Biophysical processes affecting microbial activity in soil environments

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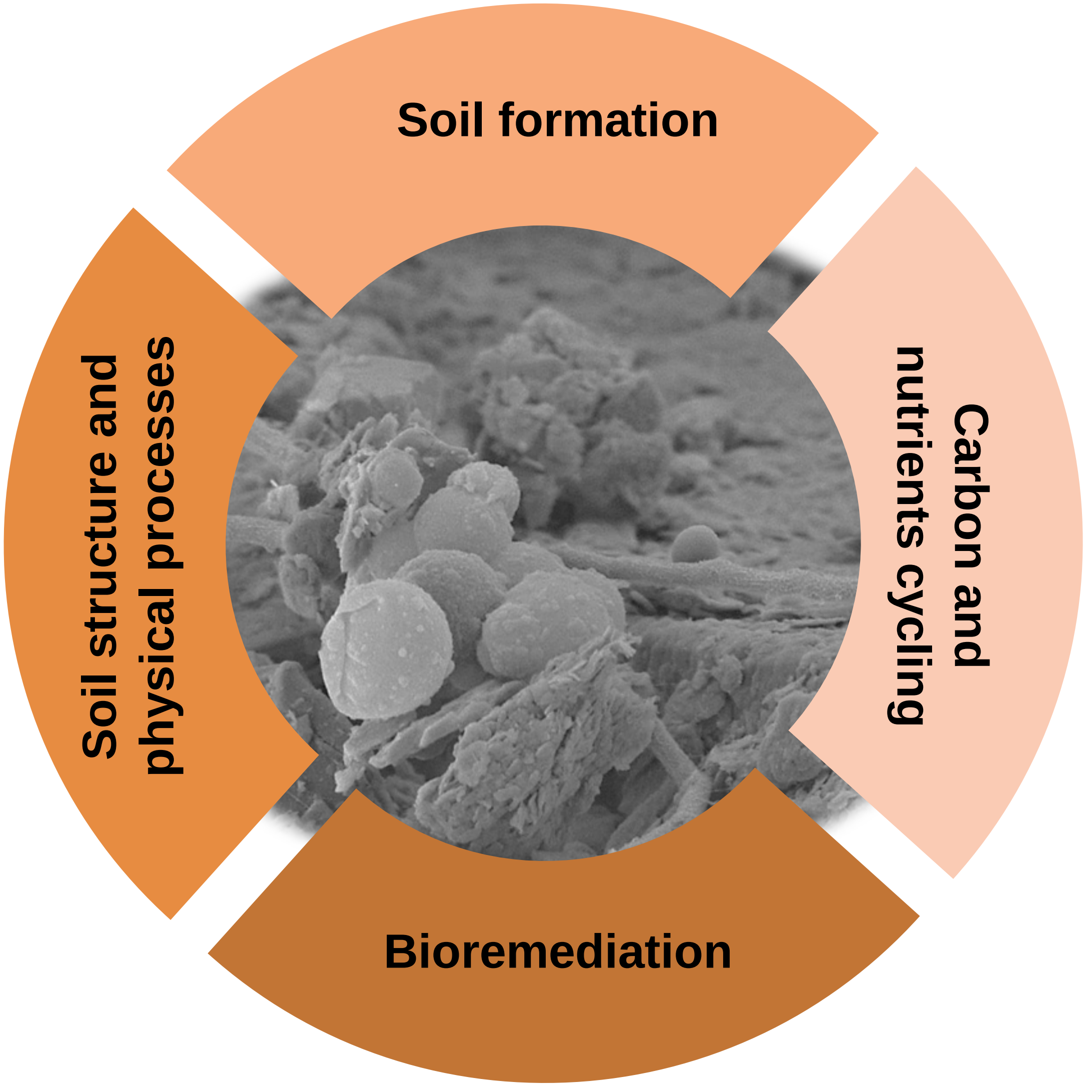
Microbial activity: an essential component of soils



Outline

- Introduction: overview of soil microorganisms
- Macro- and microgeography of soil microbes
- Soil as microbial habitat
- Consequences for microbial dispersal, activity and spatial organization
- Microbial role in soil formation, structure and physical properties

In addition: Technical notes

Reference

FEMS Microbiology Reviews, fux039

doi: 10.1093/femsre/fux039
Review article

REVIEW ARTICLE

Biophysical processes supporting the diversity of microbial life in soil

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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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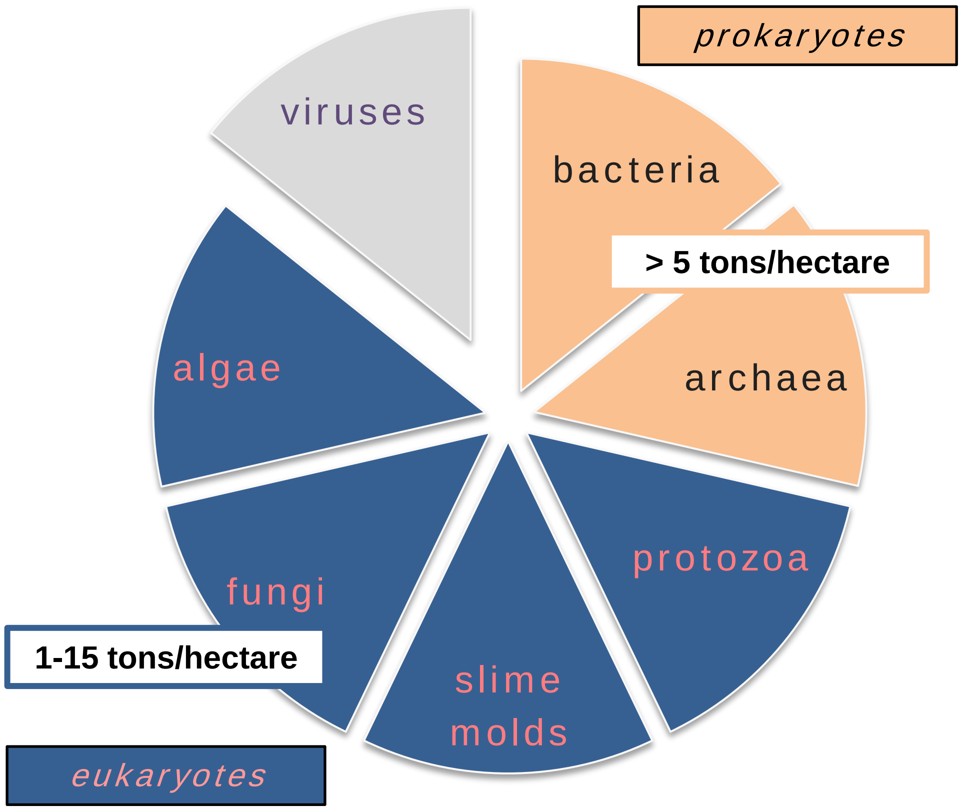
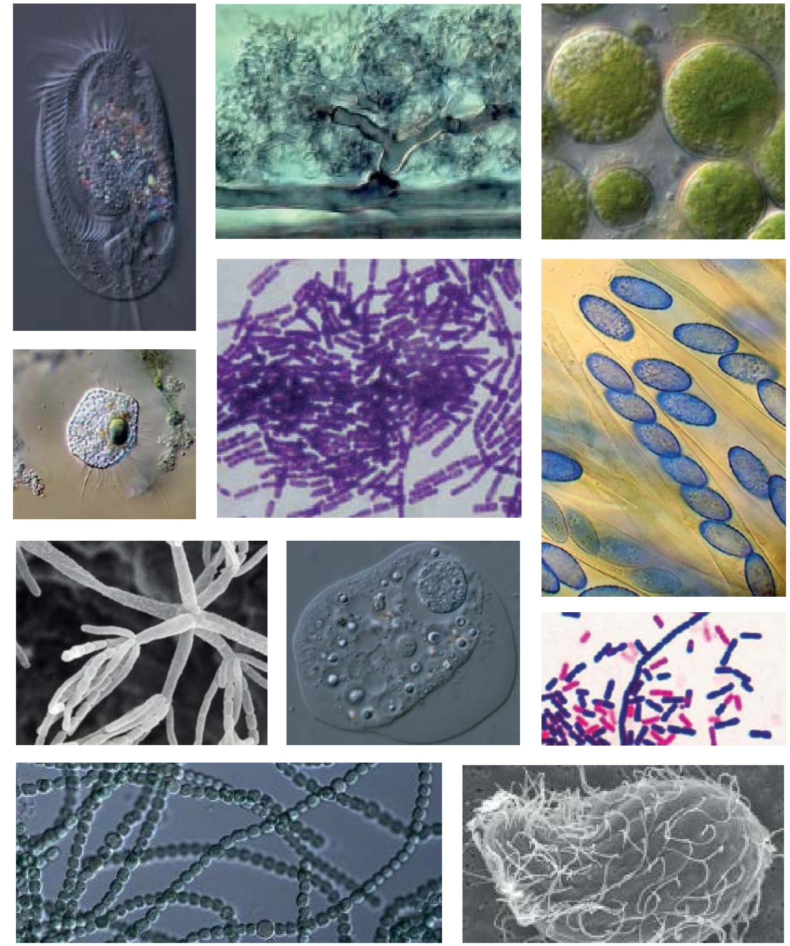
Overview of soil microorganisms

Soil microorganisms

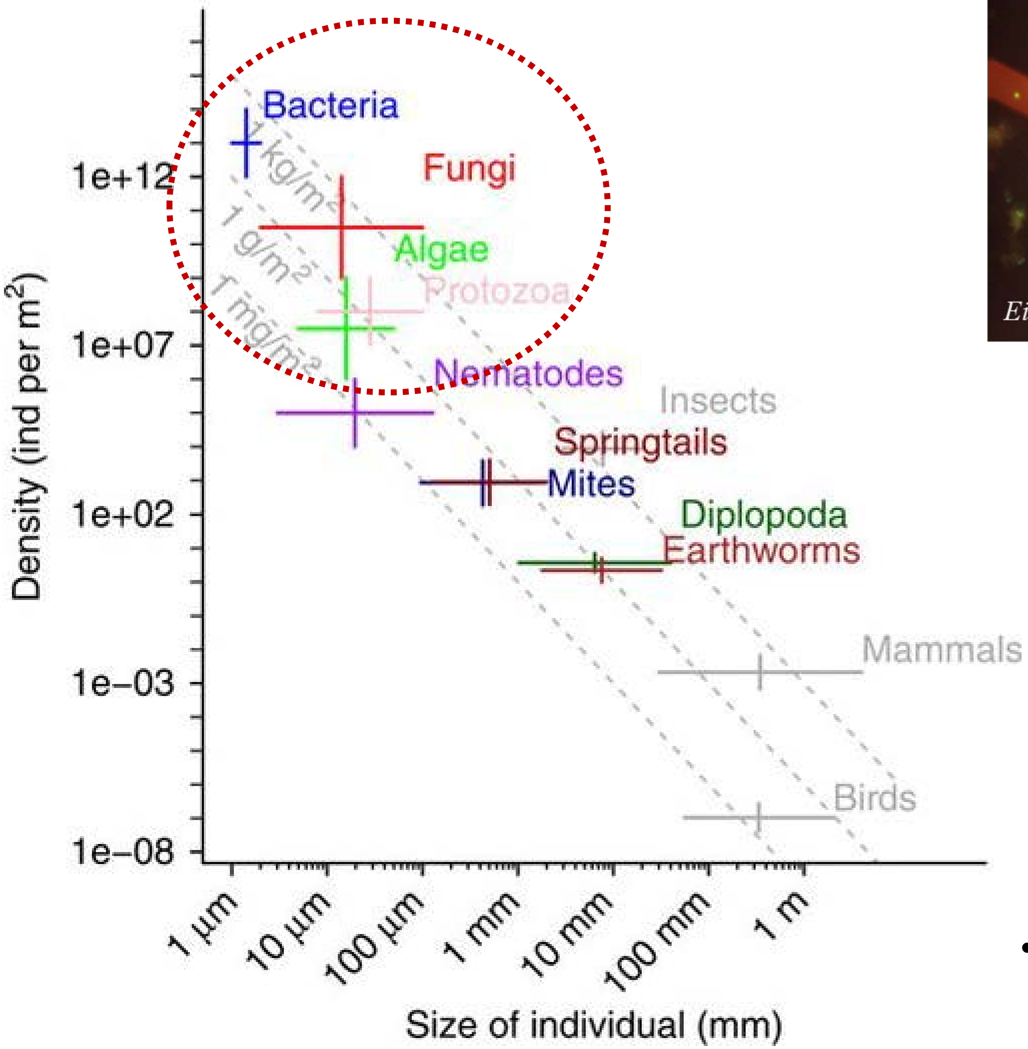




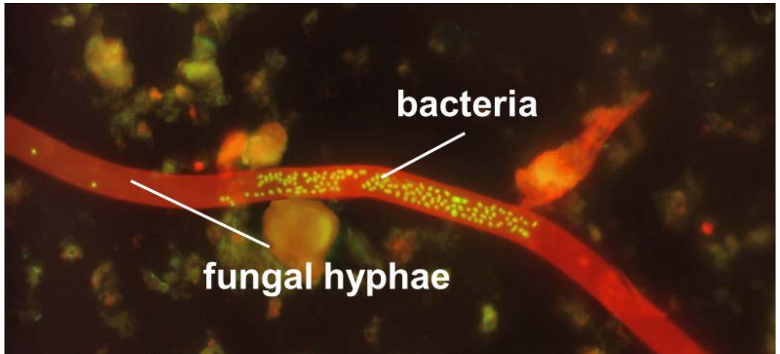
Global Soil Biodiversity Atlas, 2016

- **High abundance**: one gram of topsoil may contain 10^9-10^{10} prokaryotes (**bacteria** and **archaea**), 10^4-10^7 protists (**protozoa**, **unicellular algae**, **slime molds**), 100 m of **fungal hyphae**, 10^8-10^9 **viruses**…
- **Unequalled diversity**: highest estimates range from 1,000 to 1,000,000 bacterial phylotypes per gram of soil

