# L07b

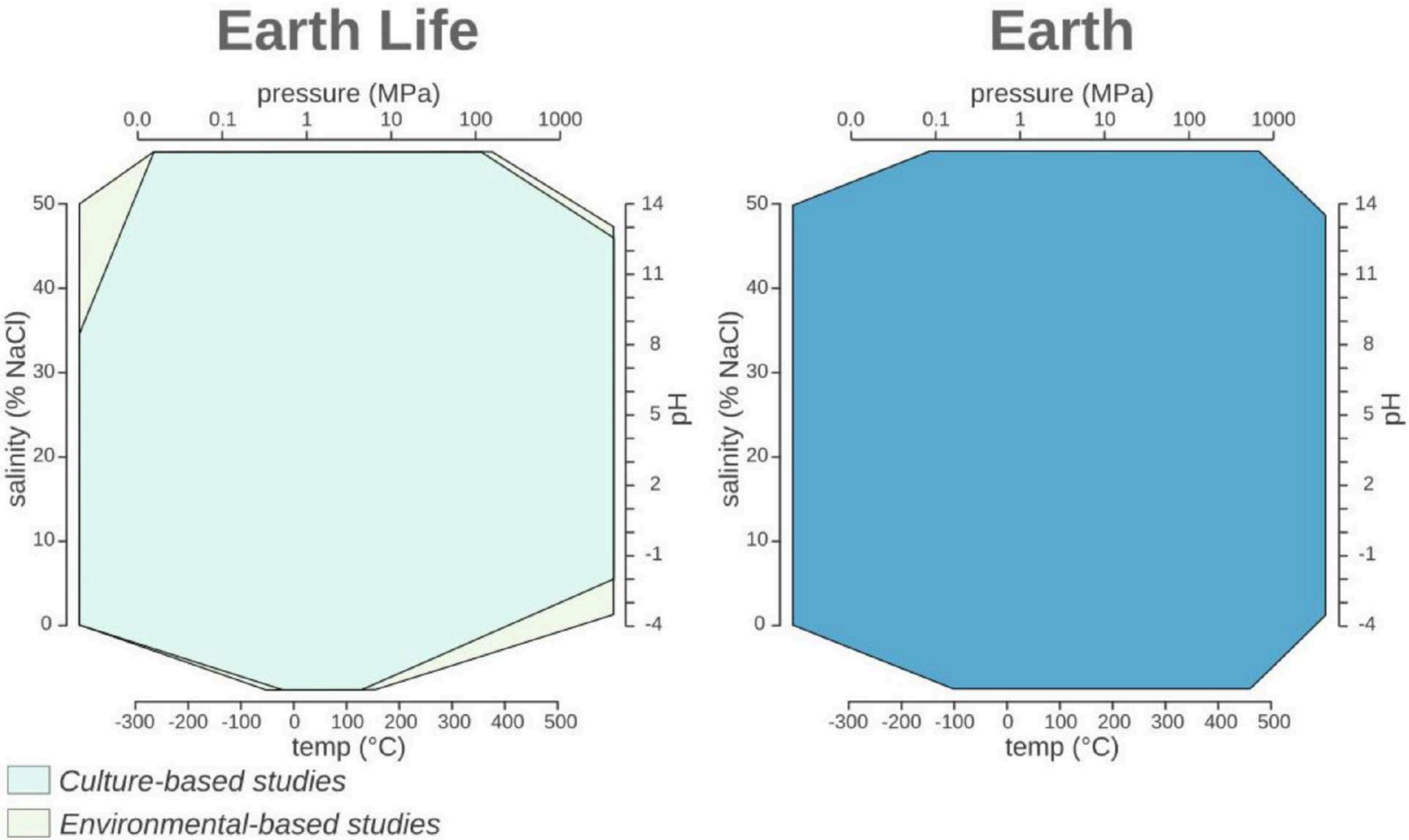
# Microbial Ecology

- Study of the **interactions** of microorganisms with their **environment (including organic matter)**, **each other**, and plant and animal species (**other organisms**) —> symbioses, biogeochemical cycles, climate change

