually drains (or dries by evaporation) following wetting, even larger aquatic habitats (not thin films) that form behind curved interfaces in crevices and at grain contacts shrink in size with decreasing matric potential and quickly become too small to support full immersion or movement of bacterial cells. Simple geometrical considerations show that the maximum size of a spherical or cylindrical microbial cell that would be fully immersed in liquid behind a curved liquid-gas meniscus is constrained by the following relationships:

$$R = r(\psi) \frac{1 - \sin \alpha}{1 + \sin \alpha} \quad (2)$$

where  $R$  is the maximum radius of a fully immersed bacterial cell,  $\alpha$  is the angle of a generic v-shaped crevice or channel on a soil or grain surface,  $r(\psi)$  is the radius of curvature of the air-liquid meniscus determined by the matric potential via the Young-Laplace equation:

$$r(\psi) = \frac{\sigma}{|\psi|} \quad (3)$$

where  $\sigma$  is the air-water surface tension ( $0.073 \text{ J m}^{-2}$ ). The simple relationship in Equation 2 suggests that for even mild unsaturated conditions (field capacity often defined at  $-30 \text{ kPa}$ ), the sizes of typical aqueous elements (as gauged by the largest radius that could be fully immersed in  $-R$ ) become smaller than average microbial cell sizes (for  $\alpha = 30^\circ$  and matric potential of  $-30 \text{ kPa}$ , application of Equations 2 and 3 yields a value of  $R = 0.81$  micron). Hence, the notion of free swimming planktonic microbial cells in unsaturated soils is limited to relatively narrow and infrequent range of wet condition near saturation (Fig. 4). Furthermore, because the sizes of aquatic habitats in angular pores are defined solely by the matric potential and pore shape and not by pore body size, prevailing notions regarding the roles of pore sizes in determining microbial activity during predation (Wright *et al.* 1995) and the movement of microbes or grazers within certain pore sizes within unsaturated soils is largely biased by the traditional view of soil pores as a 'bundle of cylindrical capillaries'. Nevertheless, the association of matric potential with certain sizes of water-filled cylindrical pores remains useful in some applications pending more rigorous representation of soil processes (Ruamps *et al.* 2013).

#### The uniqueness of the soil matric potential

The spatial and temporal organization of the soil aqueous phase within a soil is directly affected by the soil matric potential. Although often represented as an additive component of the total water potential, the role of matric potential cannot be replaced by an osmotic potential of a similar magnitude. The clear distinction of inherently different effects of these two potential components on bacterial growth and activity in unsaturated

soil remains problematic (Papendick and Campbell 1981). As explained by Potts (1994, p. 764): "There is one distinction between matric and osmotic systems [...]. The immediate environment of a cell under matric stress is the atmosphere; i.e. the surfaces of their cell walls are exposed to a gas phase, while cells under osmotic stress are bathed in an aqueous solution, albeit one of diminished water activity'. This distinction is correct but incomplete. In addition, matric potential shapes the aqueous phase configuration and with it the connectivity and other environmental conditions not captured by changes in osmotic potential.

Potts (1994) defined desiccation as removal of substantial amounts of water from bacterial cells by matric stress. However, the method and rates of desiccation play an important role in the physiological response: salt solutions in closed chambers to depress the water vapor in equilibrium with microbial cells may not necessarily mimic conditions in a drying soil. When soil matric potential is reduced through control of the soil liquid phase in the porous medium, cells or colonies may remain hydraulically connected and potential energy differences could be accommodated through mass exchange without local desiccation of cell outer membranes or substantial loss of water from the surrounding matrix made of extracellular polymeric substances (EPS). When similar changes are induced through vapor phase modification (i.e. water vapor depression by salt solution in sealed chambers), the time scales to equilibration and physiological adjustment are likely shorter and more difficult to control (see Fig. 4A for the vapor phase equivalent of water potential). Figure 4A is adapted from the excellent review by Potts (1994); it provides a general overview of relationships between key physiological processes and water potential or relative humidity. The data illustrate that at relative humidity values not far from 99%, microbial growth becomes limited, and at water potential of  $-5000 \text{ J kg}^{-1}$  ( $-5 \text{ MPa}$  or 96% relative humidity) bacterial respiration ceases (Wilson and Griffin 1975). These trends have been confirmed in recent studies concerning limitations on flagellated bacterial motion on hydrated surfaces at  $-10 \text{ kPa}$  (Dechesne *et al.* 2010; Tecon and Or 2016), and the cessation of soil microbial respiration at  $-15 \text{ MPa}$  (Manzoni, Schimel and Porporato 2012; Moyano *et al.* 2012; Manzoni and Katul 2014).

#### The physical environment for motility and dispersion in soil

Percolation theory offers simple and useful guiding principles to quantify (in general terms) the geometrical characteristics of the connected aqueous phase at scales relevant to local microbial ecology ( $10^{-5}$ – $10^{-3} \text{ m}$ ) such as within soil aggregates or over hydrated surfaces of soil grains (Sahini and Sahimi 1994; Berkowitz and Ewing 1998; Wang and Or 2013). Without requiring knowledge of pore networks or roughness geometrical detail, we may deduce useful information from consideration of the hydration conditions (e.g. expressed by the matric potential) on the sizes and numbers of separate aqueous habitats in soil pores. We illustrate the utility of this framework considering, for example, the fragmentation and shrinking sizes of connected aqueous habitats that contain sufficiently thick films to support flagellated motion. These features are described by a surprisingly simple expression that links the prevailing soil matric potential ( $\psi$ ) with the effective size of the largest connected aqueous cluster,  $R_C(\psi)$  (Berkowitz and Ewing 1998; Wang and Or 2012; Ebrahimi and Or 2014):

$$R_C(\psi) = R_0 \left( \frac{N_C}{N_0} \right)^{1/d_t} \quad (4)$$

the ingredients for the calculation require an estimate of the system size  $R_0$  (e.g. this could be the surface area of a single grain or the volume of an aggregate pore system),  $N_c$  is the number of bonds of the largest aqueous cluster (e.g. a roughness features on a surface),  $N_0$  is the number of total bonds of the system (pores in an aggregate or roughness features on a grain) and  $d_f$  is the fractal dimension related to the dimensionality of the network considered. Generally accepted (universal) values for  $d_f$  are  $d_f = 1.90$  for 2D surface roughness and  $d_f = 2.52$  for 3D pore networks (aggregates). This simple representation of the sizes of accessible aqueous habitats offers powerful insights into the maintenance of diversity, dispersion and mixing of populations, and ecological functioning in unsaturated soil—more detail is given in Wang and Or (2012), Ebrahimi and Or (2014) and Manzoni and Katul (2014). Even for non-motile soil microbes, such estimates could provide a means to assess the numbers of distinct environments, distances between colonies, typical carrying capacity of such aqueous islands and more.