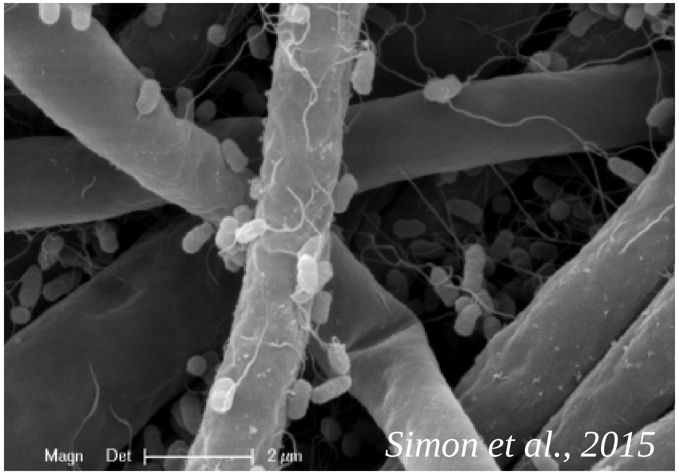
Size-density relationship



Veresoglou et al., 2015



Eickhorst & Tippkoetter http://www.microped.uni-bremen.de

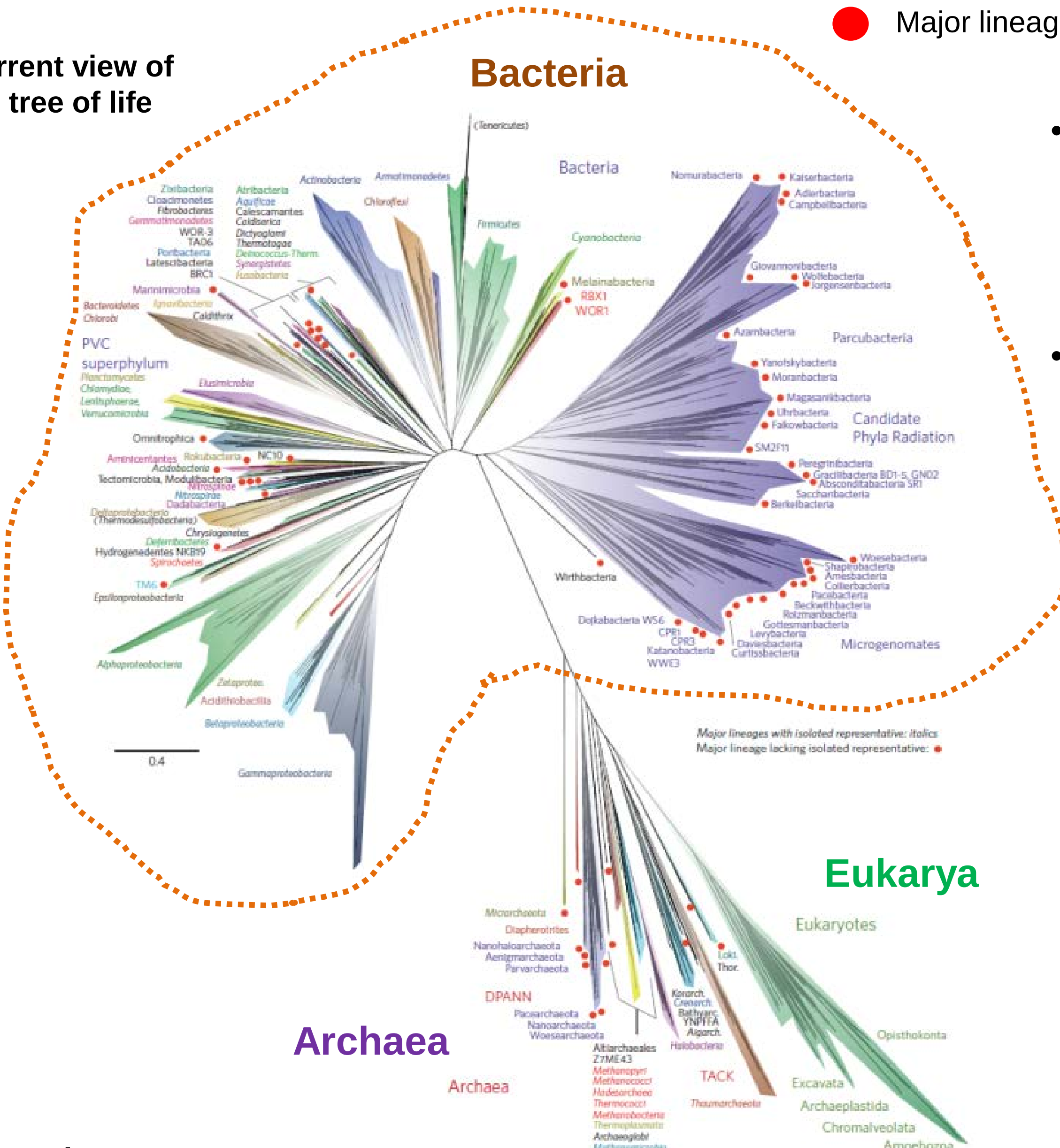


Simon et al., 2015

- **Bacteria** and **filamentous fungi** differ significantly in size and ability to disperse in soil
- **Bacteria** are <u>the most abundant organisms in surface soils</u>

Bacteria – unparalleled diversity

Current view of the tree of life

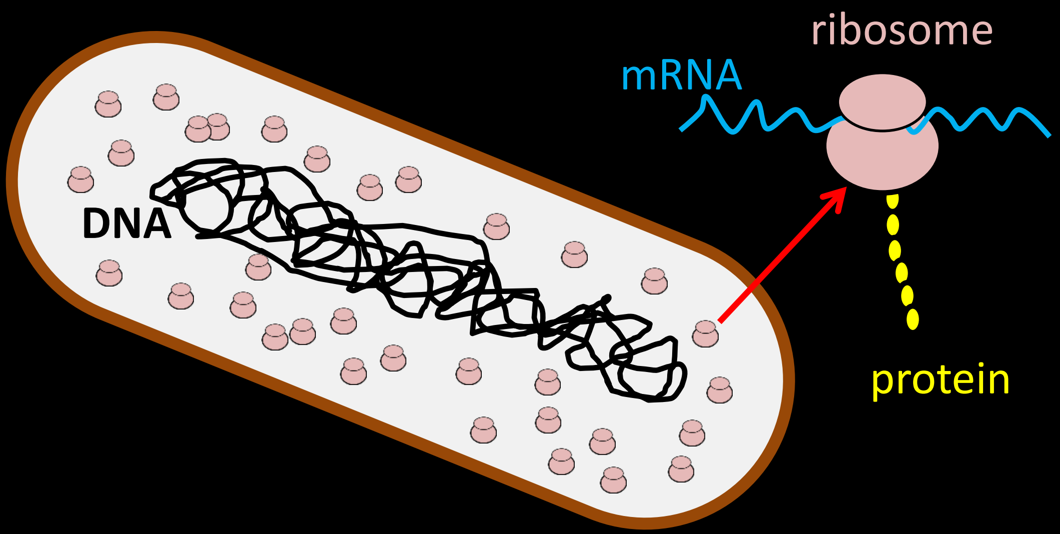


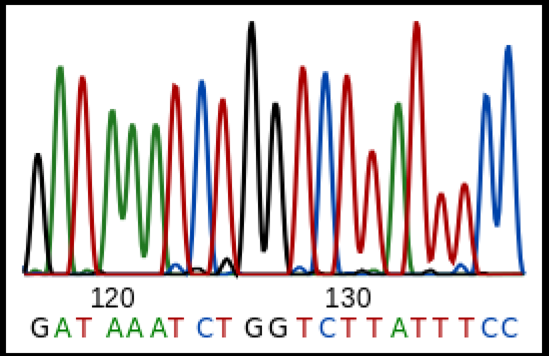
Major lineages lacking an isolated representative

- The <u>majority of bacterial diversity is only known through molecular signatures</u> in the environment (**DNA**) as many bacteria cannot be cultivated in the laboratory
- Similarity of DNA sequences in conserved genes is used to reconstruct phylogenetic trees and classify uncultured bacteria

Hug et al., 2016

Note 1: Ribosomal RNA sequence as evolutionary chronometer





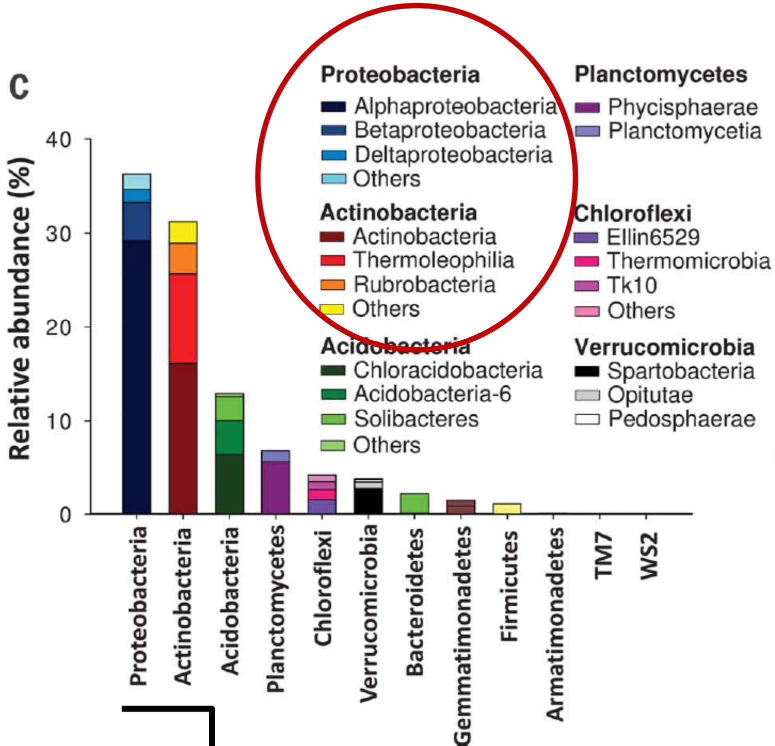
DNA nucleotide sequence

- Ribosomal RNAs (part of ribosomes) are essential and universal to all cells, and several regions have very well conserved nucleotide sequences, which makes them good evolutionary chronometers.