  - **Extreme ecosystems**
  - **Soil ecosystem**

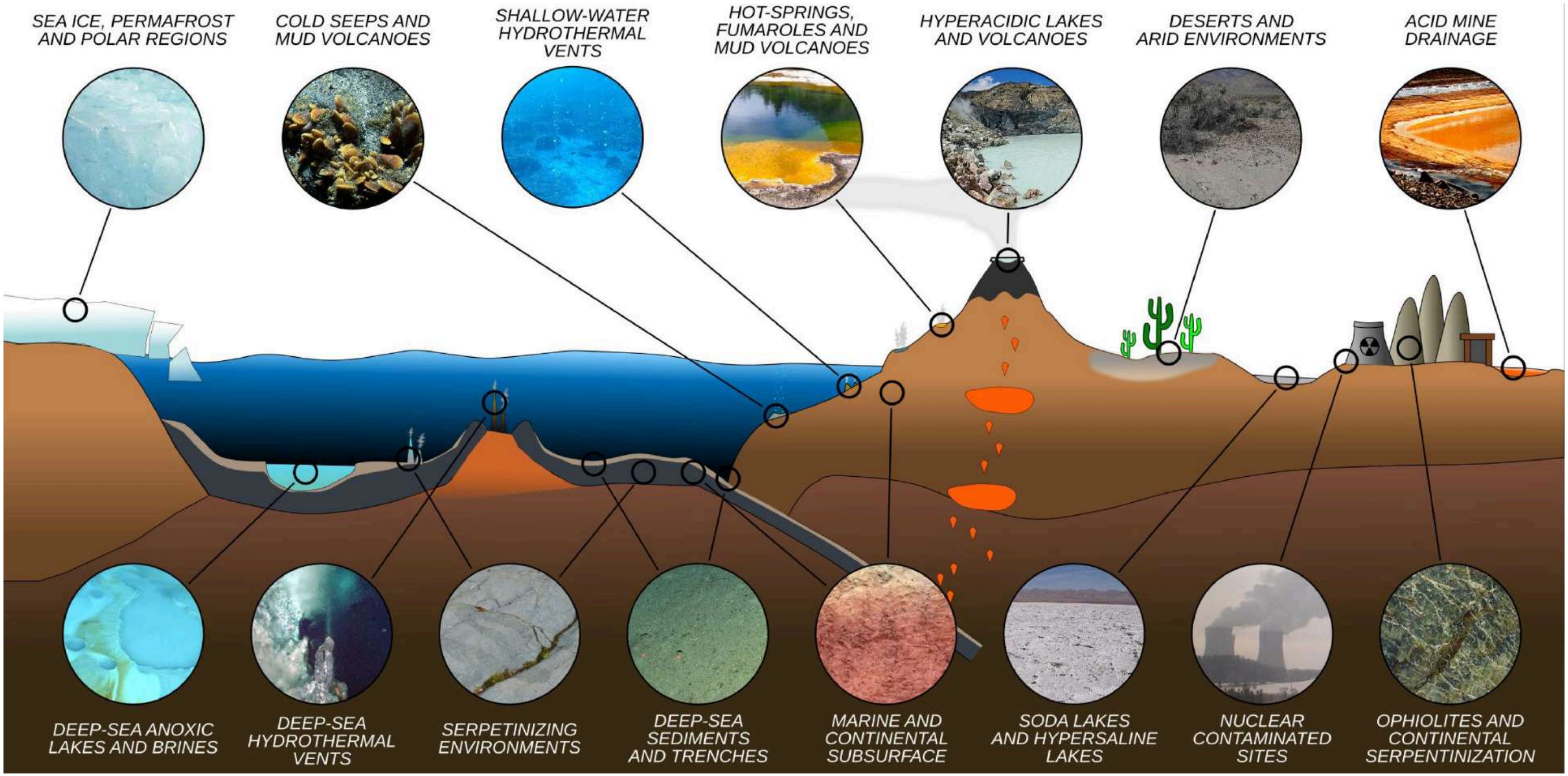
# EXTREME ENVIRONMENT ECOSYSTEMS

# Extreme microbial conditions




Merino et al. 2019

# High diversity of extreme environments on Earth

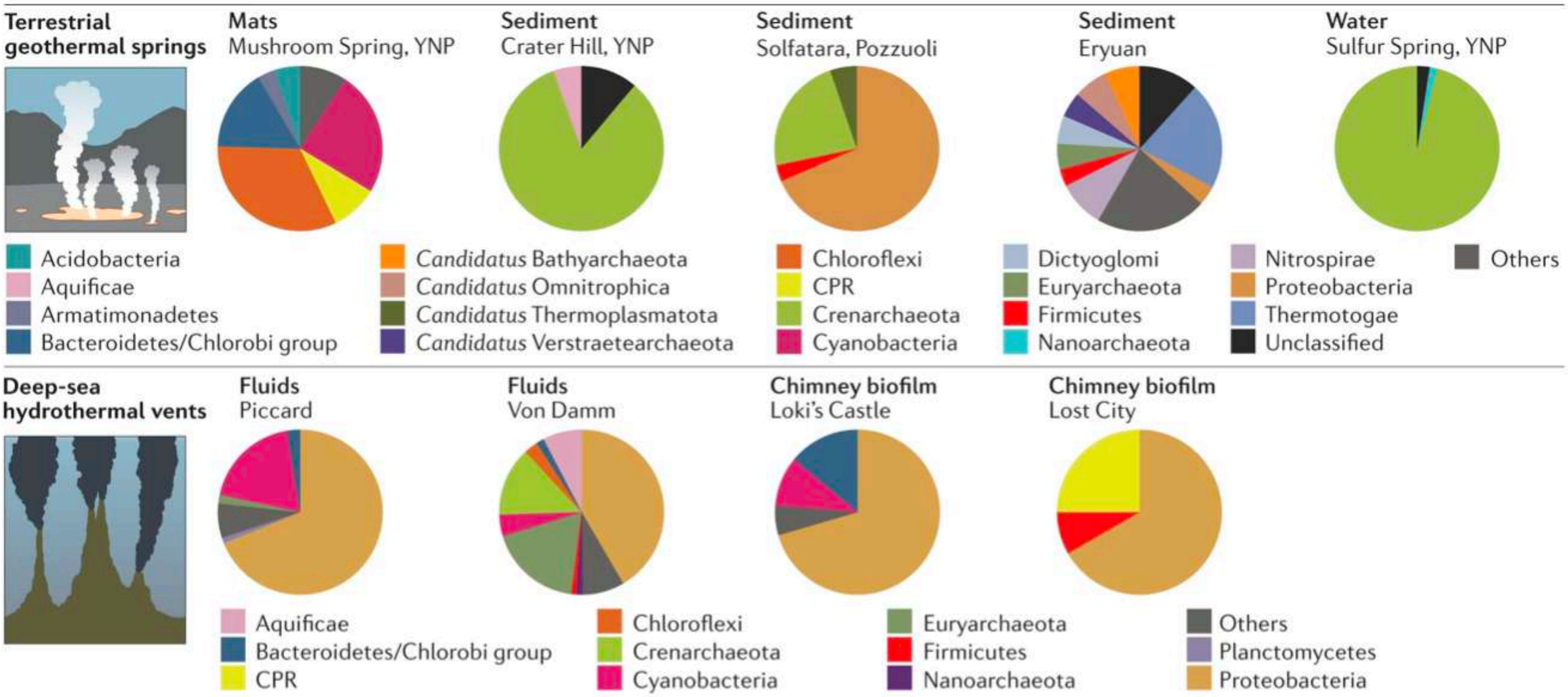



Merino et al. 2019

# Global distribution of representative extreme microbial environments

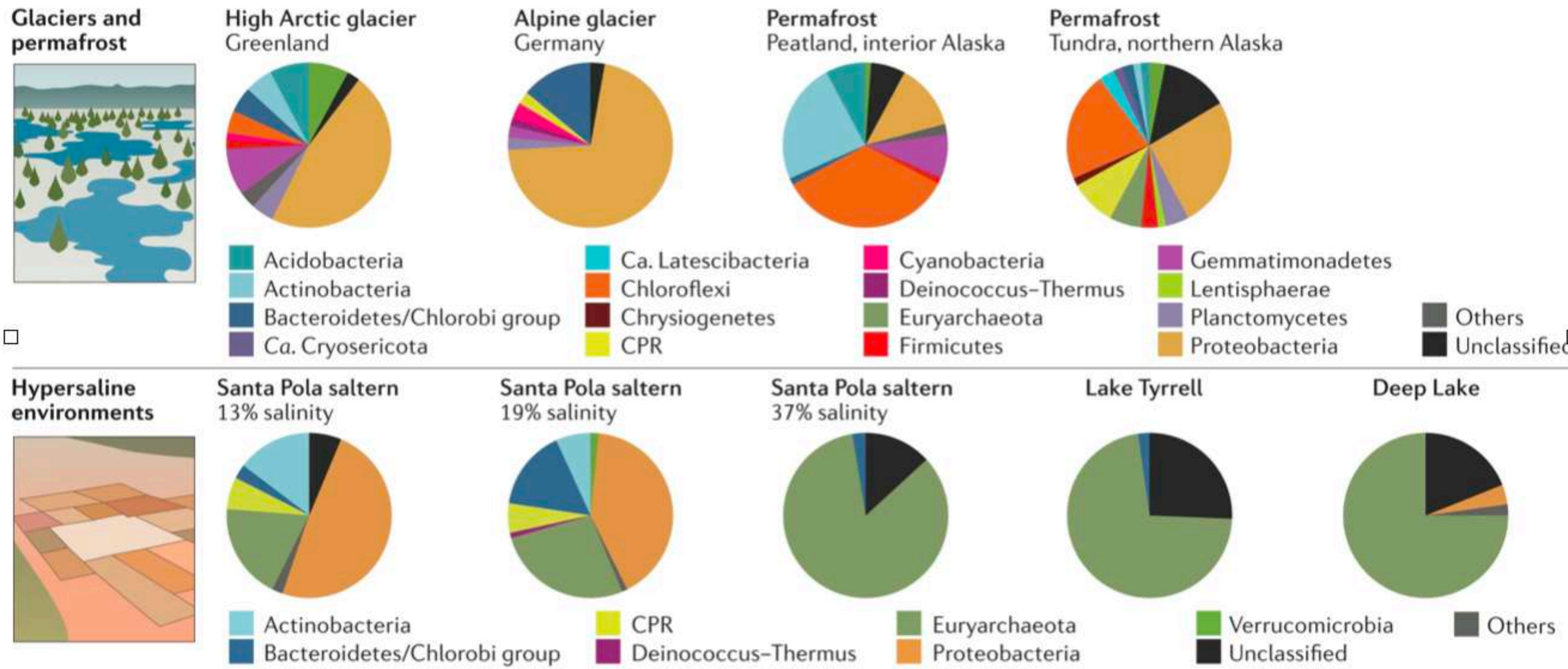

| | |
|---|---|
| Soda lake | Alkaline pH, high salinity |
| Desert | Dry, high ultraviolet solar radiation |
| Hot spring | High temperature, extreme pH, low oxygen availability |
| Cryosphere | Low temperature and water availability, low thermal energy |
| Hydrothermal vent | High temperature, high pressure, low nutrient and oxygen availablity |
| Hypersaline environment | High salt concentrations and pH, and low nutrient and oxygen availability |
| Acid mine drainage | Low pH, high metal concentrations, limited number of energy-deriving reactions |

Shu & Huang, 2020



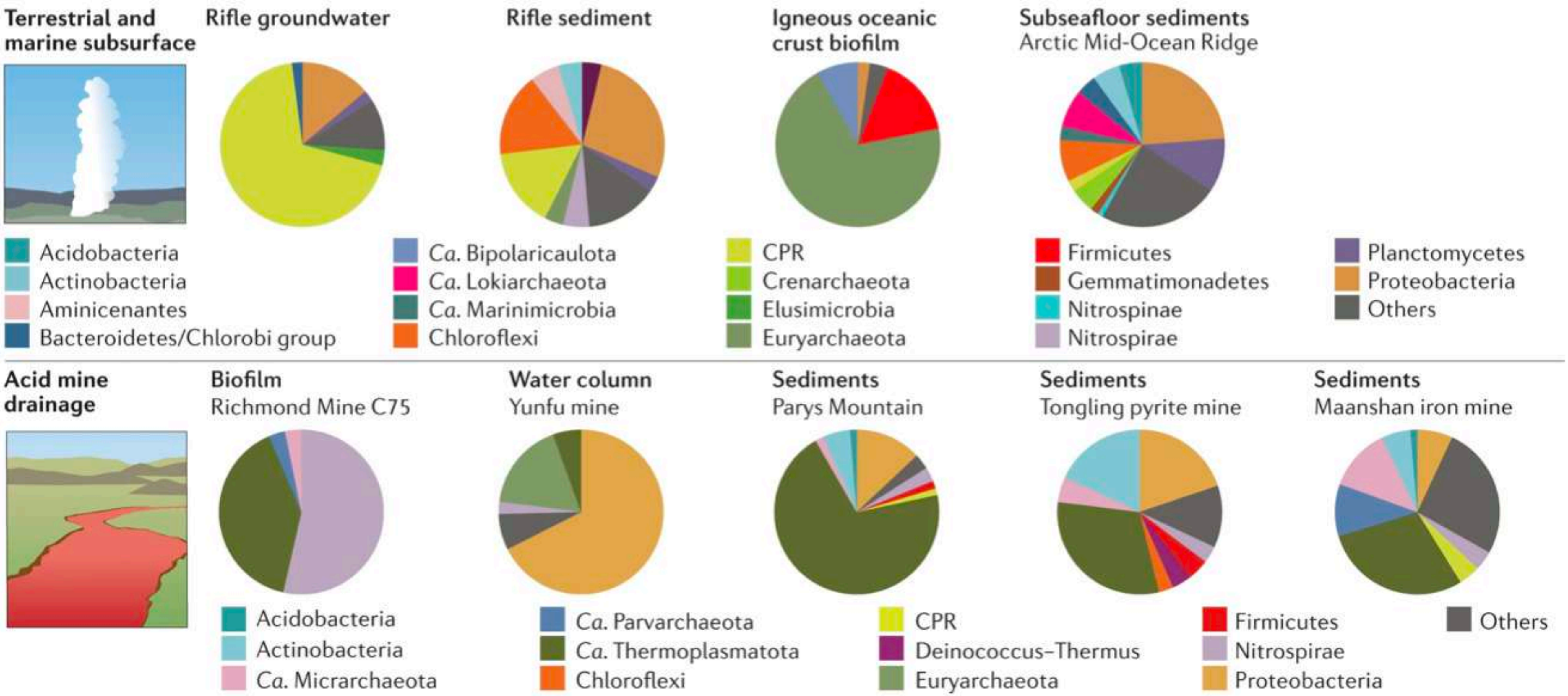

**Shu & Huang, 2020**

- Diverse environments
- Diverse microbial communities




**Shu & Huang, 2020**

- Similar adaptations for living in harsh conditions
- High biotechnological potential for new discoveries




**Shu & Huang, 2020**

- Environment with **reduced biological complexity**, overall tractability for cultivation-independent molecular analyses and **tight coupling between geochemical and biological processes**

# Adaptation of microbial life to environmental extremes: temperature

**High temperature adaptation in thermophiles**

- Modifying cell membranes by **increasing** the r**atio of saturated to unsaturated fatty acids** (bacteria) or by adopting a lipid monolayer (archaea)
- Producing **heat-shock proteins and heat-stability proteins**
- Maintaining DNA stability by having a **high G+C content or by positive supercoils** introduced by the thermophile-specific enzyme reverse DNA gyrase

**Low temperature adaptation in psychrophiles**

- Modifying the lipid composition of cell membranes (for example, **by increasing the ratio of unsaturated to saturated fatty acids**) to maintain fluidity
- Producing specialized proteins or other molecules (for example, **cold-adapted proteins, cold-shock proteins, cold-acclimation proteins, antifreeze and ice-binding proteins, and osmolytes**) that enable the cell to survive under low-temperature conditions
- **Limiting metabolic activity** by entering a **dormant state**

Shu & Huang, 2020

# Adaptation of microbial life to environmental extremes: high salt

**High salt adaptation in halophiles**

- Maintaining osmotic homeostasis by **accumulating (via a $K^+$/$Na^+$ antiporter) high levels of inorganic salts (KCl) in the cytoplasm (‘salt-in’ strategy**, found mainly in archaea)
- Achieving osmotic balance by **biosynthesizing and/or accumulating organic and compatible osmotic solutes and thus excluding salt from the cytoplasm (‘salt-out’ strategy**, found mainly in bacteria and eukaryotes)

Shu & Huang, 2020

# Adaptation of microbial life to environmental extremes: low pH and metal

**Acid adaptation in acidophiles**

- **Restricting proton influx into the cytoplasm with reversed membrane potential or highly impermeable cell membranes**, and promoting excess proton efflux with organic acid degradation or a predominance of secondary transporters
- Maintaining intracellular pH with cytoplasmic buffering, **stabilizing protein structure and functions of enzymes with 'iron rivets'**, and repairing DNA and protein damage caused by low pH with chaperones once protons enter the cytoplasm

**Metal adaptation in acidophiles**

- **Promoting efflux of the toxic metal out of the cytoplasm, sequestering metal by intracellular or extracellular binding to reduce its toxic effect, excluding metal with a permeability barrier, altering a cellular component to lower the sensitivity** of cellular targets to the toxic metal and enzymatically converting the metal into a less toxic form
- **Complexing free metals with sulfate** to prevent the entry of metal ions into the cell, and establishing **passive tolerance to metal influx** through an **internal positive cytoplasmic transmembrane potential**

Shu & Huang, 2020

# SOIL

# Biomes and Vegetation

- Latitudinal, longitudinal and altitudinal zonation (arrangement, distribution)
- Temperature, precipitation and solar irradiation