In addition to impacts on phase continuity as discussed above, lower values of matric potential result in thinner aqueous films (see Equations 1 and 2 above) that reduce the instantaneous velocity of flagellated motility in such films (Dechesne et al. 2010; Wang and Or 2010). The joint effect of slower motility (Fig. 5A) and limited ranges of dispersion (Fig. 5B and C) on variably hydrated surfaces has been demonstrated recently in a study by Tecon and Or (2016) confirming that the effects are physical and reversible. However, not all microbial life in soil is critically dependent on aqueous phase architecture for local dispersion. Fungal hyphae may grow across empty pores and bridge air gaps. This mode of growth and local spreading offers opportunities for bacterial cells, serving as local ‘fungal highways’ and thereby extending ranges of bacterial dispersion (up to 1 cm a day in laboratory experiments) (Leben 1984; Kohlmeier et al. 2005; Wick, Furuno and Harms 2010; Simon et al. 2015). Effective fungal transport depends on the hydrophilic properties of both fungi and bacteria, and on the expression of bacterial flagella enabling cell motility (Kohlmeier et al. 2005; Pion et al. 2013), although passive dispersal of non-motile bacteria attached to growing fungi has also been observed (Wick, Furuno and Harms 2010). Fungal highways may thus also be linked to the persistence of flagellar motility in soil bacteria, providing a selective advantage to the motile cells (Pion et al. 2013), a hypothesis which is not mutually exclusive with increased fitness gained during transient saturated conditions (Dechesne et al. 2010). Not only fungal mycelia, but also plant roots and soil fauna (e.g. earthworms) can mediate bacterial transport over longer distances in soil (Madsen and Alexander 1982; Vos et al. 2013). Finally, in the discussion of microbial dispersion ranges we must consider the rare but important events of cell convection by rain or irrigation water. The ranges of transport are as diverse as the preferential pathways in a soil (Bundt et al. 2001). Such pathways enable cell transport across plant root zone (circa 1 m) within minutes to hours (Besmer and Hammes 2016). Anecdotal evidence links elevated microbial activity to such preferential flow pathways in soil (Bundt et al. 2001). However, because many preferential flow pathways in soil are products of biological activity (e.g. burrowing by earthworms or decaying plant roots), microbial activity along such biological hotspots is not surprising. In other words, the stimulated microbial activity along such preferential pathways may be promoted by their biological history rather than their hydrological function; however, the relative roles of the different factors along flow preferential pathways remain unresolved.

### Dynamics of the soil aqueous phase

The soil aqueous phase is in a constant state of change: episodic rainfall or irrigation events replenish water and nutrients to different parts of the soil profile. The liquid phase may then reconnect large volumes of soil and temporarily expand ranges and rates of dispersion by cell self-propulsion, or transport bacterial cells by convection across considerable distances. For most climatic regions, wetting events are short lived and internal drainage combined with evapotranspiration restore the unsaturated and fragmented state of the liquid phase within hours to days. Nevertheless, soil wetting alters the ecology and microbial community composition within very short times (Schimel et al. 1999; Placella, Brodie and Firestone 2012) and may give rise to the formation of anoxic conditions that may persist within soil aggregates for many days after the bulk soil becomes aerated (Tiedje et al. 1984; Sierra and Renault 1996; Khademalrasoul et al. 2014). Some of the biogeochemical fluxes induced by microbial activity, in ‘hotspots’ during ‘hot moments’ (Groffman et al. 2009; Kuzyakov and Blagodatskaya 2015) of wet and well-connected aqueous phase, flourish under anaerobic conditions that are promoted by limited gas diffusion to certain volumes of soil (e.g. wet soil aggregates). Wetting events provide opportunities for microbial community spatial self-organization into favorable locations, such as proliferation in anaerobic and aerobic locations within aggregates (Ebrahimi and Or 2015), and more general aspects of self-organization to capitalize on spatial distribution of resources also along the soil profile (Rappoldt and Crawford 1999; Grundmann and Debouzie 2000; Nunan et al. 2002; Wang and Or 2014).

### Soil chemical and thermal environment

Salinity can vary spatially and temporally in soils and it affects microorganisms via changes in the water (osmotic) potential. Water infiltration (due to rainfall, irrigation) can rapidly increase the water potential in surface soil from negative MPa values to near zero. This induces a hypoosmotic stress in bacteria, which respond by releasing intracellular solutes. Dilution stress can reduce cell culturability and even lead to cell lysis (Halverson, Jones and Firestone 2000). Conversely, bacteria can experience hyperosmotic stress in soils following dry periods or the addition of fertilizers. In the long term, irrigation also contributes to increasing salinity, in particular under dry climates with high evaporative demand (Brady and Weil 2014), which has detrimental effects on microbial growth and activity (Rietz and Haynes 2003). In addition to osmotic effects, high concentrations of salts can also result in cation-specific inhibition of metabolic processes, due to iron precipitation, the suppression of microbial attachment to surfaces (via increased ionic strength) or inhibition of bacterial chemotaxis and motility (Or et al. 2007). Overall, high salinity in soil results in lower microbial biomass and lower metabolic activity (Yan et al. 2015), but it is also worth noting that, in unsaturated soils, the impact of osmotic potential on convective or diffusive nutrient fluxes is negligible compared to the impact of matric potential, which controls water diffusion pathways (Or et al. 2007). The soil redox potential can also be highly variable in both space and time (Standing and Killham 2007; Hinsinger et al. 2009), in particular due to changes in water content and associated oxygen availability, which decreases with soil saturation. Under anoxic conditions, the availability of other electron acceptors (e.g.  $\text{NO}_3^-$ ,  $\text{Mn}^{4+}$ ,  $\text{Fe}^{3+}$ ,  $\text{SO}_4^{2-}$ ) determines what types of anaerobic metabolism can take place.

Soil acidity (expressed as pH) is another factor that influences many important soil properties, such as the

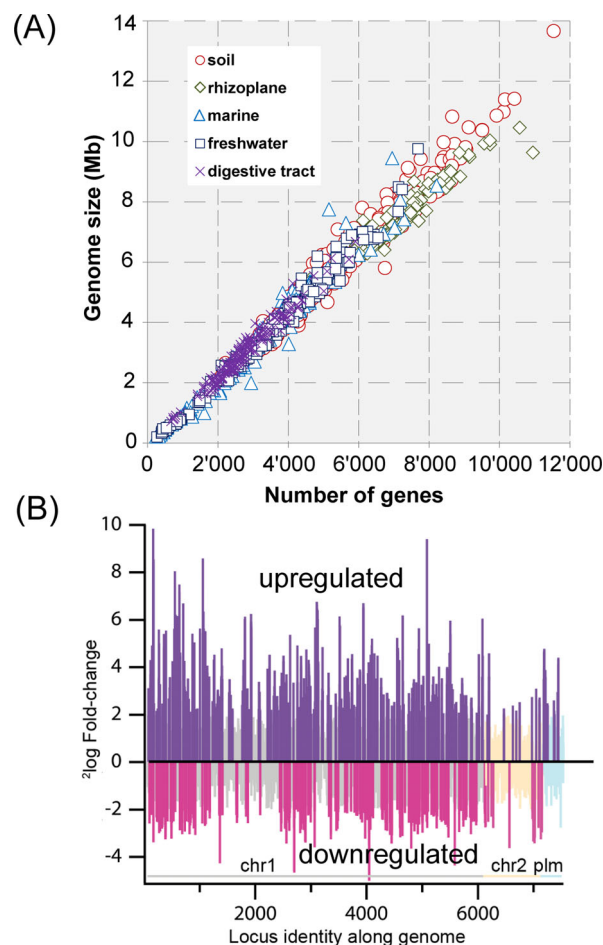
bioavailability of chemical compounds (nutrients or pollutants) to plant roots and the activity of soil microbes (Brady and Weil 2014). Soil acidification is a natural process which is influenced by the soil parent material and is favored in humid regions (forest soils) by rainfall and cations leaching. By contrast, most soils in arid and semiarid regions are alkaline (Brady and Weil 2014). At the global scale, a recent analysis has shown existence of a climatic threshold for transition from alkaline to acid soils in regions where mean annual precipitation exceeds potential evapotranspiration (Slessarev et al. 2016). Plant roots and microorganisms also contribute to soil acidification through ions uptake, respiration (concentration of CO<sub>2</sub> is much more elevated in bulk soil than in the atmosphere), nitrification or sulfur and iron oxidation. In the rhizosphere, local soil acidity can change by up to two pH units due to root activity (Philippot et al. 2013). Globally, most soils are in the range of pH 4 to 8 (Orgiazzi et al. 2016), although extreme pH values have been observed for special climate conditions and soil composition (Standing and Killham 2007). Fungi are generally more tolerant of acidic conditions than bacteria (Rousk, Brookes and Bååth 2009), which explains why fungal to bacterial ratio is higher in acidic soils. The effects of soil pH on microbial distribution and activity can be difficult to determine, since pH in microsites can differ from pH measured in the bulk soil, and surface-attached, EPS-embedded microcolonies might be protected from local acidic conditions (Standing and Killham 2007). Nevertheless, bulk soil pH is overall a strong predictor of bacterial abundance and diversity (Fierer and Jackson 2006).