- The gene encoding the small subunit (SSU or 16S) ribosomal RNA is the most commonly used for the identification and classification of bacteria

- As of today, the **Ribosomal Database Project** (RDP)'s collection contains >3,300,000 bacterial 16S rRNAs and >125,000 fungal 28S rRNAs

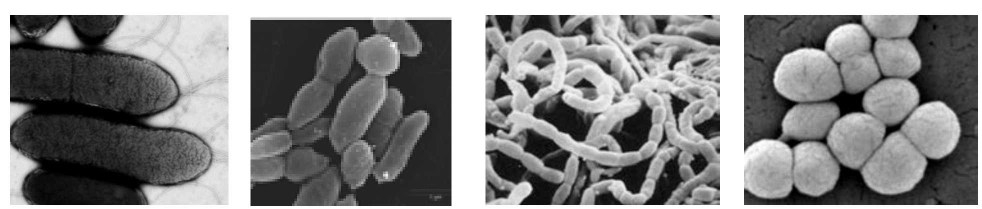
Diversity of soil bacteria – newest data



A global atlas of the dominant bacteria found in soil

Manuel Delgado-Baquerizo,[1,2]* Angela M. Oliverio,[1,3] Tess E. Brewer,[1,4] Alberto Benavent-González,[5] David J. Eldridge,[6] Richard D. Bardgett,[7] Fernando T. Maestre,[2] Brajesh K. Singh,[8,9] Noah Fierer[1,3]*

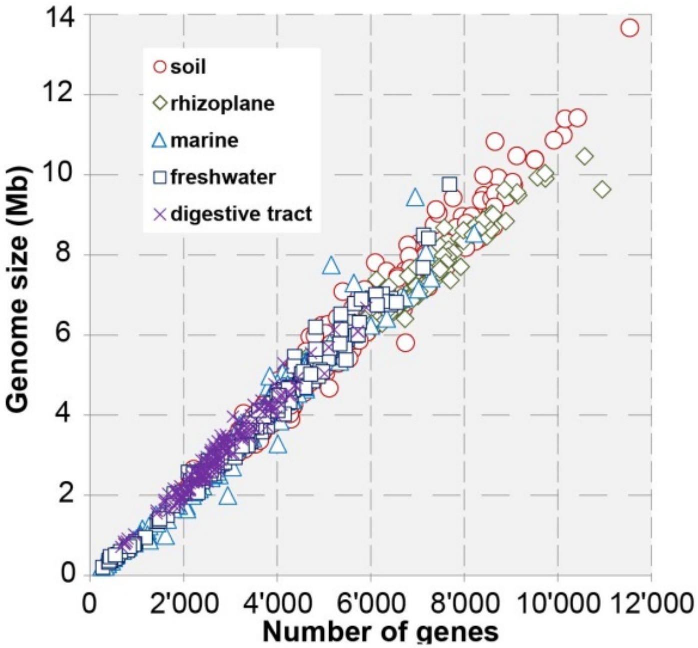
2018 Science AAAS



Proteobacteria

Actinobacteria

Genetic and metabolic diversity of soil bacteria



Data from the US *Joint Genome Institute*
(total of 1,107 genomes)

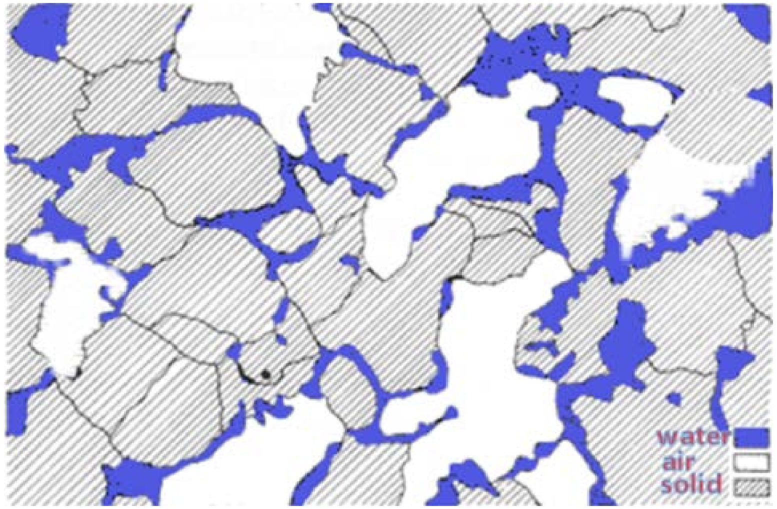
- Soil bacteria have larger genomes and contain more genes than aquatic or clinical environments
- Genomes of soil bacteria contain a large proportion of **accessory genes** (sensing, transport, antibiotics,…)
- **Gene expression** can vary greatly depending on the physical characteristics of the environment
- Such **metabolic variability and adaptability** is attributed to selection by the fluctuating soil environment

- > 80 % of antibiotics presently used in hospitals originate from soil bacteria (especially *Streptomyces* sp.)

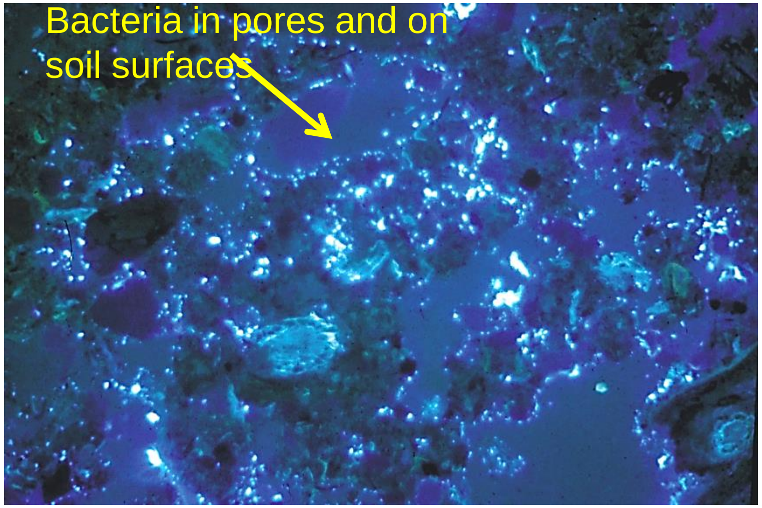
Colonies of *Streptomyces coelicolor*

Soil as microbial habitat

Bacteria colonize soil pores and surfaces

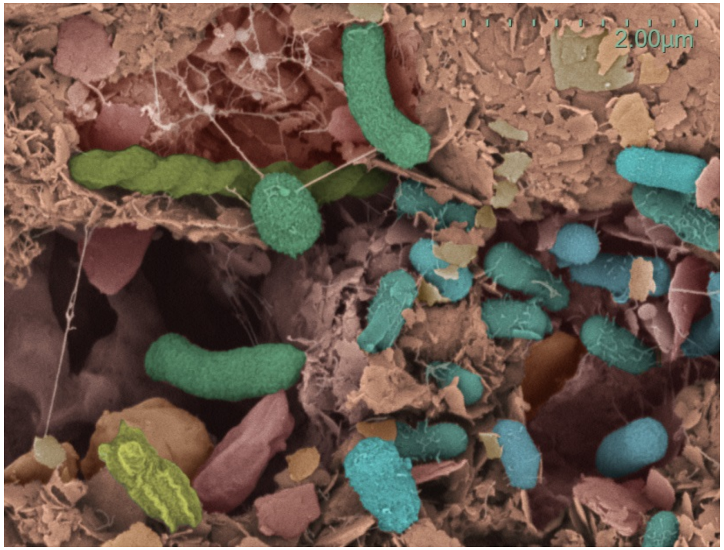


Or et al., 2007



Eickhorst & Tippkotter http://www.microped.uni-bremen.de

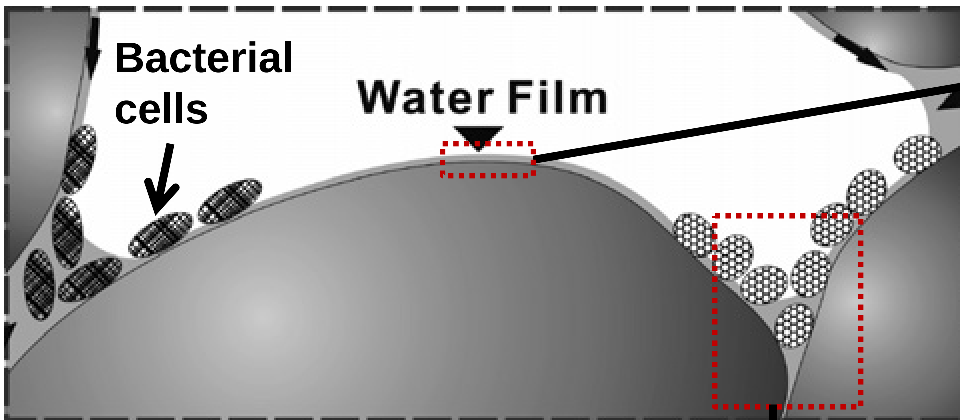
- Bacteria inhabit heterogeneous **pore spaces** and **soil grains surfaces**
- Despite high bulk cell densities, soil microorganisms occupy <<1% of all soil surfaces. Depending on soil type, 15-50% of the soil porosity is not accessible to microbes due to narrow pore throats
- Bacteria require an **aquatic environment** for their life function, but the water phase retained in soil is often fragmented and highly dynamic



Bacterial cells on soil surfaces (Zürich forest)

Water availability to bacteria in unsaturated soils

- Soil water is **retained by capillary forces in corners and crevices** between soil grains or **adsorbed as thin water films on soil surfaces.** The soil water potential, the size and geometry of soil pore spaces, and the properties of soil surfaces jointly determine the architecture of the soil aqueous phase
- Microorganisms rely on **rough elements** in soil to provide aquatic microhabitats



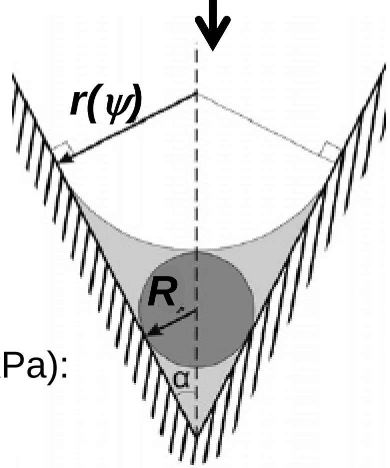
Or et al., 2007

$$l(\psi) = \sqrt[3]{\frac{A_{svl}}{6\pi\psi}}$$ (van der Waals forces)

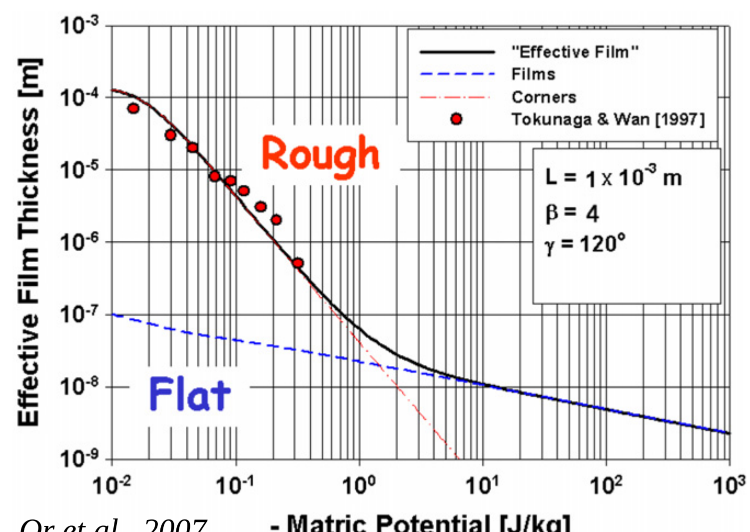
Water film thickness as function of matric potential. Values near field capacity gives film thickness of <u>10-20 nm</u> (typical bacterial cell is <u>0.5-1 μm wide</u>!)