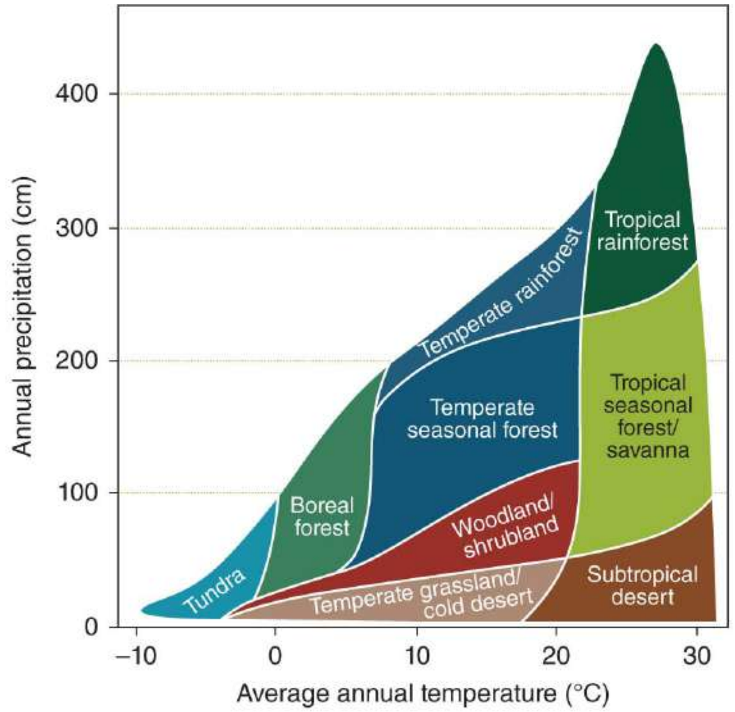



**Figure 4.3** The pattern of plant biome types showing responses to annual habitat precipitation (vertical axis) and annual temperature (horizontal axis). Boundaries between the nine plant biome types are approximate–influenced by factors that include soil type, maritime versus continental climate, and fire. (Source: "PrecipitationTempBiomes". Via Wikipedia: http://en.wikipedia.org/wiki/File:PrecipitationTempBiomes.jpg#mediaviewer/File:PrecipitationTempBiomes.jpg. After R.D. Burkett, posted to the Wikimedia Commons, based on Whittaker, R.H. 1975. *Communities and Ecosystems*, 2nd edn. Macmillan Publishing Co. Inc., New York.)

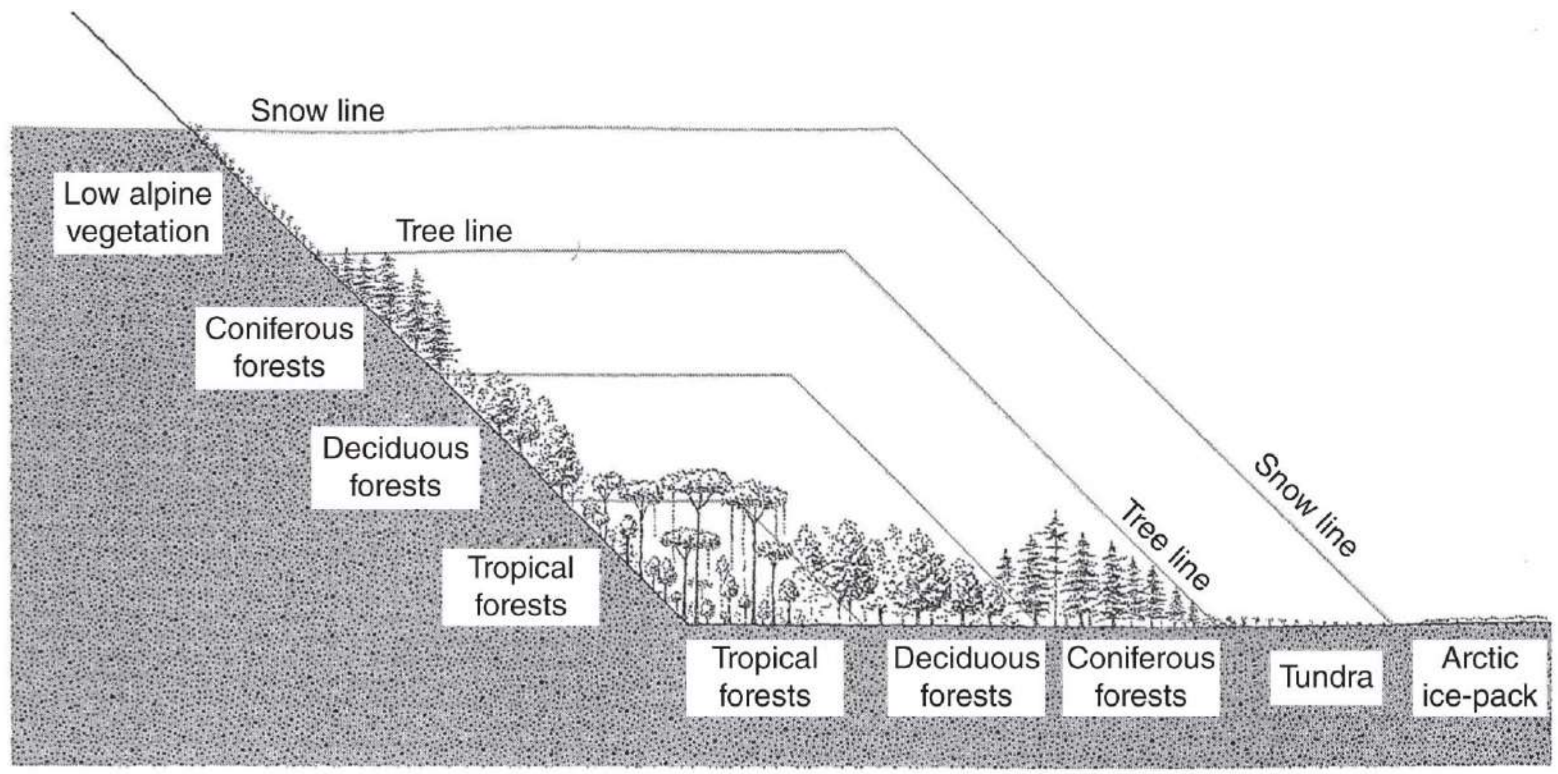



**Figure 4.2** Examples of regional and altitudinal gradients of vegetation zones in North America. The south–north gradient (right side of diagram, horizontal line) primarily reflects gradually cooling temperature regimes that extend from the hot tropics (low latitudes) to the frigid arctic (high latitudes). In parallel with the south–north gradient, many mountain ranges are hosts of similar vegetation zones that change with elevation (altitude; left side of diagram, diagonal line). (Source: Colinvaux, P.A. 1973. *Introduction to Ecology.* John Wiley and Sons, Inc., New York. Figure 2.5, page 28. Reprinted with permission.)

Madsen, 2016

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# Biomes and Soils connectivity

Madsen, 2016

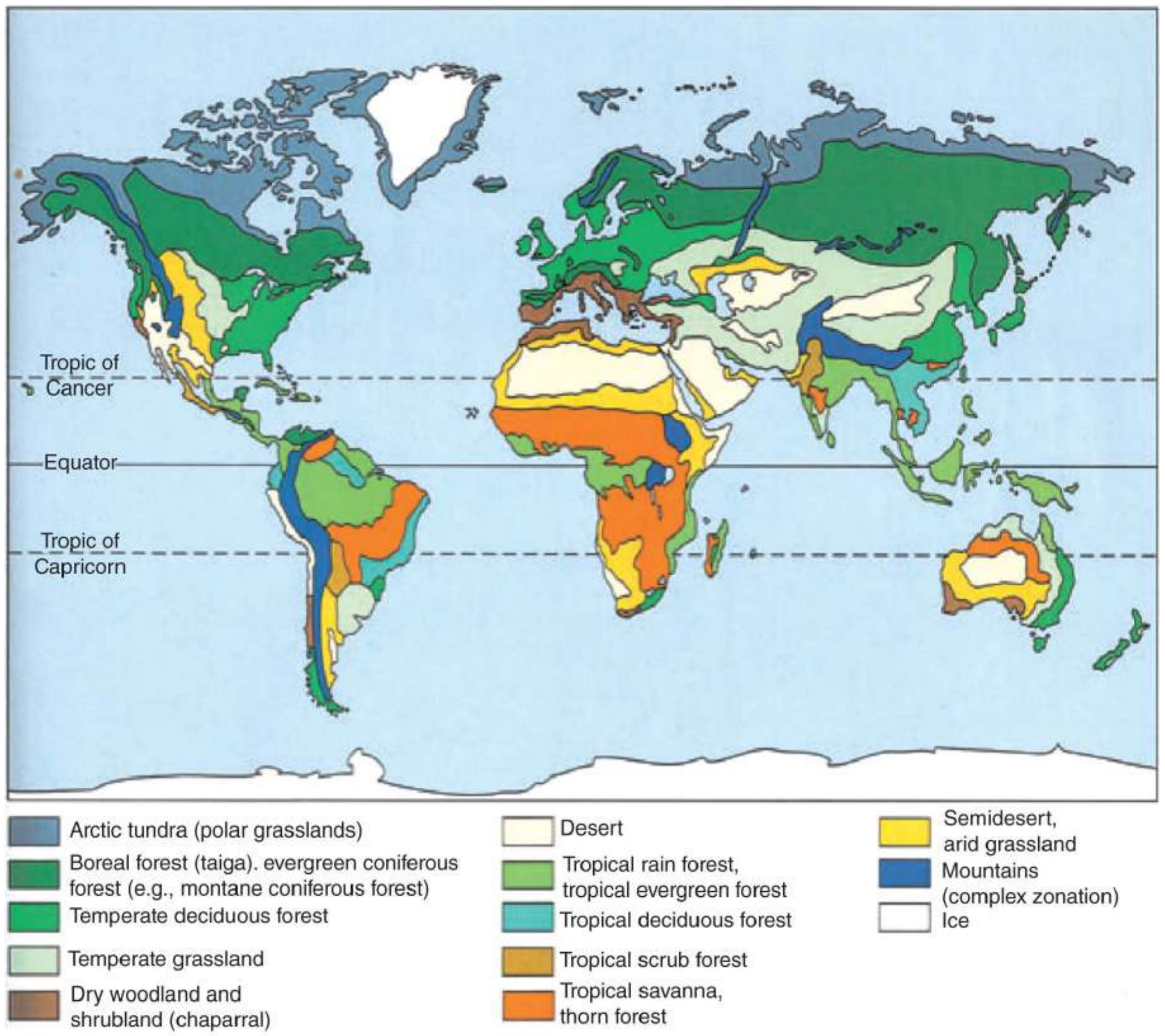



**Figure 4.1** Global map of terrestrial biomes. (Republished with permission of Brooks/Cole, a division of Thomson Learning. From Miller, G.T. 2004. *Living in the Environment*, 13th edn. Permission conveyed through Copyright Clearance Center, Inc.)