Soil thermal conditions vary daily, seasonally and spatially across the soil profile due to changes in radiation intensity, surface albedo and soil wetness (which affects heat conductance and evaporation). Typically, the amplitude of temperature fluctuations decreases in moderate climates and with soil depth, and is highest in deserts (where annual variations may reach 50°C). Microorganisms themselves can influence soil temperature: it has been shown that the production of a natural 'sunscreen' by populations of cyanobacteria inhabiting biocrusts in arid regions could reduce the soil albedo and therefore increase the surface temperature by as much as 10°C (Couradeau et al. 2016). Changes in mean annual temperature, such as observed along a latitudinal gradient at continental scale, have been shown to select for different species of cyanobacteria in biocrusts (Garcia-Pichel et al. 2013), which suggests that global warming could transform microbial communities in arid regions in the coming decades. Temperature controls the rates of chemical and enzymatic reactions, and hence influences microbial activity. Respiration rates thus nearly double for each 10°C increase (Lloyd and Taylor 1994), although temperature sensitivity may vary depending on the microbial community present in the soil (Alster et al. 2016). Studies suggest that soil warming increases microbial respiration in arctic and boreal soils, which may contribute to a positive feedback loop of CO<sub>2</sub> emissions and reduce carbon storage in soils (Dorrepaal et al. 2009; Karhu et al. 2014). In this context, there is a pressing need to understand and predict how climate change may affect the rates of microbial activity in permafrost and seasonally frozen soils, which contain a substantial amount of the total soil carbon (Nikrad, Kerkhof and Häggblom 2016).

## MICROBIOLOGY IN SOIL ENVIRONMENT

### General features distinguishing soil microbes

The diversity of microbial niches and the generally stressful and dynamic physical conditions characteristic of surface



**Figure 6.** Genomics and transcriptomics of soil bacteria. (A) Size and gene content characteristics of bacterial whole genomes from various ecosystem types. Data obtained from the Joint Genome Institute on genome projects. Bacterial genomes (classified either as 'finished' or 'permanent draft') were grouped based on the JGI classification in various 'ecosystem types'. The number of bacterial genomes per ecosystem type was 335 (soil), 123 (rhizoplane), 280 (marine), 184 (freshwater), 185 (digestive system). (B) Genes expression levels in the soil bacterium *P. veronii* change dramatically when it is exposed to a sand environment in a microcosm as opposed to a liquid culture. Positive (dark violet) and negative (pink) fold-changes indicate respectively gene up- and downregulation when in contact to sand particles relatively to liquid cultures. Graph adapted from Morales et al. (2016).

soil environments have profoundly shaped the ecology and evolution of soil microorganisms. Bacterial genomics in the past decades has revealed that the genomes of soil bacteria are relatively larger and contain more genes than those of bacteria from aquatic or clinical environments (Van Elsas et al. 2007; Land et al. 2015) (Fig. 6A). The largest bacterial genome assembled to date belongs to the myxobacterium *Sorangium cellulosum* (14.8 Mb containing 11 599 genes; Han et al. 2013). Typical soil genera such as *Pseudomonas* and *Streptomyces* tend to have genomes >6 Mb. The complexity of the soil habitat appears to promote large bacterial genomes, which usually contain a large proportion of accessory genes involved in sensing environmental fluctuations, in substrate transport and degradation, in secondary metabolism (antibiotics production and resistance) and in stress response (Guieysse and Wuertz 2012). This selection for such metabolic versatility and adaptability is attributed to continuous fluctuations in ambient conditions and variations in the limited and diverse nutrient resources. A proverbial example of metabolic versatility in soil is *Burkholderia xenovorans*

(9.7 Mb), which harbors an astounding 430 transport systems for uptake of organic substrates, 31 pathways for the degradation of aromatic compounds, more than 180 efflux systems (for drugs, heavy metals, amino acids, proteins), and about 700 sensory and regulatory proteins (Chain *et al.* 2006). The metabolic potential encoded in a bacterial genome can be differently expressed depending on physical characteristics. For example, the transcriptome of the soil bacterium *Pseudomonas veronii* (8.0 Mb; Morales *et al.* 2016) changes dramatically when it is exposed to a sand environment as opposed to a fully saturated, liquid environment (Fig. 6B). Genomic studies have also revealed that soil bacteria tend to have a higher GC content (the percentage of guanine and cytosine bases in DNA) than aquatic bacteria (Land *et al.* 2015), and some authors interpret it as a niche-specific adaptation (Wu *et al.* 2014a). Large, high-GC genomes appear to be more prone to further genetic additions by horizontal gene transfer from phylogenetically distant donors (Cordero and Hogeweg 2009), which supports the view that heterogeneous and fluctuating environments like soil select for increased genome size and metabolic versatility. Yet, not all abundant soil bacteria possess large genomes: *Candidatus Udeobacter copiosus* (phylum *Verrucomicrobia*) seems ubiquitous in soils and has a genome as little as 2.8 Mb (Brewer *et al.* 2016). (A genome size ranging 1–3 Mb is also typical of archaea; Koonin and Wolf 2008.)