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

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

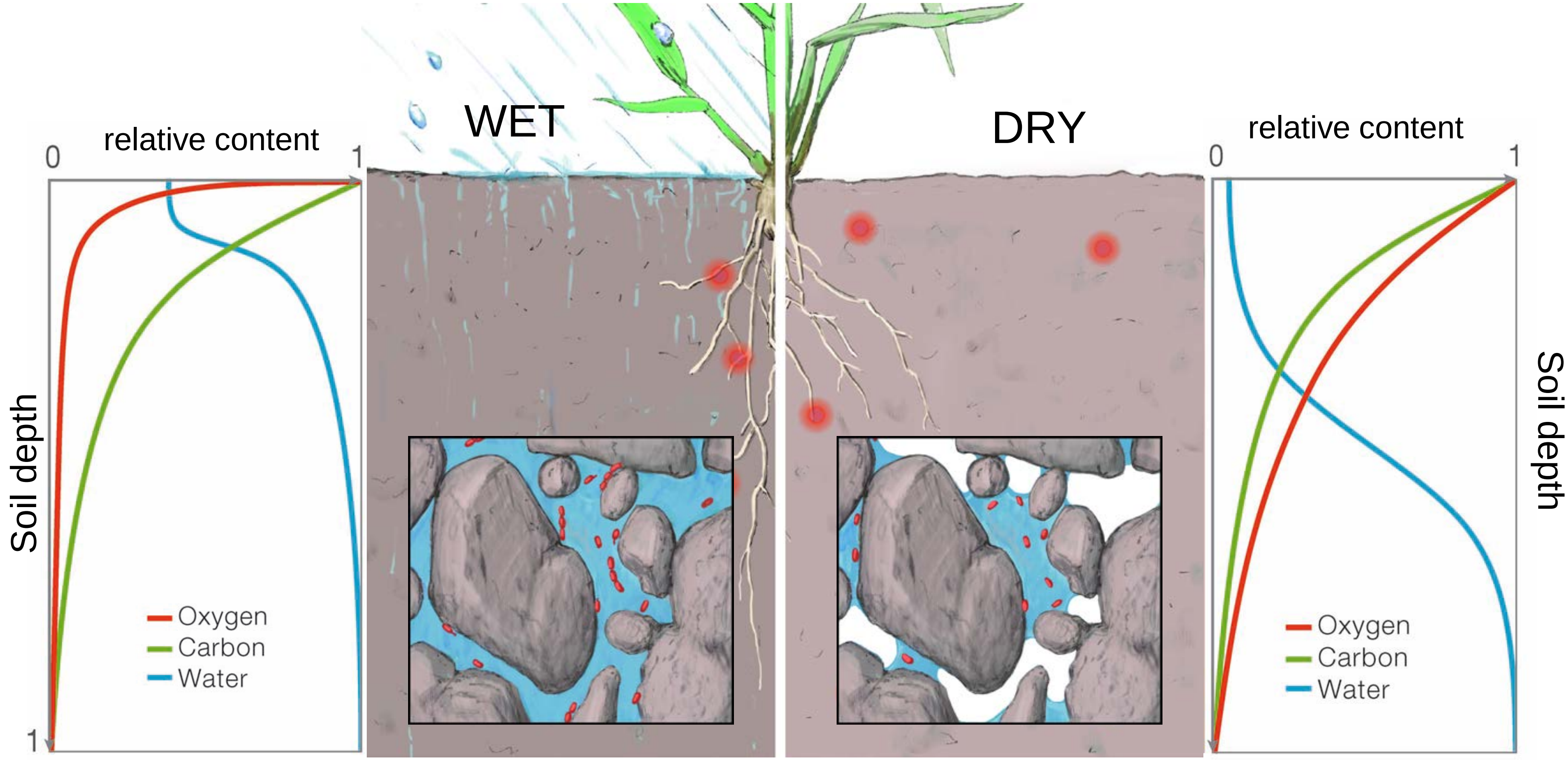


For $\alpha = 30^0$ and at field capacity (-30 kPa):
R = <u>0.8 μm</u>



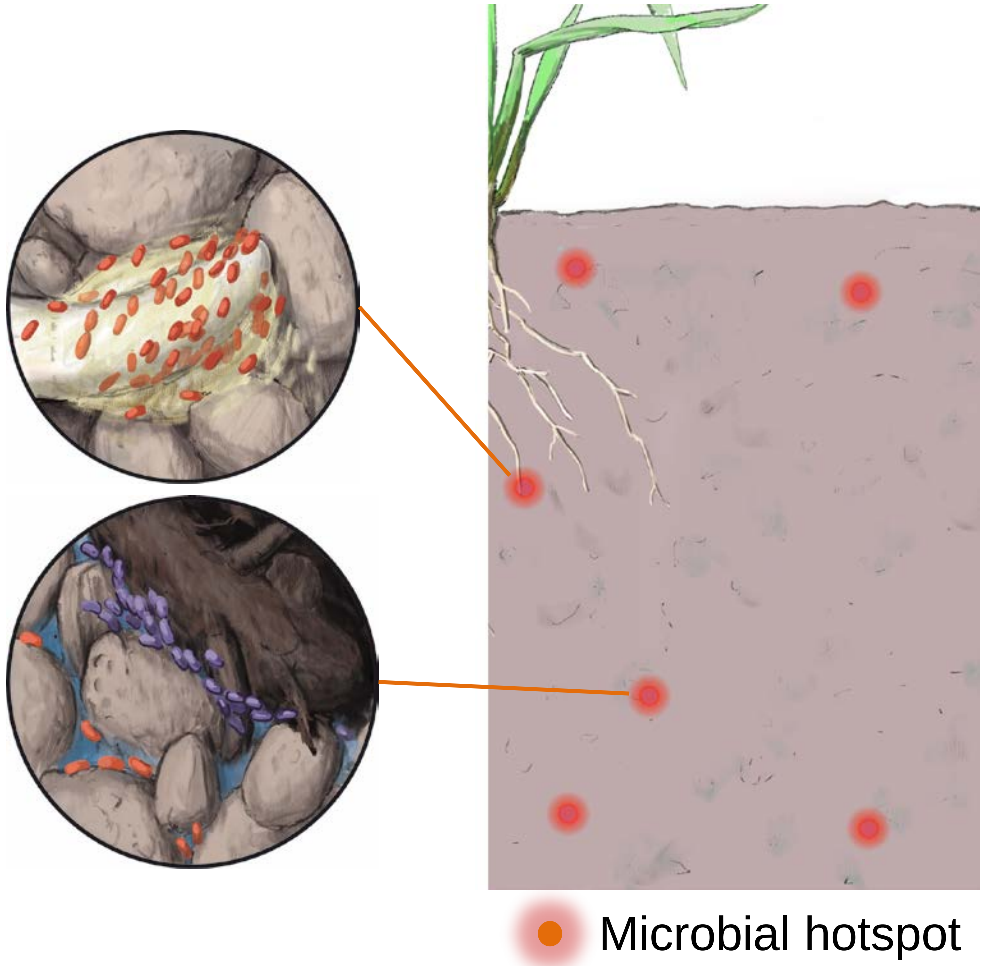
Or et al., 2007

The dynamic soil aqueous phase



- Episodes of **rainfall** and **irrigation** infiltrate water into the soil, temporarily increase soil water content and thus change oxygen and water profiles. Following drainage, evaporation and plant water uptake, soil returns to its unsaturated state (and remains so in most climatic and geographic regions most of the times)
- In most soils, microorganisms are exposed to <u>rapid, high and frequent variations in water potential and oxygen availability</u> with important consequences for their dispersion and functions

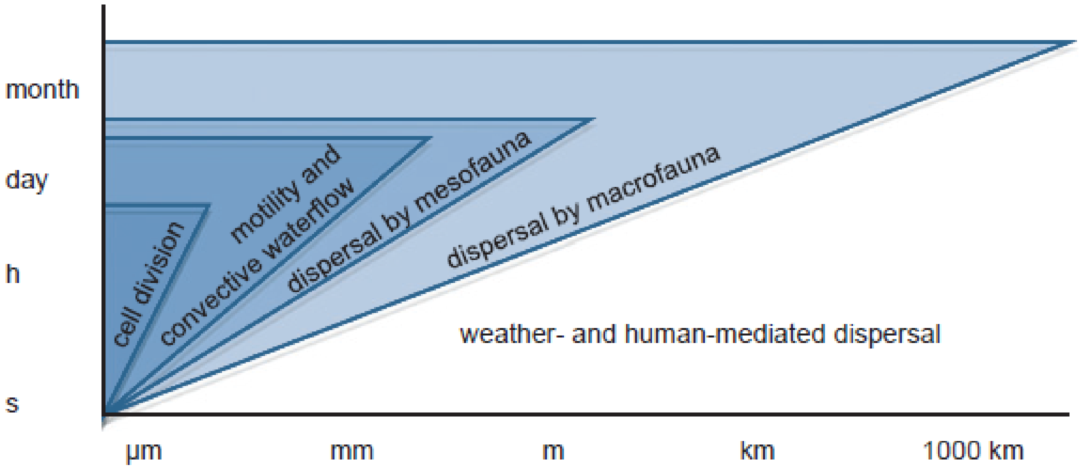
The concept of microbial hotspots in soil



- Availability of soil organic carbon to microbes is heterogeneous in space and time. Estimates suggest that **only a few % of all soil microbes are active** at a given time, the majority is inactive or dormant. Consequently, soil <u>microbial abundance and activity</u> is often associated with so-called <u>hotspots</u>, typically in the **rhizosphere** or associated with **decaying plant material**

Consequences for microbial dispersal, activity and spatial organization

Microbial dispersal in soil

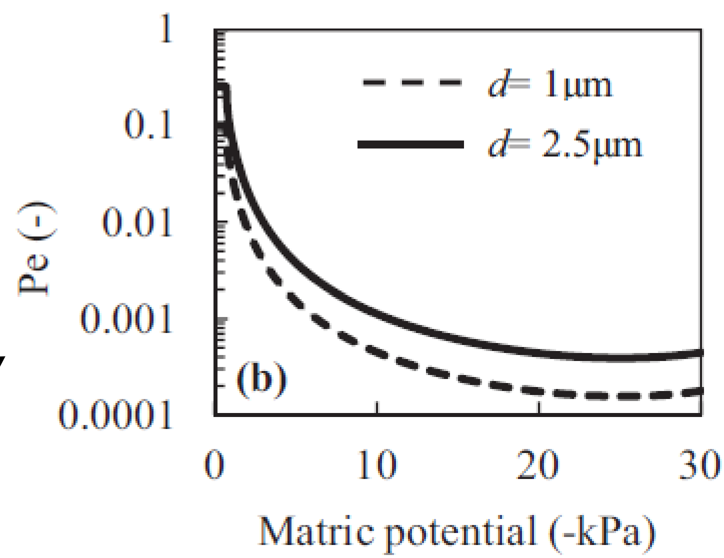


Vos et al., 2013

- Dispersal mechanisms operate at a range of spatial and temporal scales, from cell division and Brownian motion to transport across the globe
- Dispersal is **active** (motility) or **passive** through convective water flow or transport by animals or wind

Modeling results

- The advection of soil microbes is facilitated by the flowing streams of water when a soil is nearly saturated. With the exception of a few events per year, in most unsaturated soils most of the time conditions do not support advection.

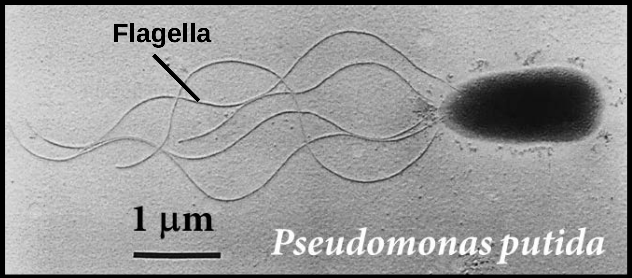


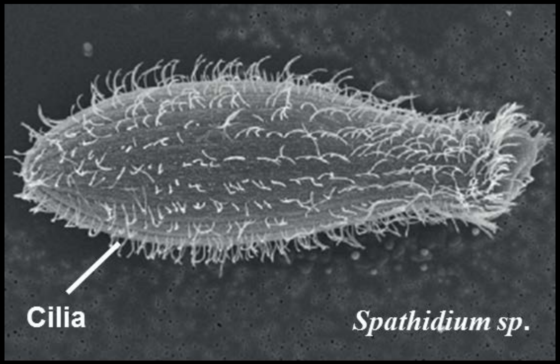
Ratio passive/active transport (convective capillary flow/chemotactic motion)

Ebrahimi & Or, 2014

Note 2: The many ways microbes move

- Many soil microorganisms are motile, thanks to rotating or moving appendages (***flagella*** or ***cilia***) that they use to move within water films
- Unlike bacteria, filamentous fungi can grow across empty pores and bridge air gaps in unsaturated soils