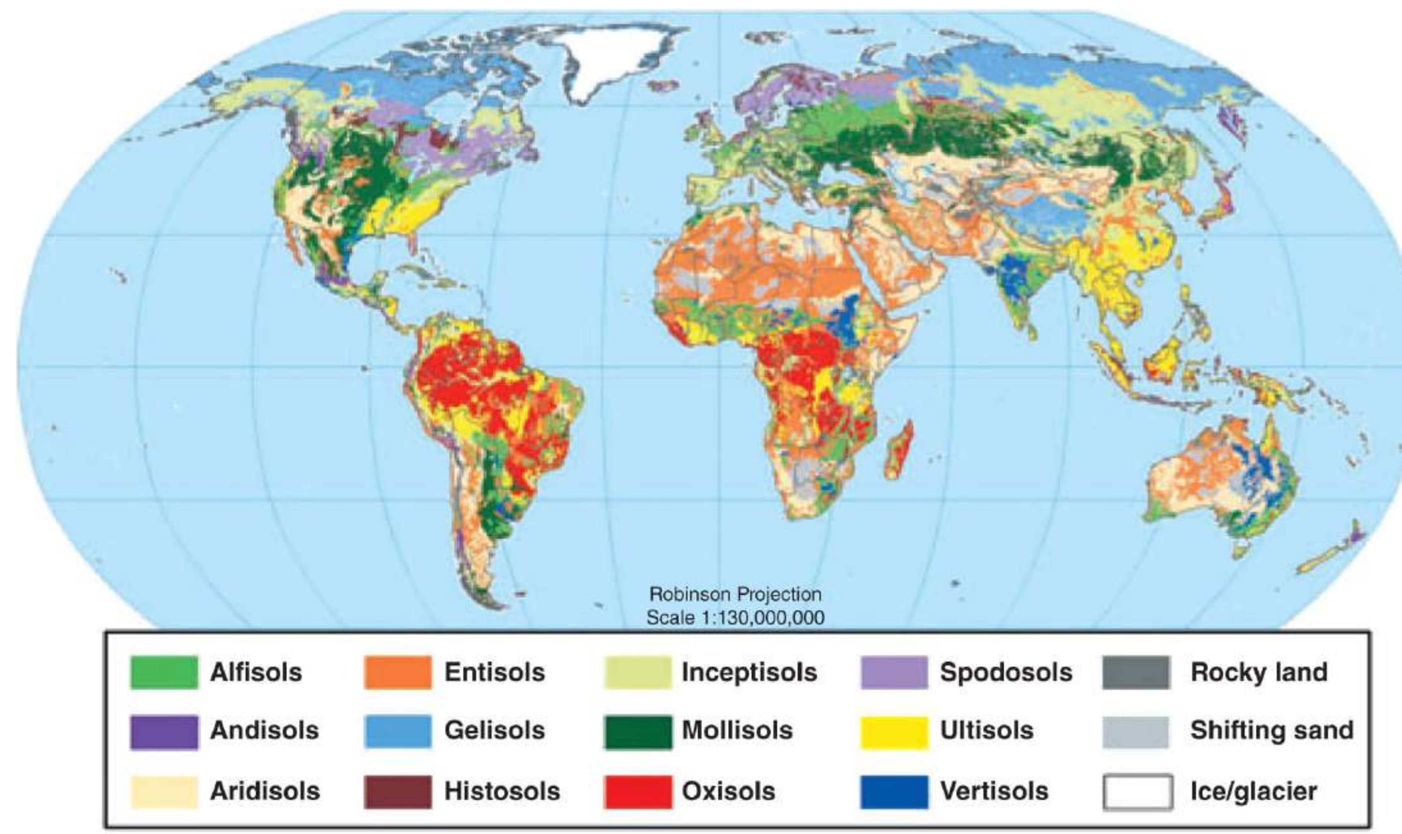
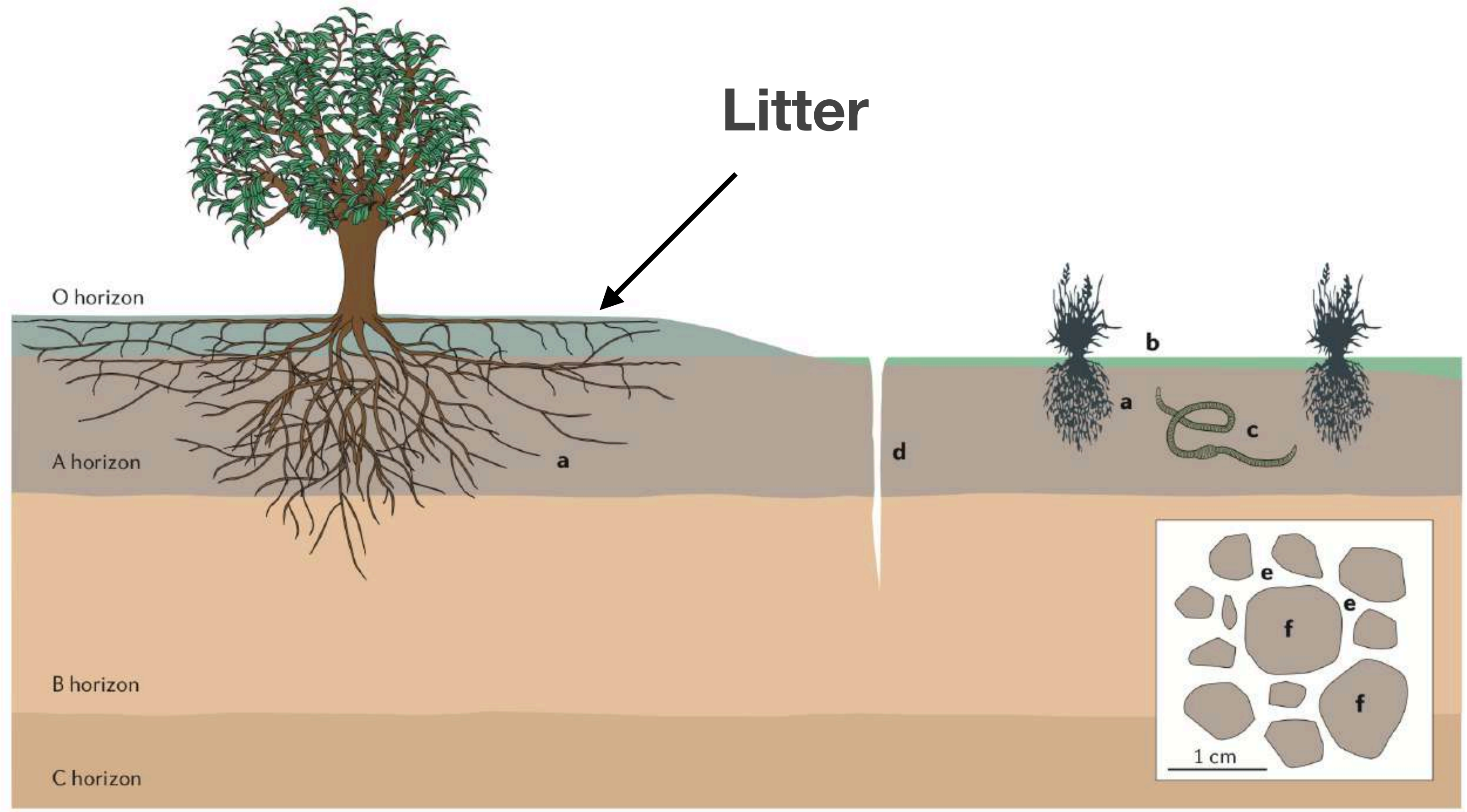



**Figure 4.4** Distribution of 12 major soil orders throughout the world. (Reprinted with permission from USDA Natural Resources Conservation Service, Soil Survey Division, World Soil Resources, Washington, DC.)

- More soil types are in a **biome** (= *a specific geographical area that can be identified by a complex biotic community characterized by distinctive plants and animal species*)
- Soil are characterized by its structure, soil-forming processes, chemical properties, organic matter

# Soil ecosystem

- pH, organic carbon concentration, salinity, texture and available nitrogen/nutrient concentration




Fierer, 2017

- Soil is not a single environment—> **a broad range of different microbial habitats**:

  a. Rhizosphere (soil in close proximity to plant roots)

  b. Surface layers that are exposed to light (the photic zone)

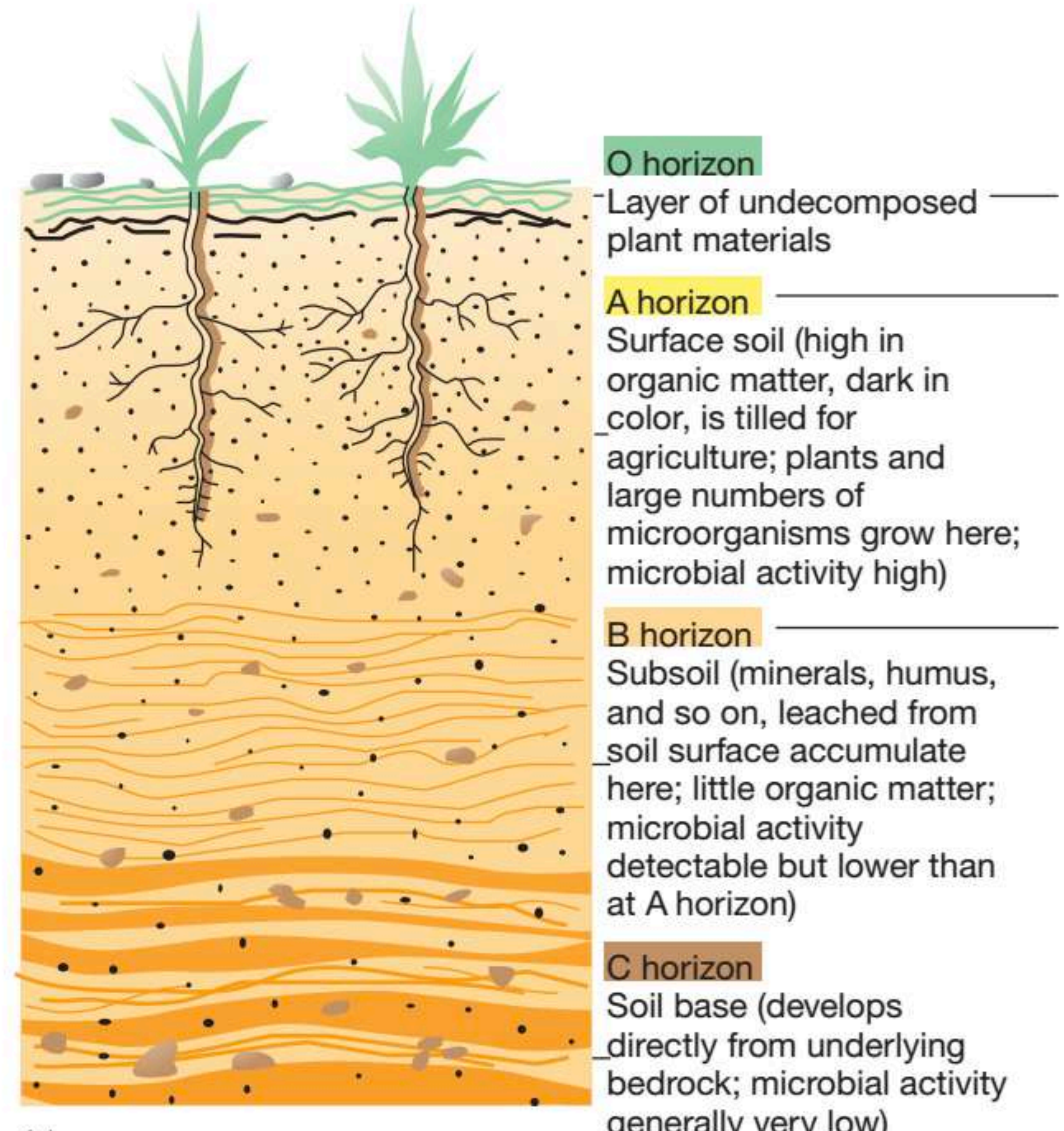
  c. Soil associated with earthworm burrows (the drilosphere)

  d. Soil found in preferential water flow paths, including cracks in the soil

# Soil ecosystem, macroscale


(b)