Evidence suggests that soil bacteria could be broadly divided into two ecological groups, namely copiotrophs and oligotrophs (Fierer, Bradford and Jackson 2007), based on their growth strategies. Briefly, copiotrophs consume easily degradable organic C, maximize growth rates when nutrients are abundant and have a high copy number of rRNA operon, whereas oligotrophs grow very slowly but steadily, maximizing yields under limited nutrients conditions and using more recalcitrant organic C, and showing low copy number of rRNA operon (Fierer, Bradford and Jackson 2007). For example, many species from the phylum *Acidobacteria* would be considered oligotrophs, while most *Betaproteobacteria* would be classified as copiotrophs. The terms copiotrophs and oligotrophs somewhat match the more ancient denominations of zymogenous and autochthonous microbes, and the ecological concept of *r*- and *K*-strategists (Panikov 1999; Prosser *et al.* 2007). In the complex environment of soil with constantly shifting strategies, such theoretical designations are naturally simplifications, and taxa may not be able to express such strategies with restricting ambient conditions; nevertheless, these provide a conceptual basis for hypothesis testing and for interpretation of empirical data. Another ecological category, associated with the so-called *L*-strategists, has been proposed to account for microorganisms adapted to stressful environments (Panikov 1999). In particular, *L*-strategists correspond to microorganisms adapted to extreme environments ( $T^{\circ}$ , pH) and to starvation-tolerant organisms that can enter a dormant state (e.g. spores, cysts) to evade unfavorable conditions. Dormancy is remarkably widespread in the microbial world and is observed in all ecosystems (Lennon and Jones 2011). Dormancy, however, is much more common in soils than in other environments: estimates suggest that about 80% of soil bacteria could be dormant, against 40%–50% of aquatic bacteria and only 20% of bacteria in the human gut (Lennon and Jones 2011; Blagodatskaya and Kuzyakov 2013). Needless to say, prevalence of bacterial dormancy in soils has enormous implications for the diversity, evolution and functioning of soil microbial communities. Dormant populations can persist in soils for long periods of time, and result in microbial ‘seed banks’ that can be revived when environmental conditions change. Finally, another common trait in soil microbes is the production of EPS that embed cells and

anchor them to surfaces. This means that sessile lifestyle and microcolony growth prevails in unsaturated soils as opposed to planktonic lifestyle (Fig. 3). Genes coding for EPS production are found in many abundant bacterial groups such as acidobacteria, myxobacteria, rhizobia, pseudomonads or Gram-positive bacteria (e.g. *Bacillus subtilis*) (Roberson and Firestone 1992; Kaci *et al.* 2005; Ward *et al.* 2009; Flemming and Wingender 2010; Berleman *et al.* 2016). The synthesis of EPS by microorganisms contributes to soil habitat formation, and it represents an important pool of reduced carbon in soil (Flemming and Wingender 2010; Schimel and Schaeffer 2012).

### Social interactions and signaling in soil

Soil microorganisms share their habitat with a vast diversity of neighbors, resulting in microbial interactions such as competition and cooperation (Little *et al.* 2008; Velicer and Vos 2009) that occur via direct cell contact or are mediated by diffusible metabolites and signals (Van Elsas *et al.* 2007). Antagonistic (e.g. via antibiotics) and predatory interactions are also common in soil: bacteria can be preyed upon by protozoa, fungi or even other bacteria (*Bdellovibrio* spp.), and can be infected by bacteriophages. Biophysical processes that control microbial distribution and dispersion in soil (see ‘soil as microbial habitat’) can thus have direct impact on microbial social interactions: species coexistence within a soil microniche would force direct interactions, whereas segregation in disconnected aquatic habitats would prevent them. Microorganisms can also influence each other using diffusible chemical signals, such as acyl-homoserine lactones (AHLs) (Papenfort and Bassler 2016). In soil bacteria, AHLs and other types of signaling molecules (e.g. small peptides) are known to fine-tune important environmental and social traits such as biofilm formation (*P. putida*), EPS production (*Pantoea stewartii*), development of genetic competence (*B. subtilis*), sporulation (*B. subtilis*, *Clostridium* spp.), symbiosis with plants (*Sinorhizobium meliloti*, *Rhizobium leguminosarum*, *Dickeya caratovora*), virulence (*Erwinia caratovora*) or production of bacteriocins (*B. subtilis*) and antibiotics (*P. fluorescens*) (Van Elsas *et al.* 2007; West *et al.* 2012). Gantner *et al.* (2006) showed that AHL signals emitted by a single bacterial cell in the rhizosphere could be detected in neighbor bacteria distant by tens of microns. Finally, microbial volatile compounds can possibly also play a role in long-distance interspecies interactions (Schmidt *et al.* 2015), and they might be of specific importance in terrestrial environments where unsaturated conditions facilitate diffusion in the gas phase. The physical structure of soils (pore geometry, air-water interfaces) plays an important role in the diffusion, exchange and activity of microbial signaling molecules, and on microbial social interactions as a whole.

### Horizontal gene transfer and microbial evolution in soil

Horizontal gene transfer (HGT) among prokaryotic species—and, to a much lesser extent, from prokaryotes to microbial eukaryotes (Andersson 2009)—is an important evolutionary driver in soil (Nielsen, Johnsen and van Elsas 2007). The frequency of HGT events naturally occurring in soil is not well characterized. On the one hand, the physical separation of microbial communities in distinct microsites and the low metabolic activity associated with limited nutrient conditions suggest that HGT should be relatively rare in soil. On the other hand, the close proximity and high cell density experienced by microbes in soil microcolonies should favor contact-mediated HGT such as conjugation, and the prolonged spatial isolation (until the next wetting

event) may help maintain transferred populations by limiting competition. To account for these in appearance contradictory views, some authors have proposed the concept of HGT hotspots in soil zones harboring relatively high cell densities, and studies have found evidence of such hotspots in the rhizosphere, in manure-amended soils or in the gut of soil animals (Van Elsas, Turner and Bailey 2003). Overall, the frequency of HGT increases with more available nutrients (Heuer and Smalla 2012). In soil, gene acquisition by conjugation could allow for faster adaptation of microbial communities to changing environmental conditions. Recently, it was demonstrated that so-called broad host range conjugative plasmids can be transferred to a surprisingly diverse fraction of the soil bacterial community, and that inter-phyla exchanges might be common (Klumper et al. 2015). These plasmids typically contain many accessory genes that encode adaptive traits such as antibiotic and heavy metal resistance, degradation of xenobiotics, efflux pumps or toxin-antitoxin systems (Heuer and Smalla 2012). Importantly, the evolutionary fate of transferred genes in soil is not only determined by HGT frequency between microbial individuals, but also by population dynamics that produces variation in the frequency of transferred genes in the community (Nielsen, Johnsen and van Elsas 2007). For example, transferred genes could become rapidly fixed in a population under strong selection conditions, even with rare HGT events. Good examples of such rapid spread include the rise of antibiotic resistance in microbial populations exposed to antibiotics selection, and the ability to tolerate heavy metals or degrade xenobiotics in polluted soils (Heuer and Smalla 2012).

### Trophic networks in soil

The soil food web has effects on the abundance and diversity of microbes, and at a larger scale on ecosystem functioning (de Vries et al. 2013). Food webs in fertile soil comprise a wide variety of organisms, including bacteria, archaea, fungi, protists, mycorrhizal and saprophytic fungi, nematodes, insects, earthworms, mammals and plants (from grasses to trees). Although plants via litter, dead roots and rhizodeposits provide the major input of organic matter upon which all other organisms depend (Schmidt et al. 2011; Bastow 2012), we will limit the discussion to the microbial actors only. Root exudates (e.g. sugars, organic acids) and mucilage represent essential carbon sources for rhizosphere bacteria and an important microbial hotspot in soil (Philippot et al. 2013). In addition, the variety of transformations of dead plant material from large and complex particulate matter to simple monomers such as glucose creates a chemical mosaic of resources and a spatial mosaic of environmental conditions (to use the terms of Moore et al. 2004). Studies have observed successional patterns on the decomposing resource, with early colonizing species differing from those arriving at a later stage (due to changes in resource 'quality'). Overall, microbial diversity associated to decomposing material increases over time, and it is generally accepted that successional specialization participates to the coexistence of high biodiversity in soil (although to what extent is difficult to determine) (Bastow 2012). In microbes, specialization often takes place at the enzymatic level, with, for example, bacterial and fungal taxa specializing in certain carbon compounds (Hanson et al. 2008; Goldfarb et al. 2011), or bacterial groups varying in their use of litter-derived nitrogen (N-fixing, ammonifiers and nitrifiers) (Torres, Abril and Bucher 2005). Metabolic specialization thus leads to the establishment of trophic preferences and dependencies, which can promote community self-organization. For example, the 'home-field advantage' hypothesis suggests that soil