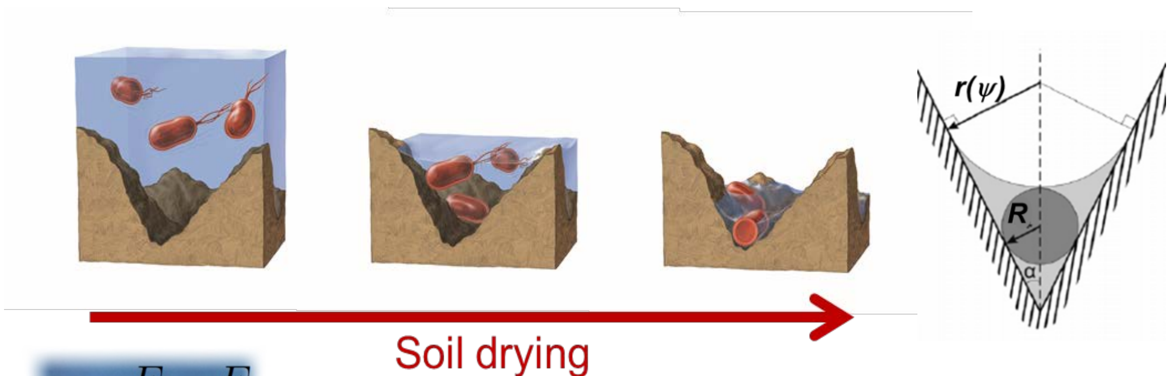


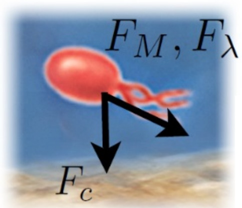
- In liquid films: swimming
- On surfaces: swarming, twitching, gliding, sliding

- Gradient-guided swimming is commonplace in soil bacteria: they orientate towards resources

Effect of matric potential on bacterial motility and dispersion

- Lower soil matric potential values result in thinner liquid films that reduce the <u>velocity</u> of swimming bacteria due to **capillary pinning forces** and **viscous drag forces**





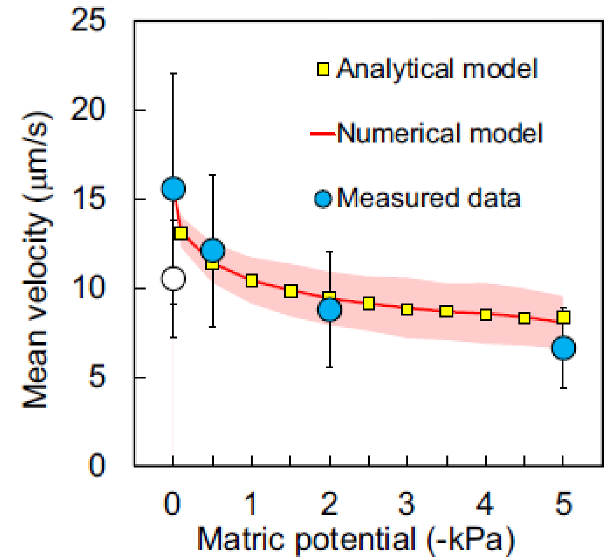
$$V = V_0 \frac{F_M - F_\lambda - F_C}{F_M}$$

F_M : self propulsion

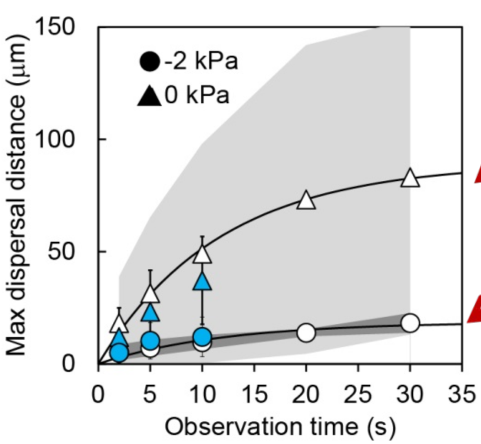
F_λ : cell-surface interaction

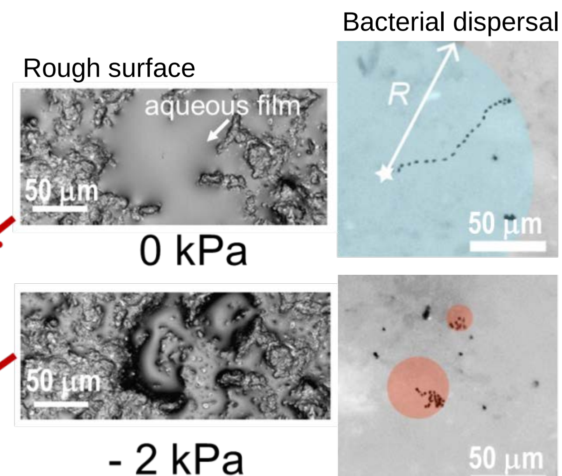
F_c : capillary pinning force

Dechesne et al., 2010



Tecon & Or, 2016

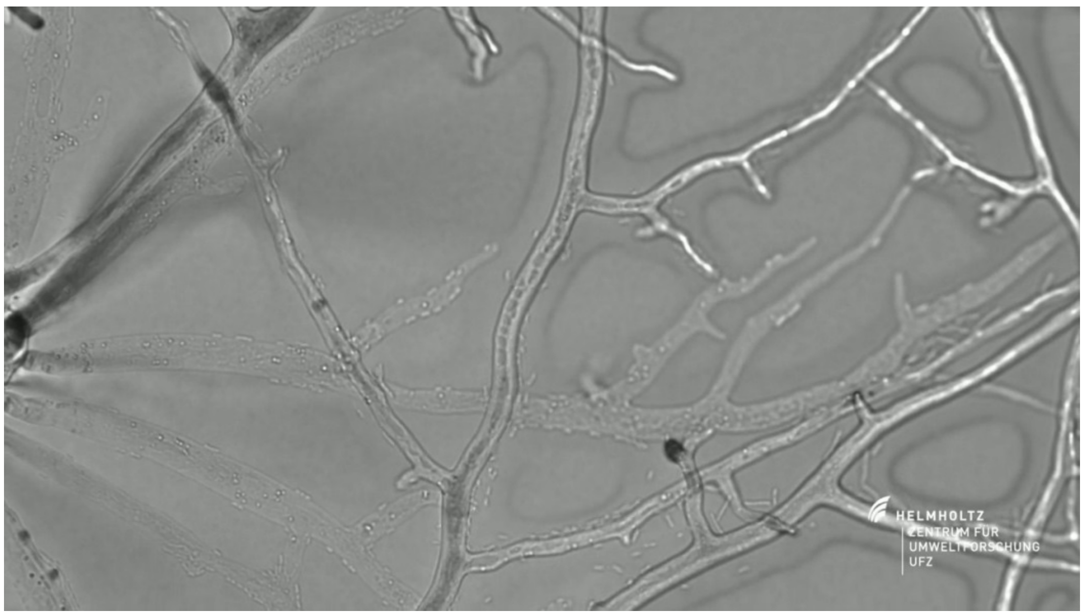


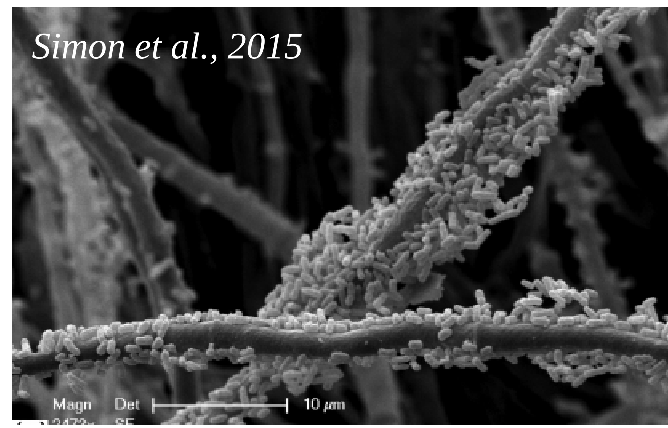


- Experiments with the soil bacterium *P. protegens* on a porous surface model show <u>dispersal</u> by flagellar motility already hindered at mild matric potential values
- Flagellar motility in soil seems to be restricted to a narrow range of very wet and short-lasting conditions

Bacterial transport on fungal hyphae

- Bacteria can use fungal hyphae as a structure for swimming (‘**fungal highways**’). This vastly increases bacterial dispersion (up to 1 cm per day in laboratory experiments). Fungal transport depends on the expression of bacterial flagella and on the hydrophilic properties of both fungi and bacteria





Movie: Tom Berthold, UFZ Leipzig

Impact of soil water potential on microbial activity

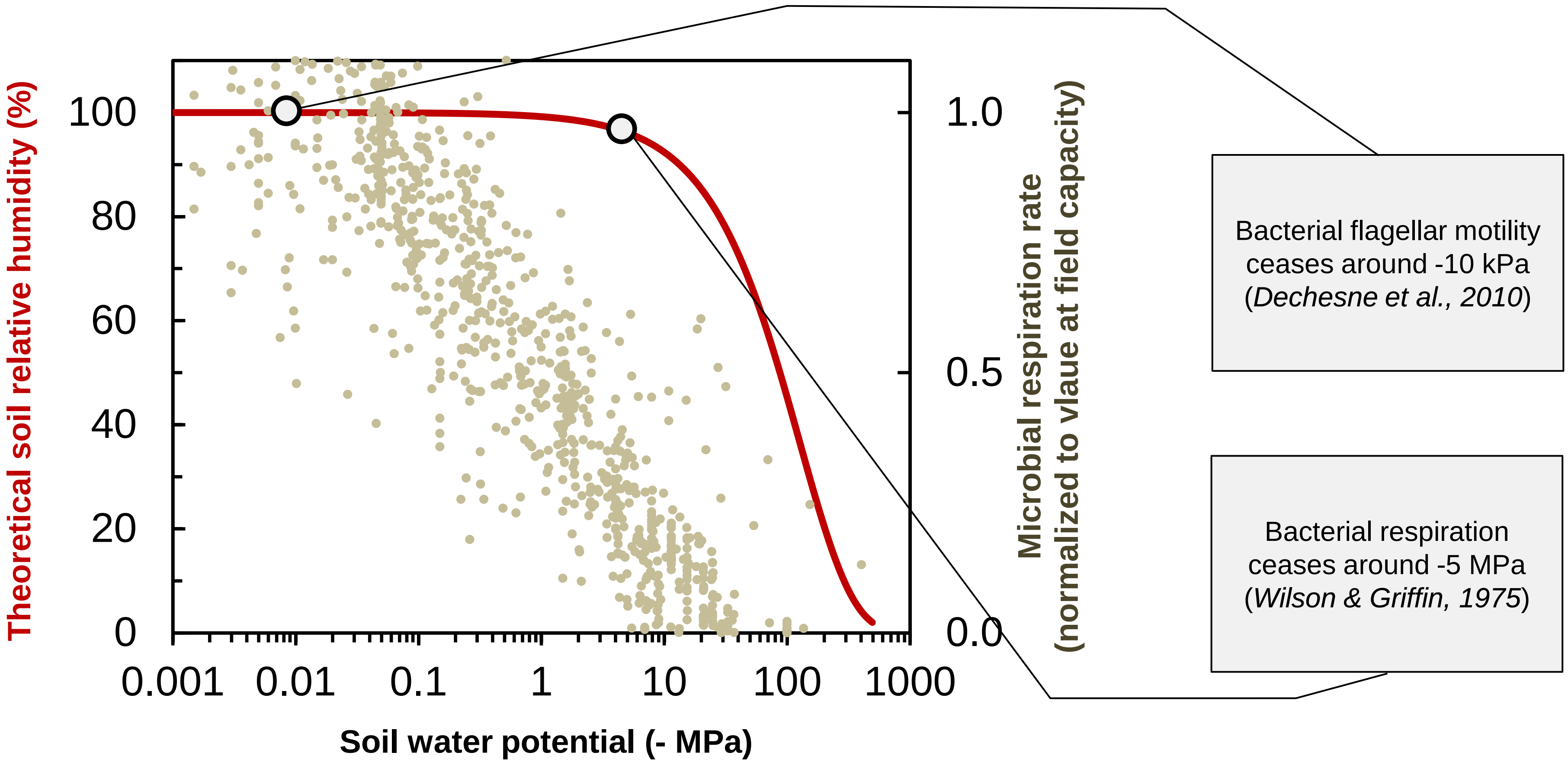
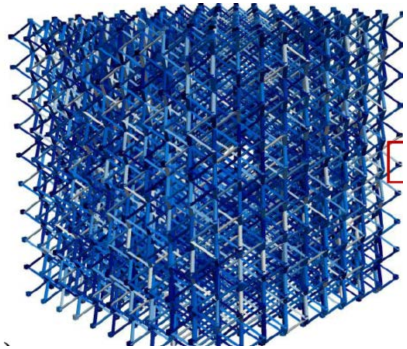