- Soils can generally be viewed as a complex 3D structure consisting of **packed aggregates and pore spaces**
- Aggregates comprise clusters of **mineral particles** and **organic carbon**
- **Forces holding the particles together within an aggregate are much stronger** than the forces between adjacent aggregates
- Allowing the **structures to persist through wetting events and mechanical disruptions of the bulk soil**

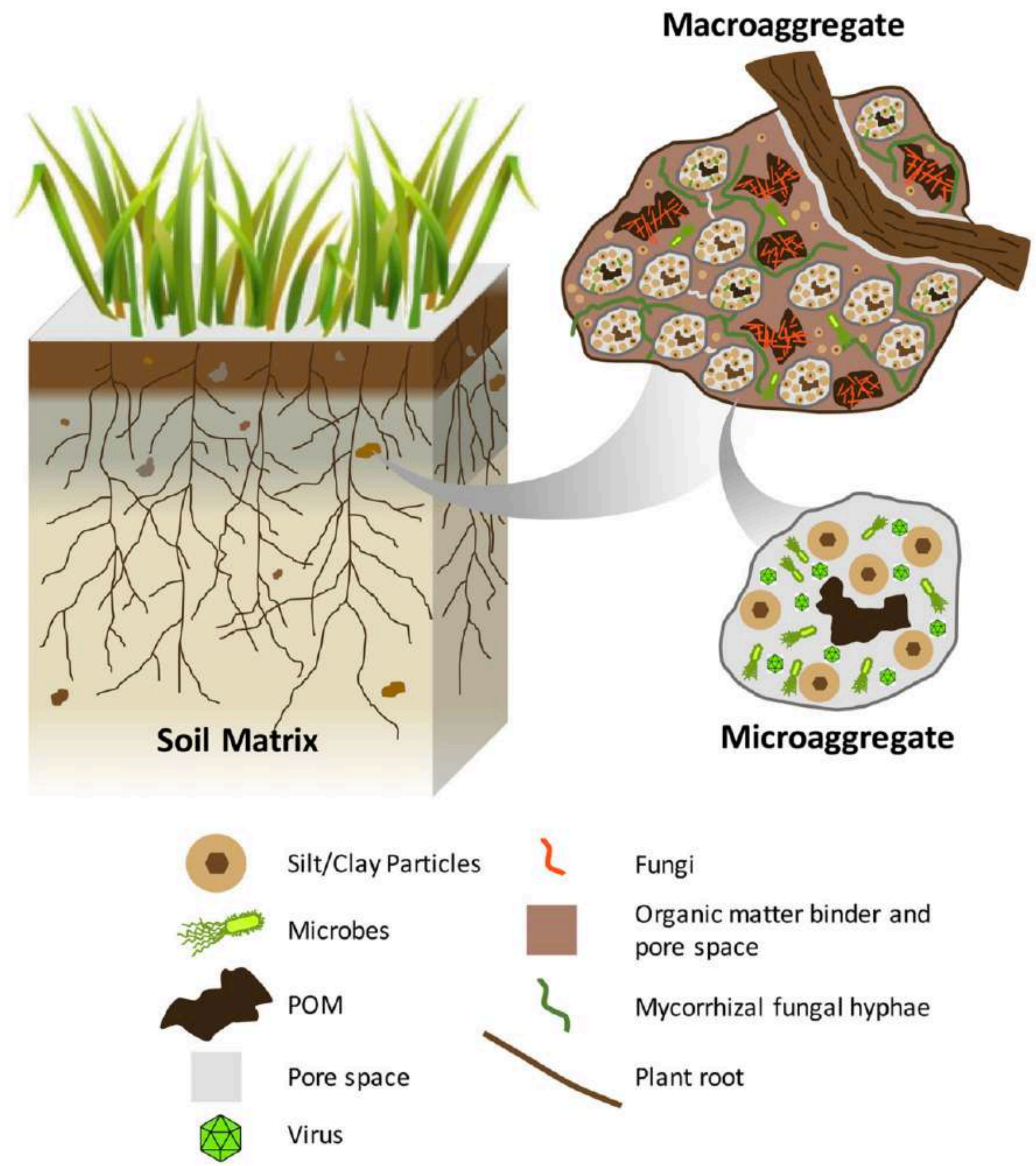



(a)

Madigan et al. 2018

# Soil ecosystem structure

- Soils are primarily composed of **microaggregates** (<250 µm), which bind soil organic carbon and protect it from removal by erosion
- **Macroaggregates** (0.25 to 2 mm), which limit oxygen diffusion and regulate water flow
- These length scales are particularly important in **shaping microbial interactions since microbial residents occupy specialized niches** (environment and function of the organisms) within the aggregate structure, with active microorganisms living both within and between aggregate particles
- **Bacteria are important for the formation of macroaggregates and microaggregates (< 250 µm), whereas fungi are most important for macroaggregate formation**



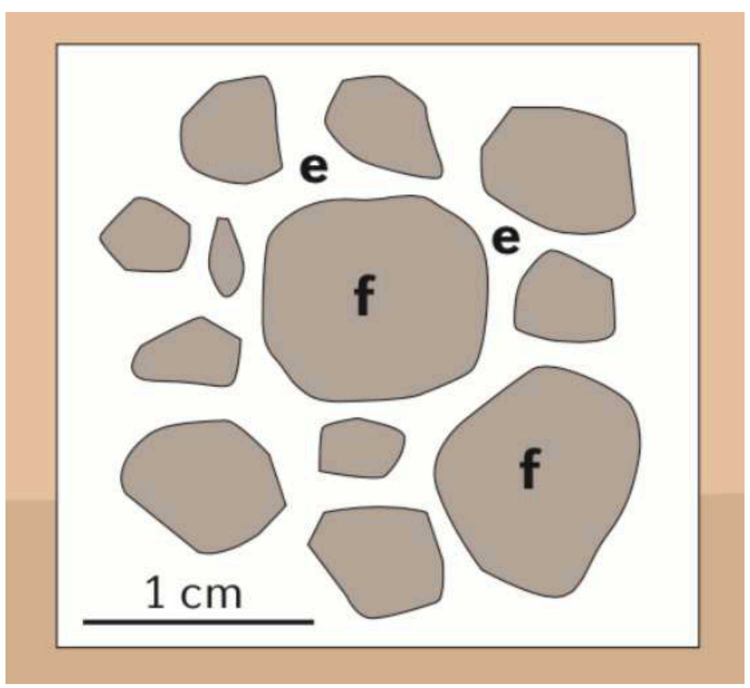



Wilpiszeski et al., 2019

# Micro-macro aggregates

- Microenvironments associated with soil aggregates
- Conditions found on aggregate surfaces or on the water films between aggregates (**e**) are distinct from the conditions found inside aggregates (**f**) (water, oxygen organic matter, redox couples)
- Hydrodynamic flow structures the dispersal of microbes (including viruses), organic matter and pollutants