microorganisms would be more efficient at degrading litter from plants they are usually associated with rather than from other plants (Veen, Sundqvist and Wardle 2015). Degradation specialization by different microbial groups increases degradation rates via coupled or parallel reactions, and in that context some level of diversity can increase ecosystem functioning. However, the relationship between microbial diversity and processing rates is complex. Very slow degradation rates can also promote chemical complexity, thus maintaining a more diverse community of microbial decomposers that contributes to a more stable soil ecosystem. For example, plant litter in tropical soils typically decomposes faster than in temperate soils. Unlike with plants and animals, prokaryotic and fungal communities are more diverse in temperate regions than in the tropics. The reduced stratification and less chemically complex habitat could thus explain the reversed latitudinal distribution of microbes. For all these reasons, it appears essential to consider the quality and distribution of primary-produced organic matter when discussing the factors that control biodiversity.

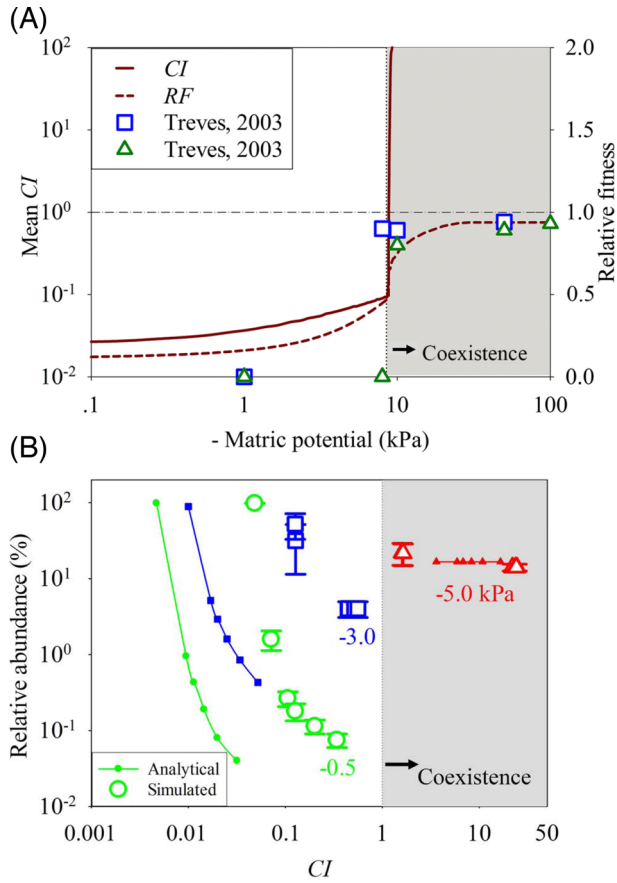
## BIOPHYSICAL PROCESSES SHAPING MICROBIAL LIFE IN SOIL

In the following section, we will provide a few illustrations of key biophysical processes affecting microbial life in soil. In the examples that follow, the soil aqueous phase plays a critical role in enabling or restricting motion, diffusion of nutrients and gases, and establishing the degree of spatial connectivity in the soil domain.

### Coexistence and diversity promoted by heterogeneity and fragmentation

The physical conditions that vary with soil hydration status greatly influence microbial motility and ranges of dispersion within this patchy environment (Dechesne et al. 2010; Vos et al. 2013; Tecon and Or 2016) (Fig. 5). The spatial environment for microbial interactions is often defined by self-dispersion of cells in this diffusion-dominated and heterogeneous environment with drastically different conditions at millimetric spatial scales (Dechesne et al. 2010, 2014; Wang and Or 2013). Although numerous studies have correctly identified the important roles of spatial and temporal microhabitat fragmentation in promoting soil microbial diversity (Or et al. 2007; Dion 2008; Vos et al. 2013), a mechanistic understanding of the processes at play remains sketchy.

Recently, a biophysical predictive index for hydration-mediated microbial coexistence in soil that integrates aquatic habitat size and connectivity, nutrient diffusion and motility rates and dispersal ranges in aqueous films has been formulated by Wang and Or (2012) (Fig. 7). The intent of this example is to illustrate the potential benefits and predictive powers of a quantitative framework without burdening the reader with all details found in the literature. The model system considered is a hydrated soil grain surface that may host diverse communities within fragmented aqueous clusters whose size and film thickness vary with soil matric potential. The connected aqueous clusters were defined by water-filled bonds whose effective film thickness remains sufficient to support flagellated motility (Wang and Or 2010, 2012). The degree of aqueous phase fragmentation is represented by the largest connected aqueous cluster with its size  $R_c(\psi)$ , which is a function of hydration status (see Equation 4) according to percolation theory (that applies to 3D



**Figure 7.** Soil matric potential impact on bacterial coexistence. (A) Analytical predictions of the coexistence index  $CI$  (solid line) and relative fitness  $RF$  (dotted line) between two model bacterial species (one dominant and one inferior) as function of soil matric potential, and comparisons with experimental data (symbols) from Treves et al. (2003) (triangles and squares correspond to two different pairs of bacterial species). A  $CI$  value above 1 corresponds to a steep increase in the relative fitness of the inferior species due to the fractionation of the aquatic habitat at a given matric potential. (B) Analytical and simulated relative abundances of the dominant species as function of  $CI$ . A steep transition is observed at  $CI > 1$ , which corresponds to lower matric potential values. Both graphs from Wang and Or (2012).

pore spaces as well). The effects of water content and matric potential on effective nutrient diffusivity for the unsaturated surfaces and soil are often expressed by:

$$D_{eff}(\psi) = D_0 \frac{(\theta(\psi))^2}{\phi^{2/3}} \quad (5)$$

the expression represents the reduction in effective nutrient diffusivity in the unsaturated soil (or hydrated surface)  $D_{eff}$ , with decreasing water content  $\theta$ , as related to the porosity  $\phi$  and bulk liquid diffusivity  $D_0$ . Thinner liquid films limit microbial motility speed and range as discussed above. Hence, the limited size of accessible aqueous habitats, the suppressed flagellated motion and the reduced nutrient diffusion rates are all linked to the matric potential and jointly affect chances of entrapped microbial community members to occupy favorable locations at the boundaries of an isolated aqueous cluster (and thus ensure nutrient supply).

In their study, Wang and Or (2012) have proposed an integrative variable termed the *mean generation length* ( $R_C$ ), which

succinctly combines microbial intrinsic-growth characteristics, motility rate and range with the hydration status (defined by matric potential),

$$\langle R_C(\psi) \rangle = \sqrt{2\langle V(\psi) \rangle^2 \tau / \mu_{eff}}, \quad (6)$$

where  $\langle V(\psi) \rangle$  is microbial mean velocity within the surface roughness (a function of the matric potential),  $\tau$  is the mean interval of microbial motility duration and  $\mu_{eff}$  is effective microbial specific growth rate. A hydration-dependent coexistence index ( $CI$ ) is defined as the ratio of microbial mean generation length ( $R_C$ ) to aqueous cluster size ( $R_C$ ):

$$CI(\psi) = \langle R_C(\psi) \rangle / R_C(\psi). \quad (7)$$

This ratio compares the cluster size (equivalent radius) with displacement distances a community member may traverse during one binary fission (generation); hence, it links net motion towards a critical boundary with nutrient interception required for cell division. The underlying assumption is that in the patchy and diffusion-limited soil environment, the boundaries of aqueous clusters are entry regions of nutrient fluxes that support microbial life within the clusters. Species capable of establishing presence along the boundaries enhance their chances for survival and intercept a larger fraction of resource fluxes relative to species within the interior of an aqueous cluster.