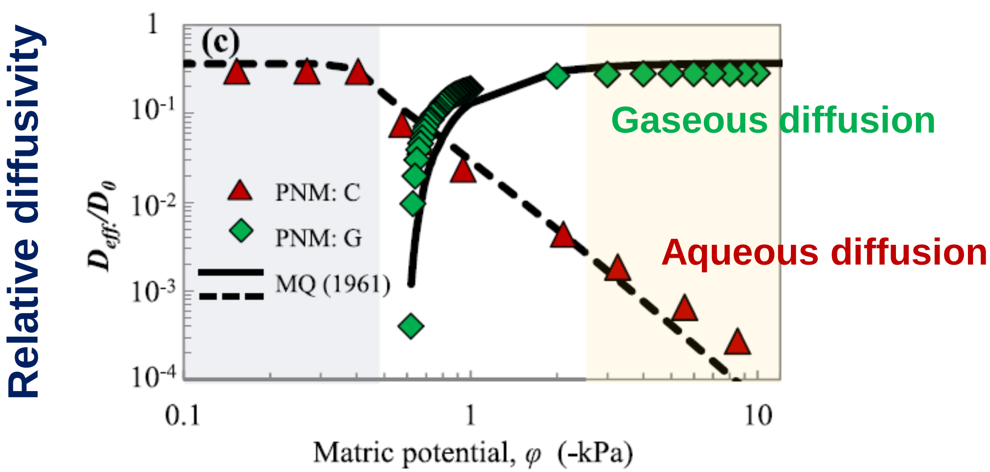
Figure adapted from *Potts, 1994*. Data on respiration courtesy of Stefano Manzoni, from *Manzoni & Katul, 2014*

- Compared to the soil water potential, the soil relative humidity exerts very little influence on microbial activity. Almost all microbial activity takes place between 90% and 100% relative humidity

Effects of water on aqueous and gaseous diffusion

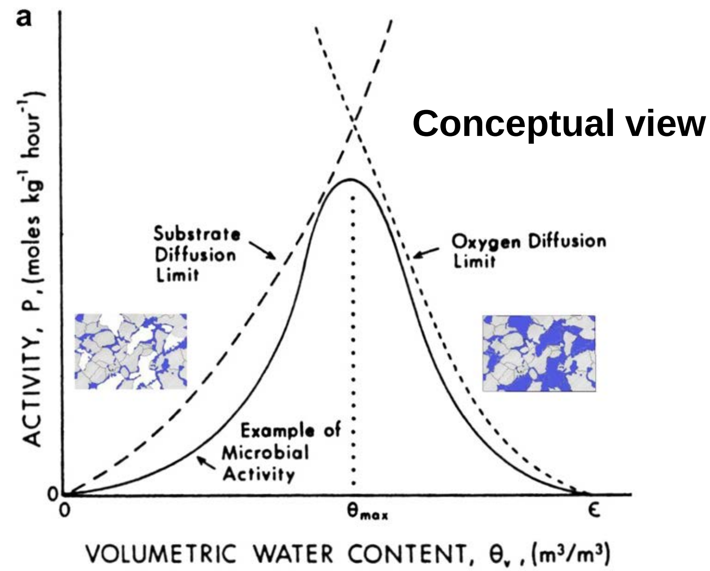
Numerical and empirical models of diffusion in unsaturated soil





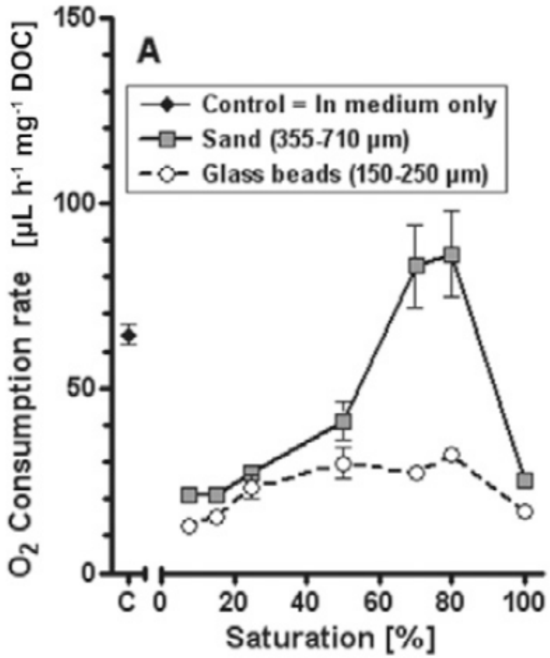
Ebrahimi & Or, 2015

- Reduction of liquid pathways as soil dries reduces nutrient transport and <u>aqueous diffusion rates</u>
- As soil dries the <u>gaseous diffusion rates</u> (e.g. of oxygen) rapidly increase
- This interplay of aqueous and gaseous diffusion can theoretically lead to an optimal water content for microbial activity at the macroscale

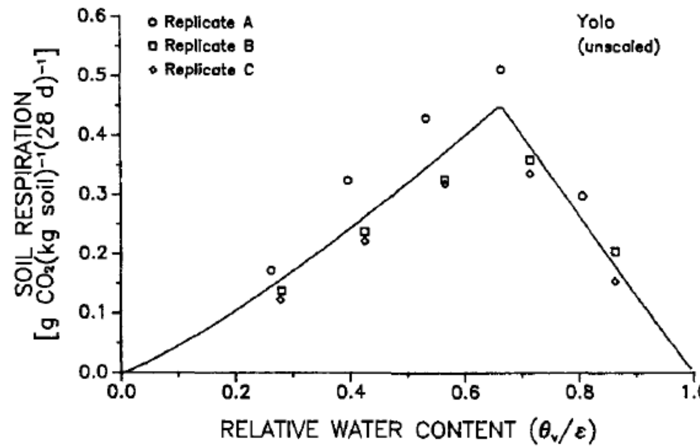


Skopp et al., 1990

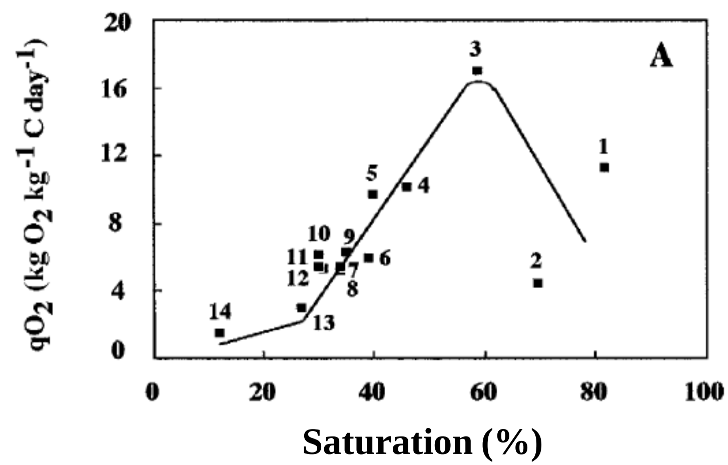
Evidence of optimal water content for aerobic respiration



Jost et al., 2011

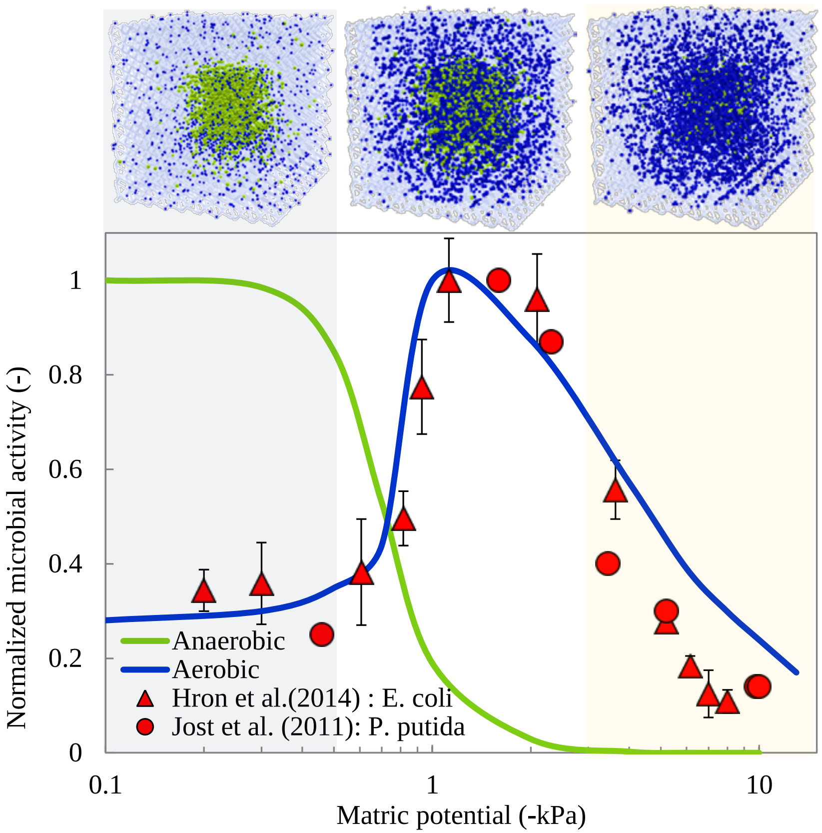


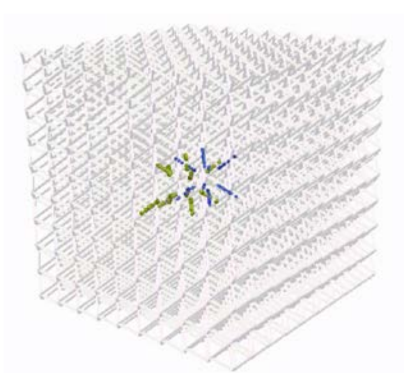
Skopp et al., 1990



Aon et al., 2001

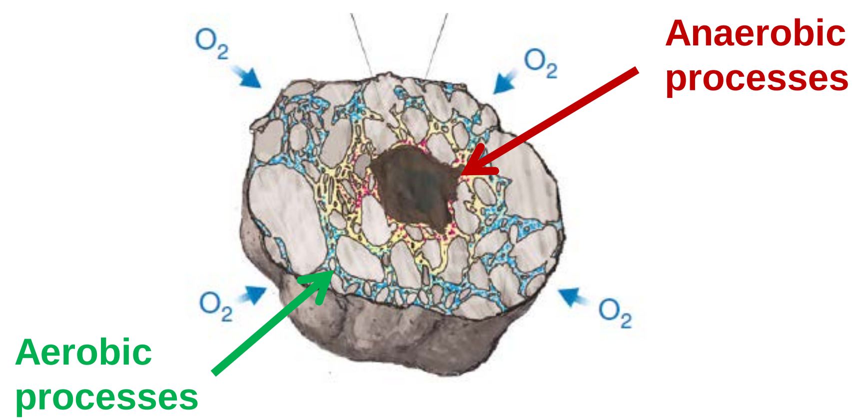
Anaerobic processes in soil – I





Ebrahimi & Or, 2015

- Under saturated conditions, <u>anaerobic respiration</u> can take place in specific microorganisms, e.g. **facultative anaerobes** that can use nitrate or nitrite as final electron acceptors and producing nitrous oxide and nitrogen gas (**denitrification**).
- **Hotspots**: 1% of soil volume may account for up to 90% of denitrification activity
- Local <u>anoxic conditions can persist even in aerated soils</u> (within soil aggregates)



Borer et al., 2018

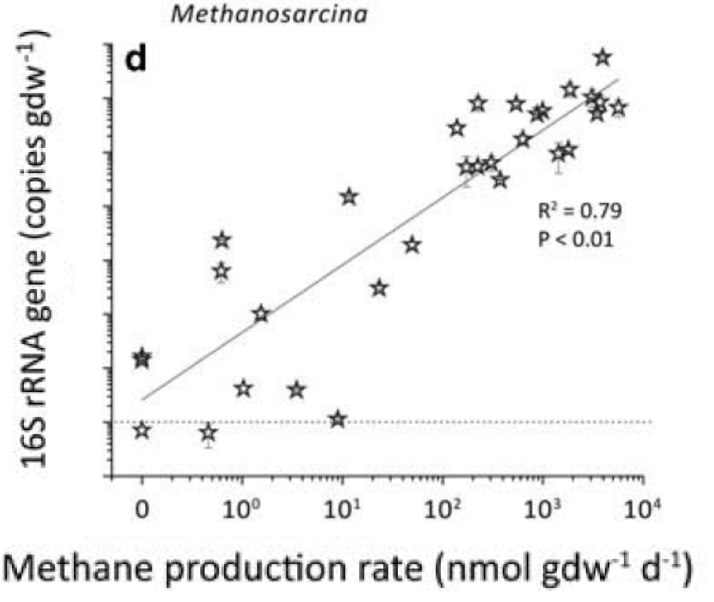
Anaerobic processes in soil - II

- In soil, anaerobic respiration is also performed by **obligate anaerobes** that are killed by prolonged contact with air. These include the groups of ***Clostridia***, **sulfate-reducing bacteria**, and **methanogens** (archaea)
- Methanogens produce almost all biogenic methane on Earth. Despite their sensitivity to oxygen, they are ubiquitous in unsaturated soils
- Peters & Conrad (1995): an arid soil from South Africa, stored under dry conditions for ~10 years, shows methanogenic activity after rewetting and incubation under anoxic conditions!