Fierer, 2017



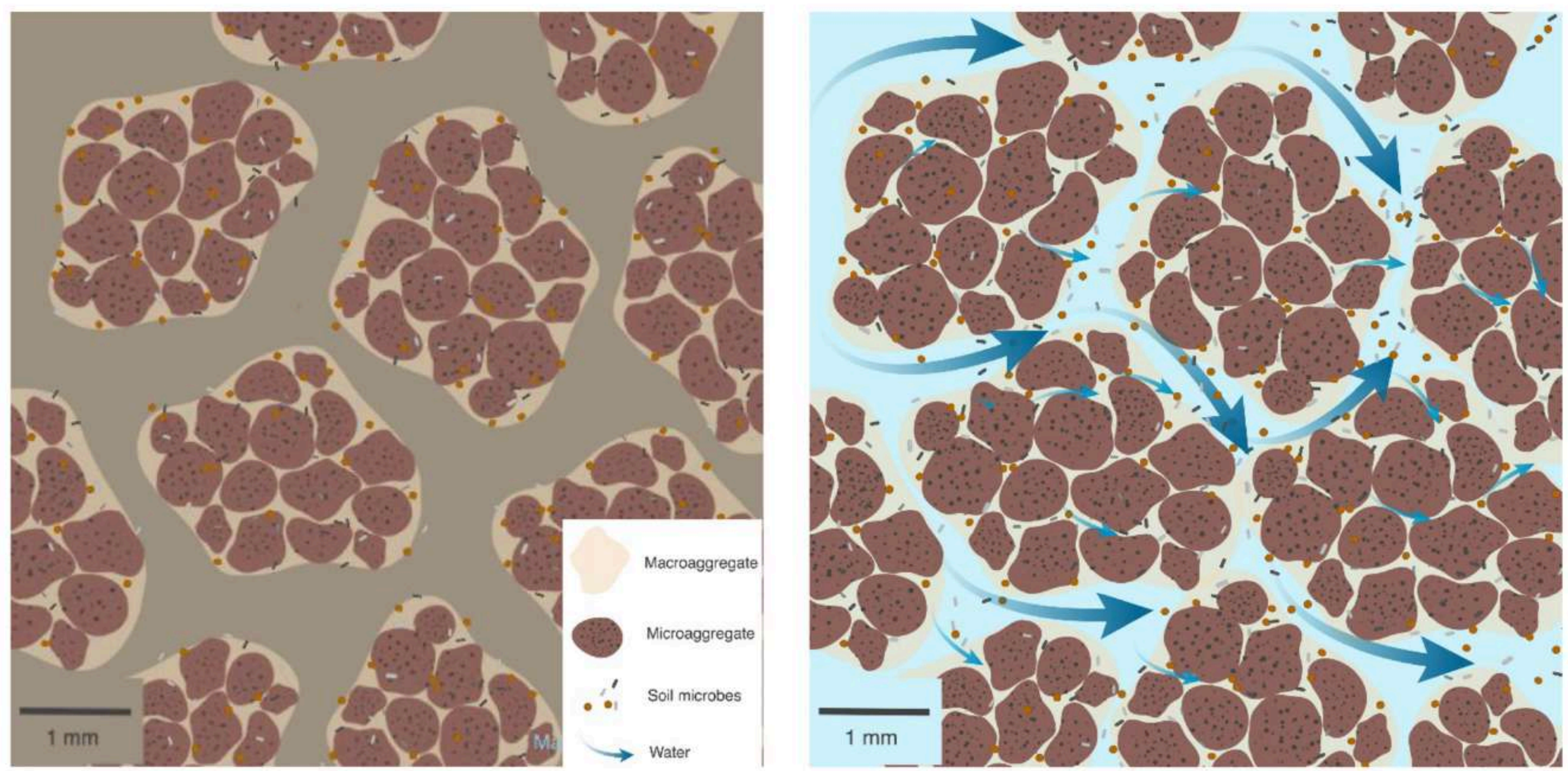



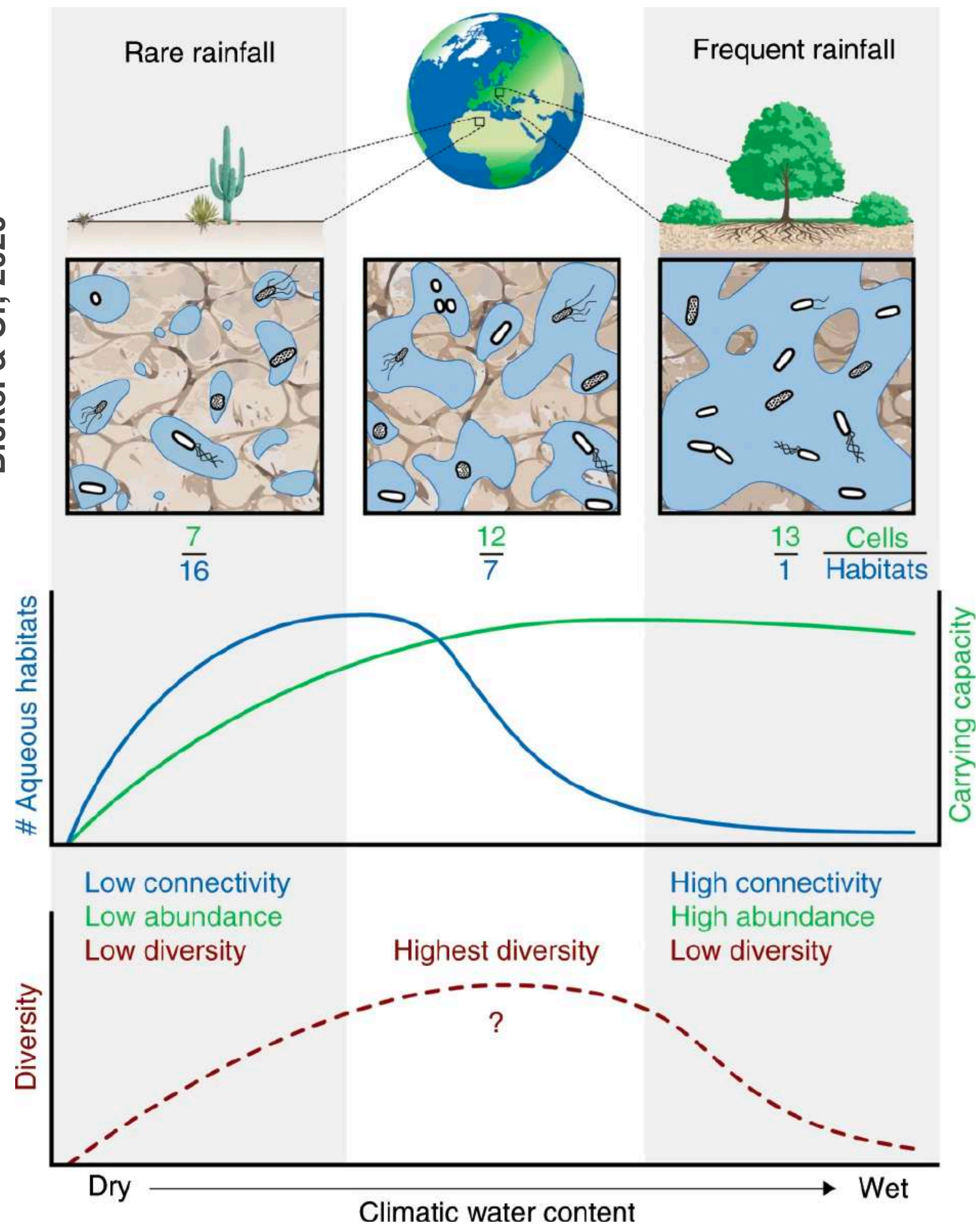

**FIG 2** Conceptual drawing of isolated micro- and macroaggregates during (left) dry conditions and (right) wet conditions. Wet conditions would allow for nutritional, microbial, viral and metabolite dispersal.



Wilpiszeski et al., 2019

# Aqueous habitat fragmentation and carrying capacity in relation to climatic water contents

Bickel & Or, 2020




- In regions with frequent rainfall, the soil **aqueous phase is largely connected** and provides a **common habitat** for different bacterial species
- In soils of drier regions, the **aqueous phase** is increasingly **fragmented** and offers a **large number of distinct habitats**
- When the soil becomes sufficiently dry, almost all aqueous habitats are **physically isolated** and might contain only a few species
- The total number of cells that can be maintained (potential carrying capacity) is reduced and smaller patches become uninhabited
- **The specific carrying capacity in a biome is based on carbon input flux and temperature that establish an upper bound on bacterial cell density (rarely realized in any particular location due to other limiting factors)**
- **Diversity** is expected to **drop** in dry regions with low cell abundance and in wet regions with high habitat connectivity

# Soil fauna across scale

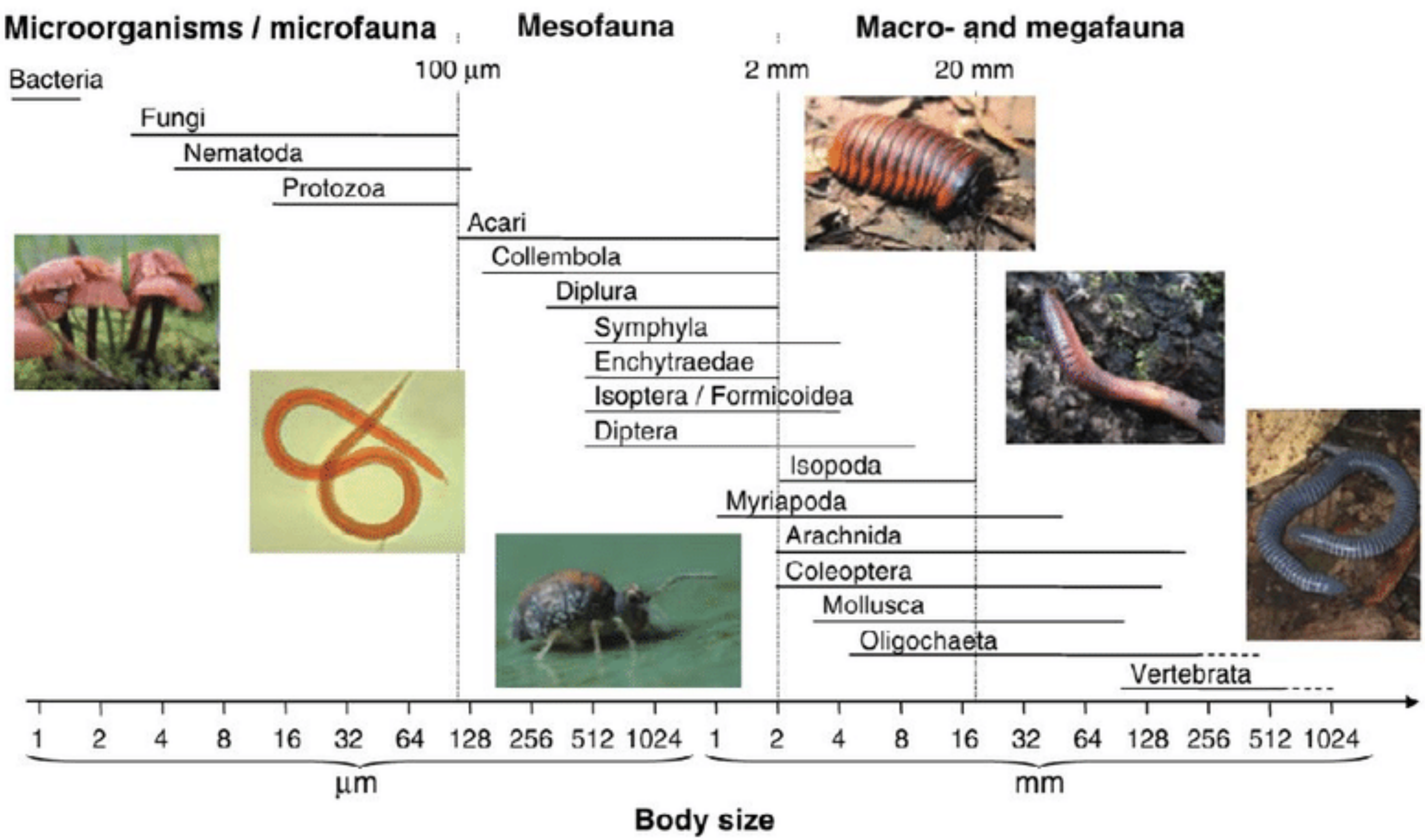
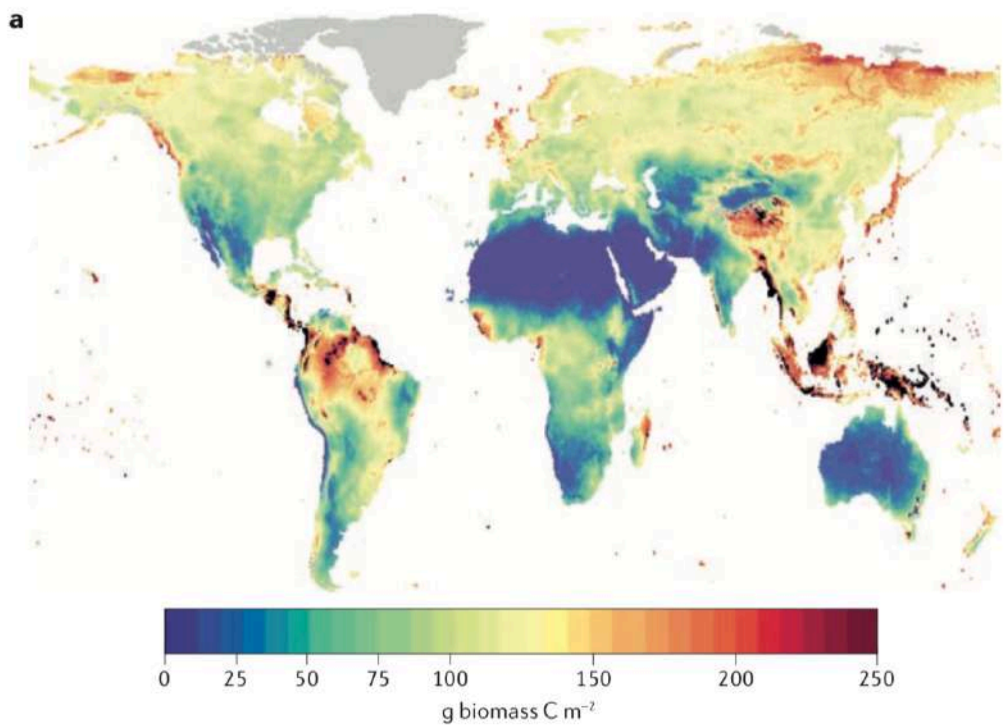
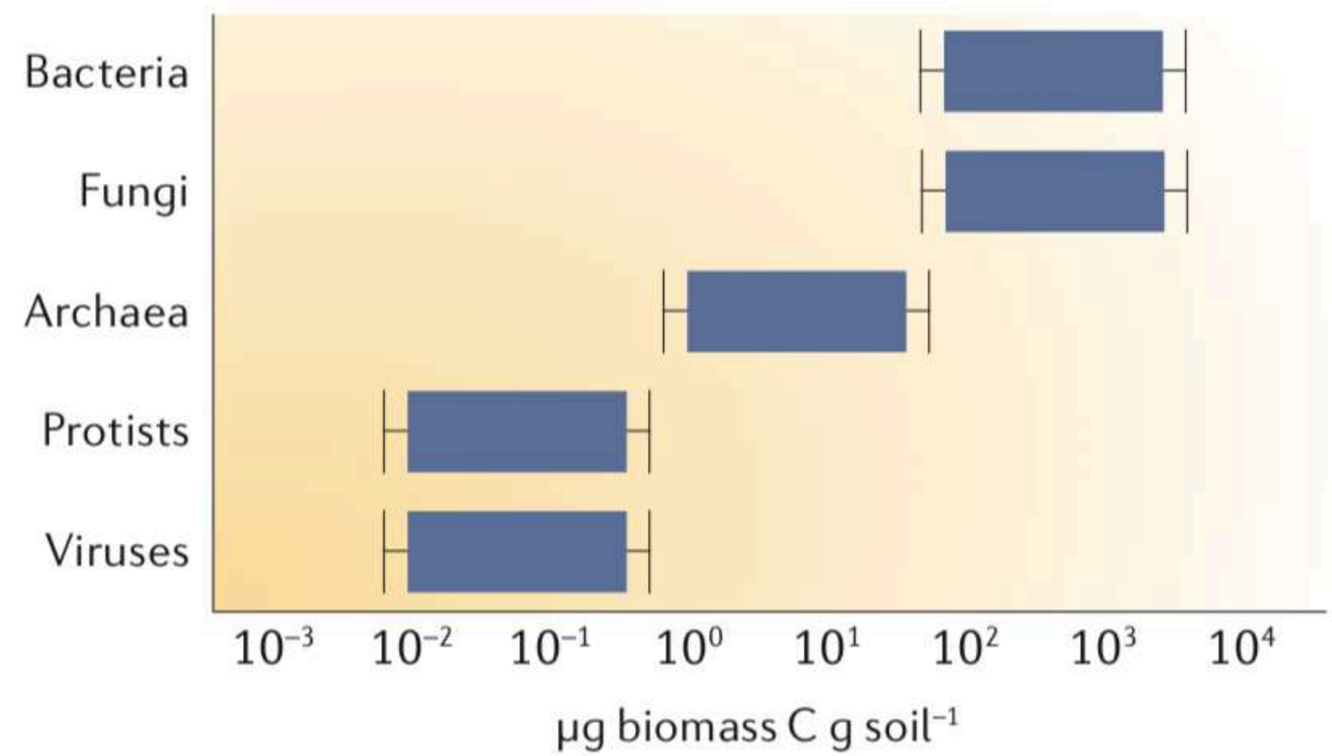