Clearly, many open questions remain that such a crude biophysical index has not addressed such as the composition and distribution of the microbial community on the surface at the onset of aqueous phase fragmentation, the dynamics (rate) of drainage leading to fragmentation, the spatial distribution of resources and more. Remarkably, simulation results of randomly distributed multispecies on rough hydrated surfaces with different characteristics, with no a priori assumptions regarding fitness or coexistence outcome, yield consistent results that confirm coexistence in agreement with predicted values of the  $CI$  (where a ratio  $>1$  marks onset of coexistence) as seen in Fig. 7. Recasting the experimental results of Treves et al. (2003) in terms of the proposed  $CI$ , considering 3D aqueous clusters in the unsaturated sand used in their studies, supports the predicted transition towards species coexistence for  $CI$  values close to 1. Moreover, simulation results using multiple species (the term ‘species’ refers to individuals with prescribed Monod parameters drawn from a range of reported values—see Wang and Or (2012, 2013) for more details) confirm that, with the transition to coexistence mode, the relative species abundance within the simulation domain (consisting of many clusters) evens out as also predicted in some theoretical and observed in experimental studies (Treves et al. 2003; Sloan et al. 2006; Quince, Curtis and Sloan 2008).

The species coexistence example above is only one of many other lines of evidence for the centrality of this metric of soil hydration status in shaping microbial life. In Fig. 4A, we represent milestones in biological activity as a function of water potential (dominated by the matric potential component in unsaturated soil). The impact of matric potential on bulk soil respiration is deduced from experimental results compiled by Manzoni, Schimel and Porporato (2012) and Manzoni and Katul (2014) shown in Fig. 4A. Wolf et al. (2013) and others have explored other effects of hydration status on soil microbial activity; undoubtedly, many additional studies will be reported regarding the centrality of the matric potential for microbial function in soil.

The proposed coexistence metric presented above illustrates the centrality of the matric potential in the spatial organization and other characteristics of the soil liquid phase. Next, we explore the ramifications of constraints imposed on cell dispersion on several aspects of soil microbial ecology (Kerr *et al.* 2002; France and Duffy 2006; Reichenbach, Mabilia and Frey 2007). With the exception of organisms forming mycelia, microbial cells rely on the liquid phase for motion and nutrient diffusion. For issues related to public safety or bioremediation activities, one is interested in predicting travel distances of soil bacteria from a release point. The primary mechanisms for bacterial dispersion in soil are advection by flowing water, facilitated transport by other organisms (earthworms, protists, fungi) and self-propulsion by various modes (Heijnen and Marinissen 1995; Thorpe *et al.* 1996; Harshey 2003; Jarrel and McBride 2008; Rubinstein *et al.* 2015). The advection of soil microorganisms is facilitated by the flowing streams of water when a soil is nearly saturated. With the exception of a few events per year for most soils and climates, during which the soil is very wet and supports significant advection, most of the time and in most unsaturated soils conditions do not support advection. Nevertheless, such episodic advective events are important for resource mixing and long-distance transport along preferential pathways, at rates that could exceed  $1 \text{ m day}^{-1}$  (Fontes *et al.* 1991; Wang, Bradford and Simunek 2013). The advected bacterial cells could be introduced to new surfaces, and such wet conditions may rejuvenate dormant soil microbes and promote temporary anoxic conditions suitable for anaerobic communities. For most conditions, bacterial dispersion would occur across ranges and at rates compatible with foraging distances of protists (Rubinstein *et al.* 2015) or earthworm burrow networks (Heijnen and Marinissen 1995; Thorpe *et al.* 1996) and by self-motion through sufficiently large aqueous films. Under unsaturated conditions, self-dispersion is limited to short distances (0.01–0.1 m) aided primarily by flagellated motility (Issa, Wood and Simmonds 1993; Turnbull *et al.* 2001), but also by gliding, twitching and swarming (Harshey 2003; Jarrell and McBride 2008).

Notwithstanding the relatively slow modes of motion and limited ranges of dispersal in unsaturated soil, the ability to change position plays an important role in the maintenance of microbial diversity (Kerr *et al.* 2002; Wang and Or 2013) and is an essential trait for the formation of complex microbial communities in the rhizosphere (Martiny *et al.* 2006; Dumbrell *et al.* 2010; Lindström and Östman 2011). Motion is also important in many biological and ecological processes, including soil organic matter cycling (Azam 1998; Wardle *et al.* 2011; Philippot *et al.* 2013), bioremediation of contaminated soils and aquifers (Harms and Bosma 1997; Harms and Wick 2006; Banitz *et al.* 2011), promoting the plant rhizosphere and root function, and controlling the spread of pathogenic bacteria (Beattie and Lindow 1995; van der Wal *et al.* 2013). We mention in passing that dispersion along hydrated hyphae that grow across empty pores could extend the effective dispersion ranges of other soil microbes (Wick, Furuno and Harms 2010; Simon *et al.* 2015); the ecological implications of such range extension are yet to be studied.

Simulation results of cell dispersal in 3D pore networks (Ebrahimi and Or 2014) revealed that the average travel time is reduced drastically from  $100 \text{ mm day}^{-1}$  for saturated pore spaces (no advection) to less than  $10 \text{ mm year}^{-1}$  under  $-35 \text{ kPa}$  in agreement with measured values from the literature (Wong and Griffin 1976; Arora 1986; Bashan and Levanony 1987) shown in Fig. 5C. Not surprising, chemotaxis plays an important role in significantly reducing travel times through tortuous and

fragmented unsaturated pore networks (relative to traversing the network in a random walk).

### Resource gradients and diffusion pathways shape soil microbial organization and activity

The macroscopic manifestation of the degree of microbial activity in soil is often quantified by fluxes of biogeochemically evolved metabolic products (e.g.  $\text{CO}_2$  or  $\text{N}_2\text{O}$ ). These activity metrics respond to variations in soil conditions such as temperature, aeration or water content, and often exhibit a non-monotonous response with clear optimal conditions. We will discuss here microbial response to changing macroscopic soil water content (keeping other conditions constant). The increase in the fraction of water-filled pores results in a reduction in gas diffusion pathways while increasing diffusion pathways of dissolved nutrients. Consequently, these two opposing macroscopic processes give rise to an optimal water content where aerobic microbial activity is maximal as shown in Fig. 4B (Young and Ritz 2000; Or *et al.* 2007; Moyano, Manzoni and Chenu 2013). The optimal water content for a particular soil is derived theoretically from consideration of solute and gas diffusion coefficients in soil and generic assumptions regarding microbial consumption rates (see Moyano, Manzoni and Chenu 2013 for additional details). Unlike the optimum emerging with variations of temperature or pH that are linked to intrinsic physiology of the microbial cells, this optimum is mediated by conditions imposed by the porous medium.