Methanogenic archaea are globally ubiquitous in aerated soils and become active under wet anoxic conditions

Roey Angel, Peter Claus and Ralf Conrad
Department of Biogeochemistry, Max Planck Institute for Terrestrial Microbiology, Marburg, Germany

2012



Note 3: Microbial seed banks

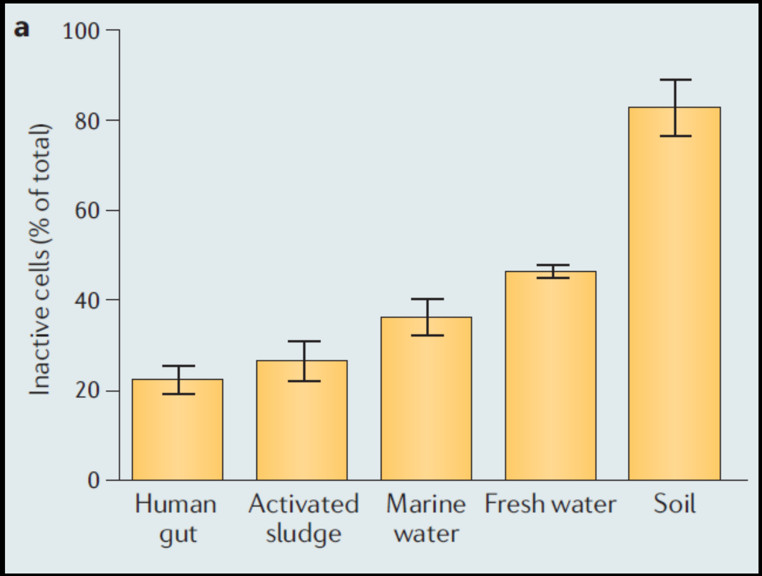
- Various estimates suggest that the majority of soil microorganisms are not active
- Inactive cells are **dormant**, with some species forming **spores**

Seed bank: 'reservoir of dormant individuals that can potentially be ressucitated in the future under different environmental conditions' (Lennon & Jones, 2011)

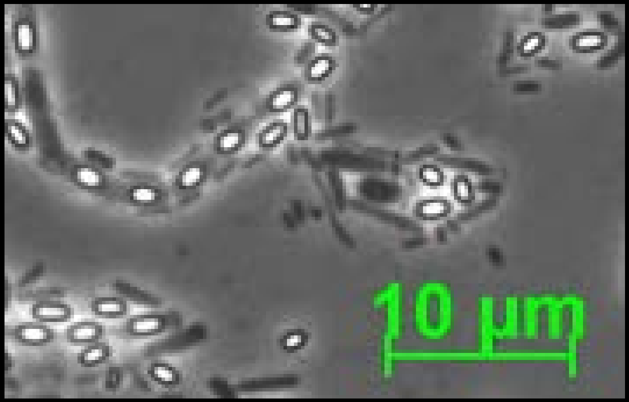
Dormancy: non-spore-forming ('persisters') and spore-forming

Endospores: Bacilli and Clostridia

Conidia: Filamentous Actinobacteria and filamentous fungi



Lennon & Jones, 2011

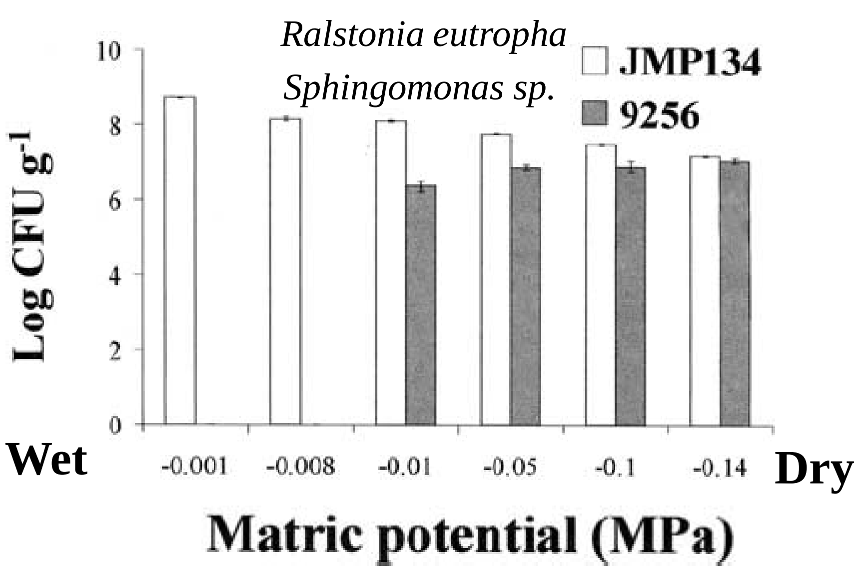


Endospores and soil bacteria

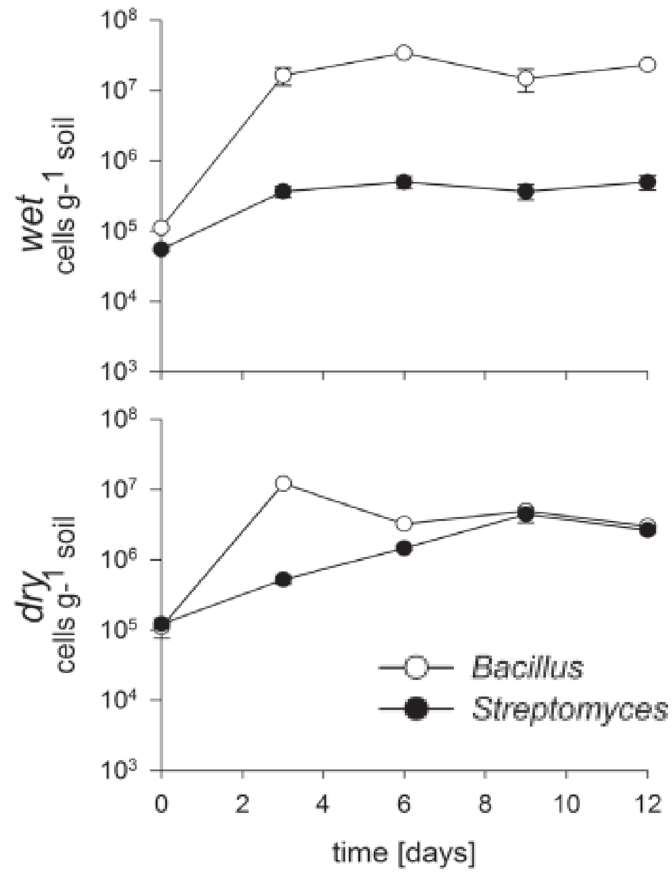
Species coexistence and diversity

- Microcosms experiments suggests that , in unsaturated soils, spatial isolation of microbes due to low water content would favor species coexistence and diversity by reducing competitive interactions
- But: mechanistic understanding of the processes at play remains sketchy

Sand microcosms

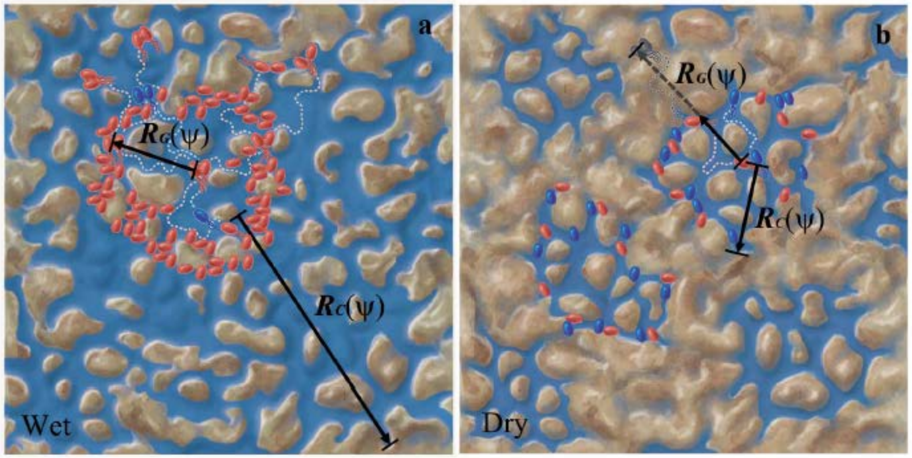


Treves et al., 2003



Wolf et al., 2013

A model for a bacterial coexistence index (CI)?

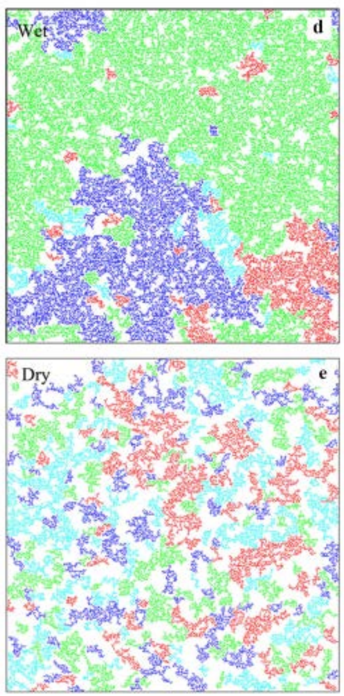


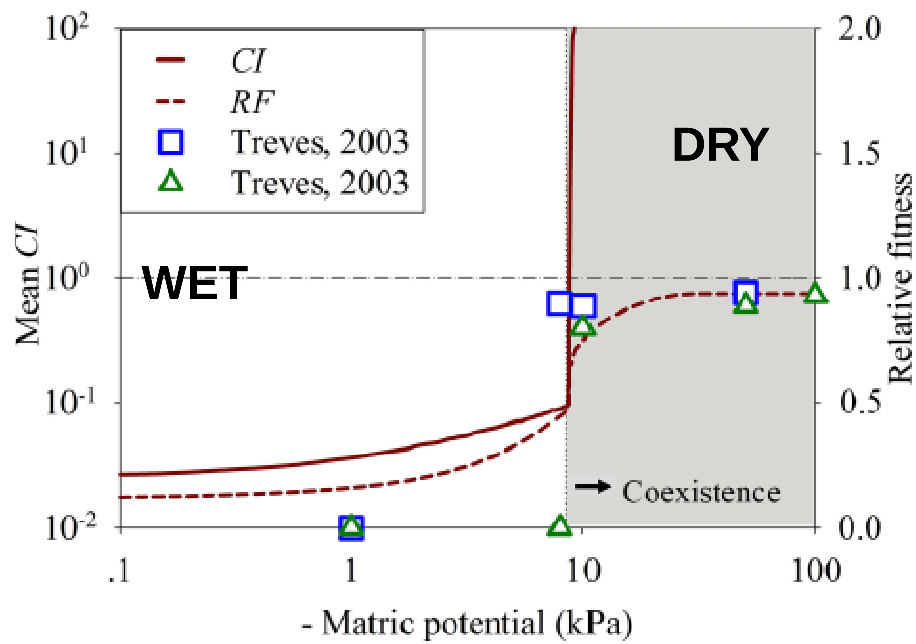
$$CI(\psi) = \langle R_G(\psi) \rangle / R_C(\psi).$$

- R_G: mean generation length (distance a cell can travel during a generation time)
- R_C: effective size of largest connected cluster radius