**Figure 1:** Representation of the main taxonomic groups of soil organisms on a body-width basis (Reprinted with permission from John Wiley and Sons after Swift et al., 1979) from Decaens (2010) and Barrios (2007) (all photo credits: Flickr, http://www.flickr.com/)

# Soil microbial biomass



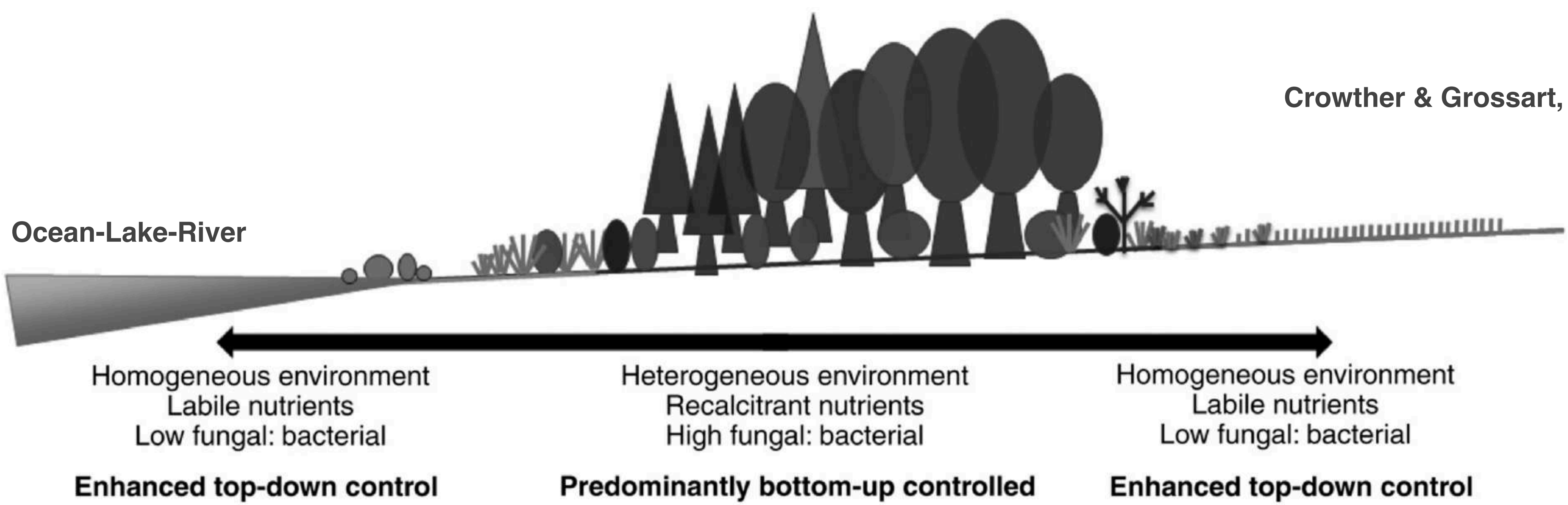

Fierer, 2017

- Microbial biomass (approximation), the sum of all microbial groups: bacteria, fungi, archaea, protists and viruses varies across the globe
- **Biomass can vary** substantially across soils, and the biomass of protists and viruses is highly uncertain
- **>90% of soil viruses seem to be strongly adsorbed** to clays and other soil surfaces
- Unclear what viruses % that are found in soil are even capable of infecting their microbial prey

# Soil microbial communities

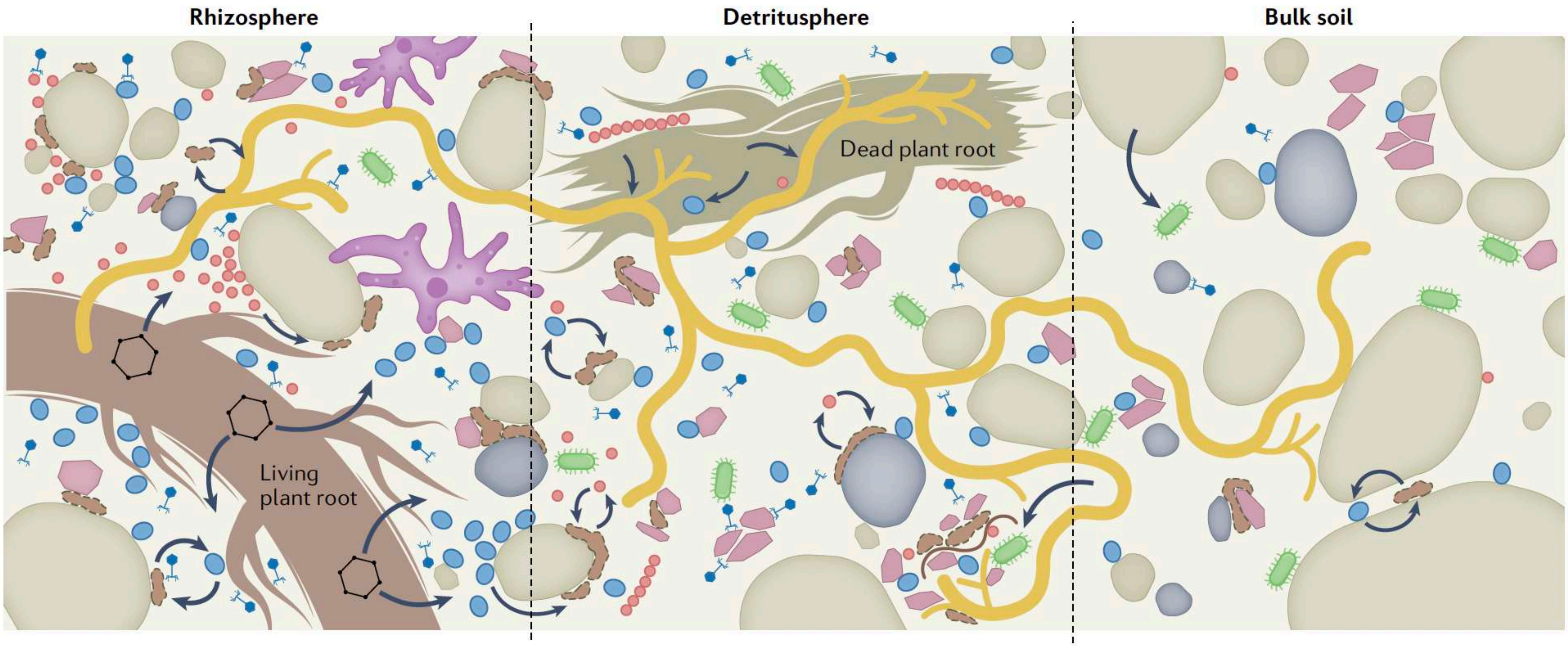
- **< 1% of the available soil surface area is typically occupied by microorganisms**
- **Biotic or abiotic constraints on the microbial colonization** of soil surfaces
- **>95% of total microbial biomass pool are dormant/inactive** at a given point in time
- Marked shifts in microbial communities and abiotic conditions with soil depth (more studied in surface soil horizons)
- Communities found in the litter layer (or O-horizon) are often **distinct** from those found in underlying mineral soil horizons (A and B horizons) and deeper saprolite (C horizons)