A similar type of biophysical mediation of microbial activity due to effects of water content and soil properties is manifested at smaller scales of individual soil aggregates. Limitations to oxygen diffusion into wet aggregates pore spaces (at the mm scale) may give rise to formation of anoxic microsites even within an aerated bulk soil. The process is reinforced by aerobic activity at the periphery of aggregates that give rise to formation of hotspots where aerobic and anaerobic microbial communities coexist (Sexstone, Parkin and Tiedje 1988; Renault and Sierra 1994; Brune, Frenzel and Cypionka 2000) (Fig. 2). The sizes, distribution and activity in these anoxic hotspots remains a subject of active research motivated primarily by their role in soil greenhouse gas emissions (Davidson, Savage and Finzi 2014; Kuzyakov and Blagodatskaya 2015) and other important biogeochemical functions. Representation of microbial hotspots in soil is possible without linking these processes exclusively to soil aggregates (Davidson, Savage and Finzi 2014). However, soil aggregates are common and form the soil structure backbone, mediate soil carbon architecture and protection (Schmidt *et al.* 2011; Six and Paustian 2014), and provide 3D pore spaces where soil bacteria reside and self-organize along oxygen and carbon gradients. Studies suggest that microbial communities within aggregates are spatially structured (Chenu, Hassink and Bloem 2001) and that community size and probably organization vary with aggregate size (Kanazawa and Filip 1986; Richaume *et al.* 1993; Blaud *et al.* 2014; Gupta and Germida 2015). Recent modeling studies by Ebrahimi and Or (2015) in artificial 3D pore networks provide additional insights into potential mechanisms for spatial self-organization of aerobic and anaerobic microbial communities. In particular, the delicate dynamic balance they strike in terms of carbon fluxes from the aggregate core that leaks out of the anaerobic region to support aerobes that form a shell and intercept oxygen fluxes and, in turn, maintain an anaerobic core even in an aerated soil. Evidence of anaerobic core hosting various activities is abundant (Kuzyakov and Blagodatskaya 2015), and theoretical studies suggest that the architecture of the carbon

sources is critical to the coexistence of communities. Ebrahimi and Or (2015) modeling results suggest that when the carbon source is external to the aggregates, anaerobes become extinct irrespective of anaerobic conditions (a postulate pending experimental confirmation).

### Sessile microbial life and microbial spatial self-organization in soil

The ubiquitous unsaturated state of soils with severe limitations on cell motion implies that commonly observed sessile microbial life associated with surfaces is not an option (such as in water saturated systems where biofilms may form) but a mandatory condition imposed by the physical environment. This means that sessile lifestyle and surface-associated growth prevails in unsaturated soils as opposed to planktonic lifestyle (Fig. 3). The conditions for the cessation of flagellar motility occur at relatively wet conditions ( $\sim 10$  kPa, Fig. 4A) even before the onset of the so-called soil field capacity (a hydration state where internal drainage becomes negligible) that often occurs within a day after rainfall or irrigation. This relatively narrow window is important for positioning and spatial structuring of microbial communities on surfaces.

The emergence of spatial patterns in multispecies consortia is common in many natural systems (Cordero and Datta 2016; Nadell, Drescher and Foster 2016), and it is considered a hallmark of trophic dependencies and various types of community interactions. Theoretical and experimental considerations suggest that non-random microbial patterns and structures would also emerge in soil through self-organization processes (Nadell, Xavier and Foster 2009; Wang and Or 2014; Tecon and Or 2017). In particular, heterogeneous organic substrates, restricted diffusion paths, oxygen gradients and complex cell trophic interactions likely promote spatial arrangements that optimize the microbial exploitation of soil resources. Heterogeneous chemical and nutrient gradients can be further stabilized by species distribution and activity within the extracellular matrix (Flemming et al. 2016). The emergence and persistence of spatial patterns require a period of self-organization (motility), physical anchoring of consortium members on surfaces or within biofilms, limited mixing and relatively stable diffusion fields. One type of stable spatial segregation has been discussed in the context of aerobes-anaerobes inhabiting soil aggregates or hotspots, and evidence suggests that spatial patterns are common and are manifested at various scales (Dechesne et al. 2003; Vos et al. 2013). There is a certain ambiguity in terminology used to describe microbial community structure—some studies refer to community membership and composition, whereas others refer to spatial organization. Recent studies (Momeni et al. 2013; Wang and Or 2014; Tecon and Or 2017) have illustrated the emergence of persistent spatial self-organization of microbial community induced by trophic interactions (Cordero and Datta 2016; Dolinšek, Goldschmidt and Johnson 2016; Nadell, Drescher and Foster 2016). To investigate microbial self-organization in soils is a formidable challenge, but it is of utmost interest for future development of explanatory and predictive models of soil microbial activity.

## THE ROLE OF MICROBIAL LIFE IN SOIL FORMATION, STRUCTURE, AND FUNCTION

Microbial activity affects soil structure and formation rates at various time and spatial scales. From long-term increase in global soil respiration and associated loss of soil carbon

(Cox et al. 2000; Davidson, Savage and Finzi 2014) that adversely impact soil structure and susceptibility to water and wind erosion to facilitated mineral weathering by surface-adhered microbial colonies affecting soil formation (Warren and Kauffman 2003; Uroz et al. 2009; Goudie and Viles 2012). At shorter time scales, microbial interactions within hotspots (aggregates or rhizosphere) greatly impact the soil physical environment (Philippot et al. 2013), especially via excretion of sticky and mechanically stable biopolymers (EPS) that bind particles and promote formation of stable structures (Chenu and Guerif 1991; Chenu 1993; Oades 1993). Arguably, the most prominent microbial group for soil structure formation is filamentous fungi due to their central role in soil carbon cycling, the formation of hyphae that enmesh soil particles and form stable microaggregates (Oades 1993), and the strong feedback on microbial niche formation (de Boer et al. 2005). Evidence suggests that hyphae of arbuscular mycorrhizal fungi, obligate symbionts of higher plants, produce glomalin, a recalcitrant protein that protects hyphae and extend their intact mechanical enmeshing function thus contributing to soil aggregate stability (Steinberg and Rillig 2003; Wu et al. 2014).

The spatial arrangement of soil particles and soil carbon that are important factors in the biological feedback associated with formation of soil structure (Nunan et al. 2003; Young and Crawford 2004; Kravchenko et al. 2014). The stabilization of soil structure and the acquisition of soil strength due to cumulative effects of microbial activity is linked to special mechanical properties of bacterial and plant derived EPS (see below), and to the properties and longevity of hyphae and fine roots. The sensitivity of EPS and other biopolymers to hydration status (Billings et al. 2015; Flemming et al. 2016) is reflected in the mechanical behavior of the reinforced soil elements (e.g. soil aggregates). The tensile strength and the Young's modulus of biopolymers increase by several orders of magnitude as the soil dries, while the biopolymer transforms from soft and ductile material when wet to stiff and brittle when dry. The microbial contribution to soil structure formation and stabilization is best understood in the ecological context where strong feedbacks shape the resulting spatial self-organization of soil elements and niches within (Nunan et al. 2003; Young and Crawford 2004) that, in turn, serve as the scaffolding for soil microbial life.