WET

DRY





Wang & Or, 2012

Microbial role in soil formation, structure and physical properties

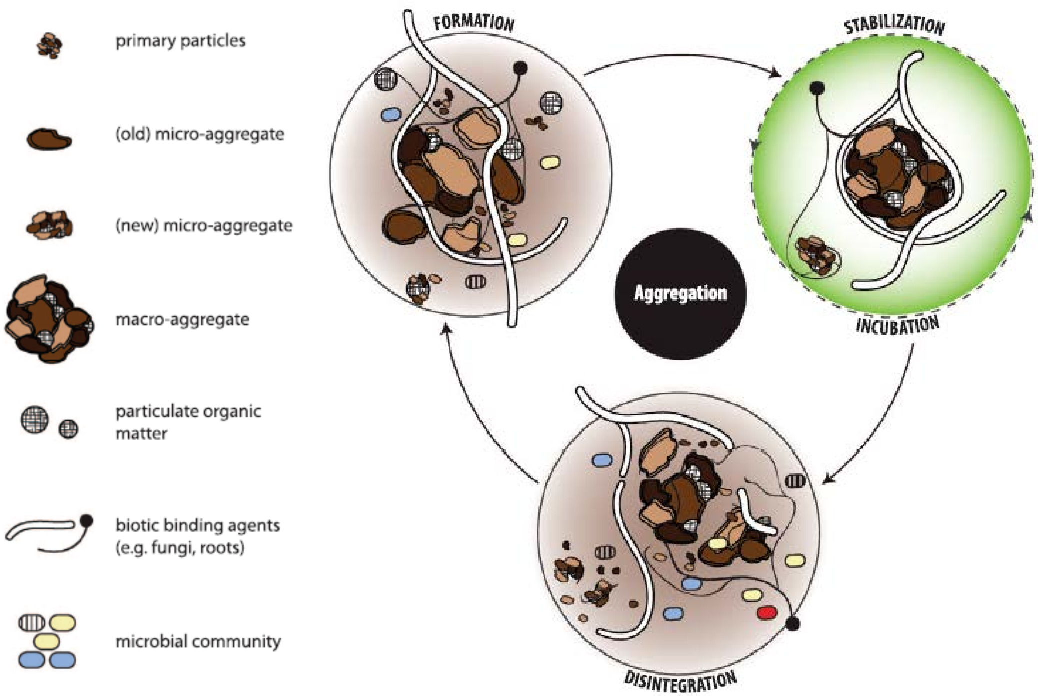
Role of microorganisms in soil formation and structure

Soil microorganisms

Possible interactions with soil particles

Weathering
Formation of new minerals
Biodegradation of organic particles
Formation of organo-mineral association
Rearrangement and aggregation

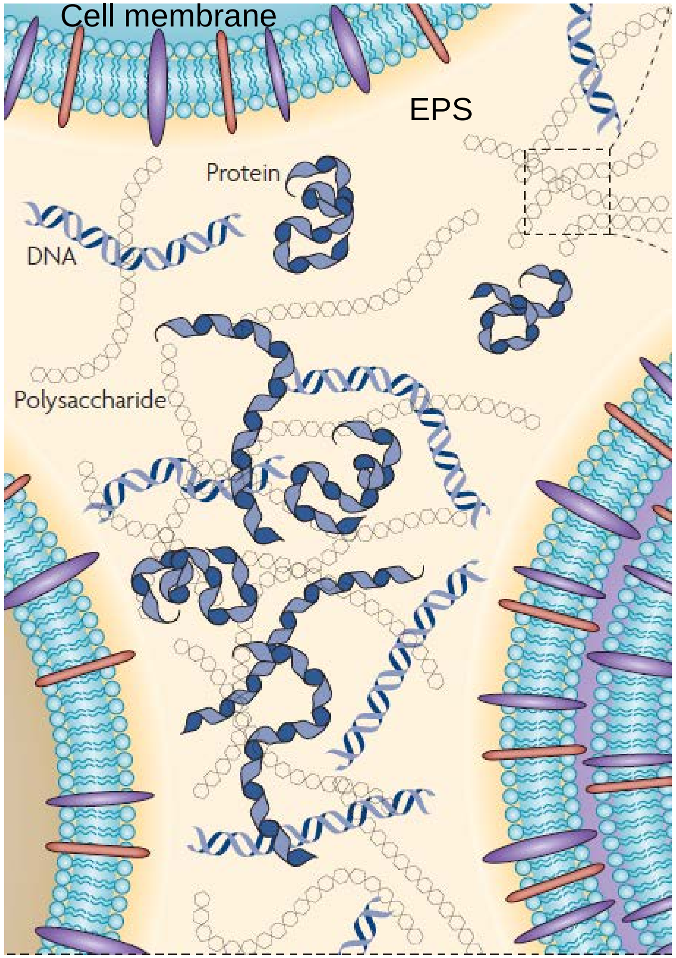
Chenu & Stotzky, 2002



Rillig et al., 2017

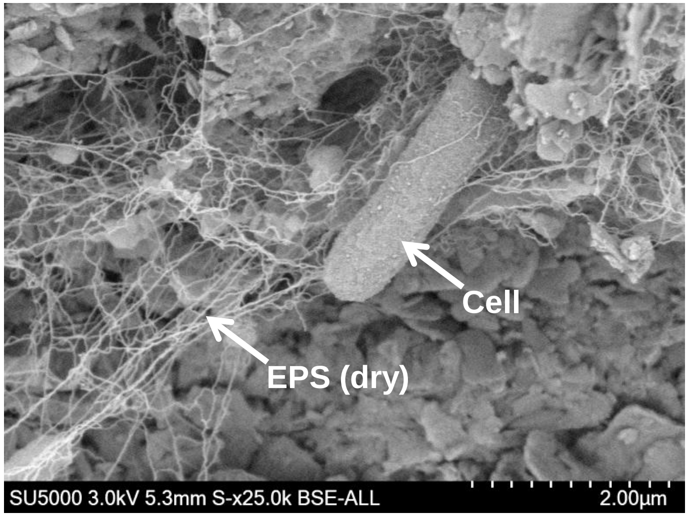
- Soil biota is the main driver of aggregate formation: microbial exudates (EPS) glue together organic and inorganic particles, while fungal hyphae and plant roots contribute to holding aggregates together
- Dynamic aggregate turnover

Microbial extracellular polymeric substances (EPS)



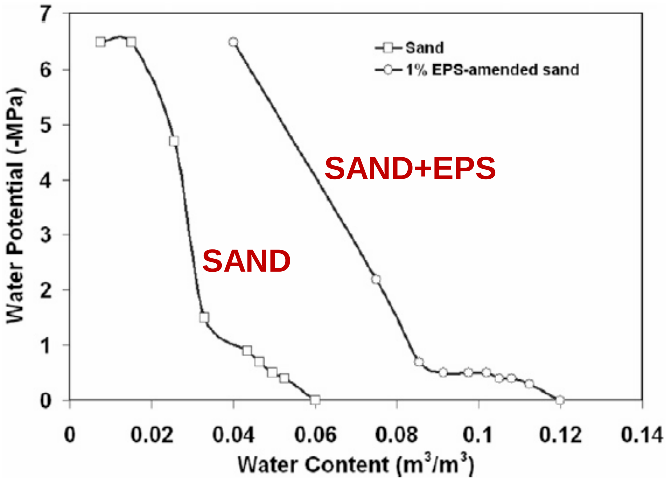
Flemming & Wingender, 2010

- Bacteria, archaea, algea and fungi can produce a matrix of hydrated biopolymers ('slime') known as extracellular polymeric substances or **EPS**
- EPS is a complex mixture of **polysaccharides**, **proteins**, **DNA** and **lipids.** The exact composition can vary significantly across producing species and strains
- EPS has an exceptional capacity to retain water (more than ten times its weight when saturated), and it can remain water-saturated at matric potentials as low as -1 Mpa
- Microorganisms live embedded in EPS matrix, which anchor them to surfaces, protect them from desiccation and from toxic substances

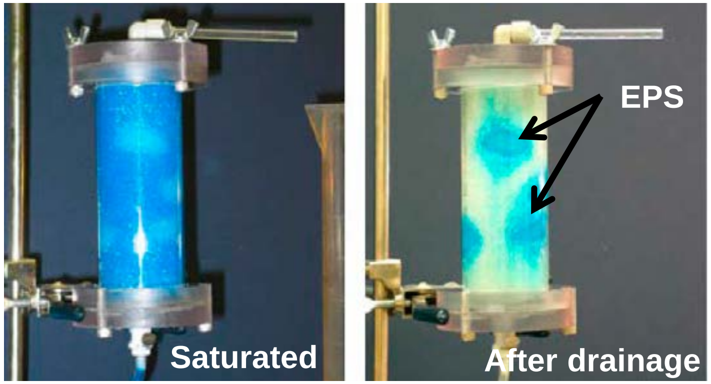


Effect of microbial EPS on hydrological processes

Water retention



Hydraulic decoupling (glass beads column)



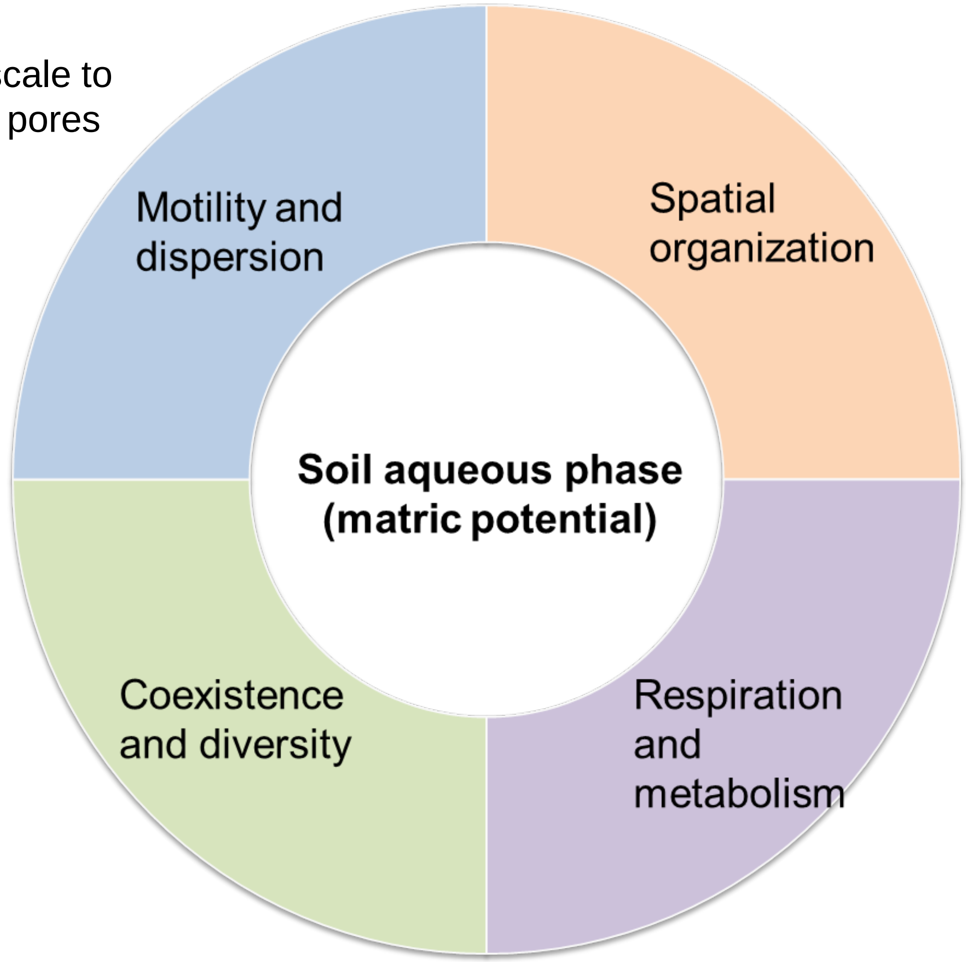
Or et al., 2007

- Microbes producing EPS modify **microhydrological conditions** due to increased water retention, which also likely influence soil water content at macroscopic scale
- The EPS matrix can reduce by up to one order of magnitude the **diffusion of solutes** relative to diffusion in free water (relative diffusivity)
- BUT: at low matric potentials relative diffusivity of solutes (e.g. glucose) is higher in EPS matrix than in unsaturated soil pores, which maintains nutrient fluxes to cells in dry soils
- The EPS matrix can reduce by up to five orders of magnitude **hydraulic conductivity** in porous media
- The EPS matrix can result in **hydraulic decoupling** in soil: maintain local hydrated areas during drainage, or moderate effects of rapid wetting during rainfall
- EPS represents a stabilizing interface between biological and physical soil components

Take-home messages

- The **dynamic soil aqueous phase** exerts a central and unifying control over microbial activity and processes in soil, and its spatial and temporal organization is directly afffected by the soil matric potential

- Soil water influences microbiological processes **at all scales**, from global scale to soil profile to the scale of microscopic pores and grains



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