### Biophysical properties of EPS

EPS are a complex mixture of biopolymers: primarily polysaccharides, but also lipids, proteins and extracellular DNA (Flemming et al. 2016). Although EPS production has been well studied in bacteria and fungi, relatively little is known about archaeal EPS (Flemming and Wingender 2010). The mass of EPS can exceed the mass of the microorganisms that produce them, and it is generally accepted that EPS production enhances microbial fitness in soil environments (Chenu 1995; Or et al. 2007). A variety of mechanisms have been shown to confer a competitive advantage to EPS producers, including protection from desiccation, facilitated surface attachment and diffusion barrier against toxic substances (Tamaru et al. 2005; Chenu and Cosentino 2011). In addition, the EPS matrix can retain and accumulate extracellular degradative enzymes, therefore acting as an 'external digestion system' for the embedded cells (Flemming et al. 2016). The chemical and physical properties of the EPS matrix vary depending on its polymeric composition and structure, but it broadly consists of hydrated macromolecules organized as interconnected strands longer than 100 nm (Chenu and Cosentino 2011) (Fig. 3C). The strands network attracts water via surface,



osmotic and capillary forces, and its structure gives EPS an exceptional capacity to retain water (EPS can absorb more than 10 times its weight in water when saturated) (Roberson and Firestone 1992). Drying modifies the morphology of the EPS matrix, but it can remain fully water saturated at matric potentials as low as  $-1$  MPa (Chenu and Roberson 1996). In soil, microorganisms producing EPS modify the local microhydrological conditions due to increased water retention, which also likely influence soil water content at the macroscopic scale. A physical consequence of the water-binding capacity of EPS is the reduction by up to one order of magnitude of the aqueous diffusion coefficients of solutes in the matrix relative to their diffusion coefficients in free water (relative diffusivity), as well as a steep reduction of hydraulic conductivity (up to five orders of magnitude) in porous media (Or et al. 2007). However, at low matric potentials, the relative diffusivity of solutes such as glucose is higher in the EPS matrix than in unsaturated soil pores (Chenu and Roberson 1996; Or et al. 2007), which maintains nutrients diffusion fluxes to EPS-embedded cells even in dry soils. In addition, reduced hydraulic conductivity and increased water retention in the EPS matrix may result in hydraulic decoupling in the surroundings of EPS-producing microbes, that is, it could maintain local hydrated areas protecting the cells during drainage, or conversely it could moderate effects of rapid soil rewetting during rainfall, hence decreasing the osmotic stress experienced by soil microbes (Or et al. 2007). Structurally, EPS production by microbes creates a stabilizing interface between biological and physical components in soil, as EPS possess high affinity to clay and other mineral particles (Chenu and Cosentino 2011). Following intense colonization of the wheat rhizosphere by EPS-producing bacteria, Amellal et al. (1998) observed significant increase in soil aggregation and concluded that *Pantoea agglomerans* plays an important role in soil water regulation by improving soil aggregation. The EPS matrix is mechanically stable thanks mainly to its polysaccharides components, their adhesion to soil surface and strand cross linking all contributing to its strength and viscoelastic properties (Flemming and Wingender 2010; Billings et al. 2015; Flemming et al. 2016). Microrheology, which studies spatiotemporal changes in EPS mechanic properties at the microscale (Rice, Wuertz and Kjelleberg 2016), could in the future improve our understanding of the organization of EPS-producing microorganisms in soil. Altogether, the biophysical properties of the EPS matrix play a fundamental role, both structural and physiological, in the soil-microbe complex. EPS-induced changes in hydrological conditions protect cells against desiccation, facilitate nutrient diffusion under dry conditions and influence soil water content at the macroscale, while EPS matrix holds cells together and favor soil aggregation.

## SUMMARY AND OUTLOOK

Contemporary environmental microbiology endeavors to systematically harness the wealth of genetic tools and fuse new insights into mechanistic models that enable generalization and predictions. The services provided by soil microbial life rely on a delicate balance within, and proper management of the environment where they live, the soil. The long-term success of agronomic operations can no longer be measured by biomass or yields alone, with the growing recognition for the importance of a 'sustainable subsurface management' (Brussaard 2012; Bardgett and van der Putten 2014) where soil biota and microbiota are considered a critical part of the soil capital deserving special attention and management considerations. The

sustainability of soil ecosystem services and soil management necessitate improved understanding of how the various components of this complex ecological machine fit and function together. We have reviewed the roles of water and its dynamics, complex pore spaces, carbon and resource architecture within such pores, and how microbes interact in this environment and with other biota (plant roots, earthworms and more).

The review highlighted the central role of the soil aqueous phase, a highly dynamic and fragmented environment essential for microbial life. Theoretical and experimental evidence suggests that the sizes and connectivity of these dynamic microhabitats shape nutrient diffusion pathways, cell motion and dispersion distances, thereby promoting the large microbial biodiversity found in soil. Differences in climatic conditions and in the biomes that develop on soils have a strong effect on the composition, abundance and activity of soil microbial communities, with certain factors (e.g. soil pH) exerting stronger influences on microbial life—the reasons for such strong influences are not yet fully understood. Soil bacterial communities are dominated by a relatively small subset of phyla that seem to be present in all soils and climates (Lauber et al. 2009). For this reason, bacterial communities across continents and soil types are globally more similar to one another than to communities in other ecosystems, which may reflect very ancient selection for soil colonization at the phylum level. On the other hand, species diversity within this subset of soil phyla is unparalleled, which reflect extreme niche partitioning and spatiotemporal isolation in soil habitats. While the review focuses on factors and properties of prokaryotic cells, we recognize the diverse roles of other microbial groups, especially fungi and protists. These and other microbial groups (viruses) have adapted different ecological strategies to cope with fragmentation of the aqueous phase. For example, the ability of fungal hyphae to extend across empty pores and thus bridge the fragmented aqueous environment greatly extend the range of soil moisture conditions for their activity and the ranges of their dispersion (Ritz and Young 2004; Falconer et al. 2015). Clearly, all microbial actors play a role in the soil complex ecology, and combining new insights from all microbial groups with their diverse temporal and spatial preferences and life strategies would undoubtedly enhance understanding and elucidate important interactions that are presently ignored, or not yet understood.

The key remaining challenge is how to continue the transformation of soil microbiology from an empirical science to a quantitative discipline capable of making predictions and offering evidence-based soil management strategies. Efforts are underway in different research groups to formulate quantitative frameworks that harness the explosion in molecular tools for constructing detailed metabolic networks (Harcombe et al. 2014), track individual cells and populations in virtual soil-like environments (Resat et al. 2012; Kreft et al. 2013; Ebrahimi and Or 2015; Kaiser et al. 2015; Kim and Or 2016) and in turn, provide guidance to better use of new experimental and monitoring activities (Widder et al. 2016). In terms of ecosystem functioning, one way ahead is to integrate dynamic soil processes into mechanistic models (Bradford and Fierer 2012). For example, York et al. (2016) recently proposed a 'holistic rhizosphere' perspective in order to apprehend the complex interactions and feedbacks between soil, root system and microorganisms. Such integrative efforts demand more interdisciplinary research, a trend that we expect to continue steady in the future. In particular, knowledge transfer from microbial ecology to biogeochemical models may prove essential to understand how local microbial diversity affects soil processes at larger scales. The past decade

has proved highly fruitful in advancing theoretical concepts, developing new mechanistic models and reducing the boundaries between research disciplines concerned with soil processes. The awareness of the fundamental role of soil has grown markedly in the past years, both in the scientific community and in the public eye (2015 has been designated the international year of soil by the UN). In this challenging and promising context, we look very much forward to the flourishing of the field in the years to come.

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