**Crowther & Grossart, 2017**



# Soil microbiome

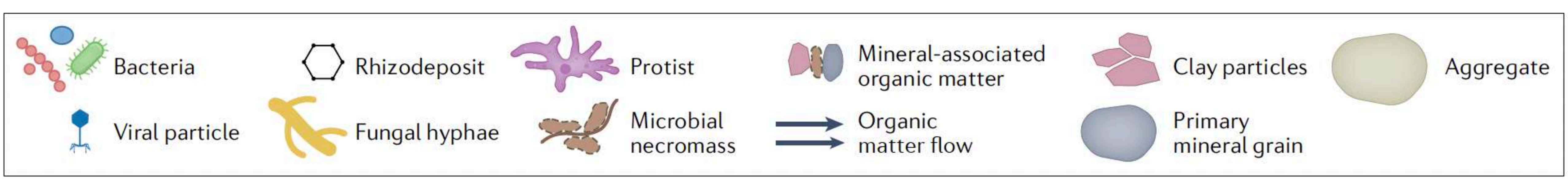
Sokol, 2022




- Organic matter inputs from living root (rhizodeposits)
- Higher microbial biomass and activity
- Lower microbial diversity
- Fast biomass turnover; high rates of organic matter flow
- Increased predation

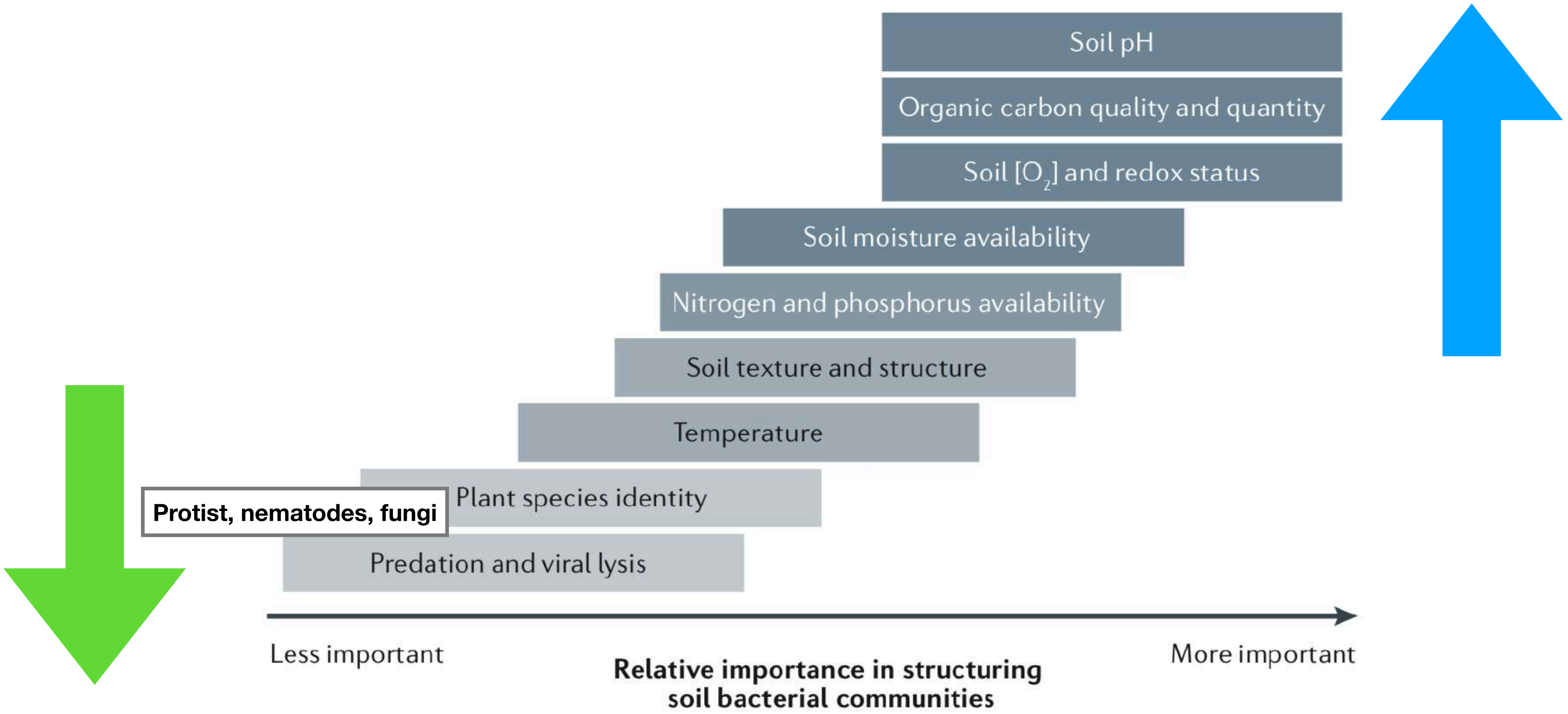
- Organic matter inputs from dead litter
- Higher microbial biomass and activity
- Higher prevalence of saprotrophic fungi
- High rates of organic matter flow

- Lower microbial biomass and activity
- Higher microbial diversity
- Slower biomass turnover and rates of organic matter flow



# Soil: Top-down & Bottom-up

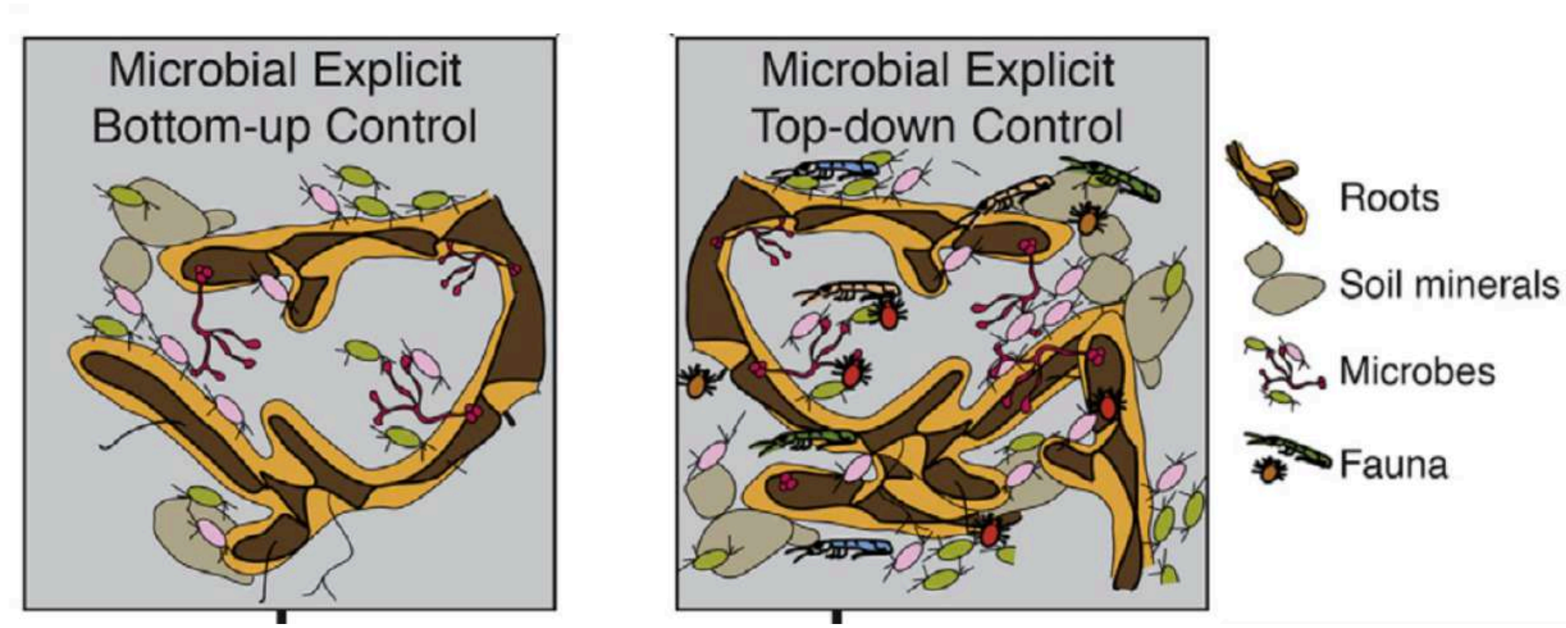
- Biotic and abiotic factors that can **influence** the composition of **soil bacterial** communities
- The shading of each box qualitatively indicates how well we understand the specific effects of each factor on bacterial communities; darker shades highlight factors that have been reasonably well-studied




Fierer, 2017

# Top-down control

- **Microbivory by microarthropods and fungal- and bacterial-feeding nematodes** provides a constraint on microbial community size and physiology and thus SOM formation




Grandy et al. 2016

**TABLE 1** Length scales relevant for interactions between soil particles and microbes

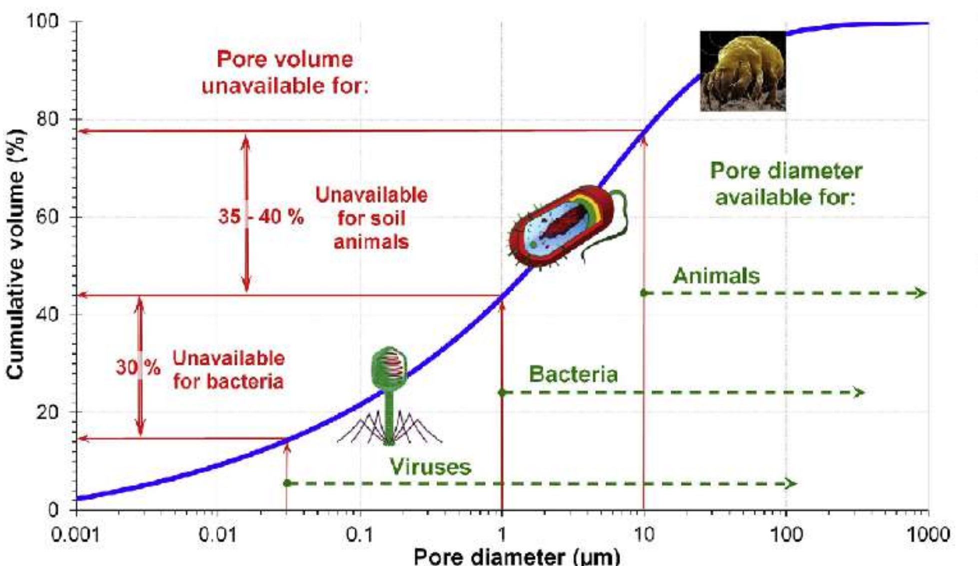
| Size (μm) | Biological relevance | Soil relevance | Interaction |
|---|---|---|---|
| <1 | Viral particle sizes,[a] *E. coli* cells deform (300 nm)[b] | Particle surface roughness promotes selective adhesion of specific bacterial species (10–100 nm)[c] | Lysogeny and gene transfer,[d] bacterial shape deformation,[b] surface attachment[c] |
| 1–2 | Bacterial cell size[b] | Pores within soil microaggregates[e] | Nitrogen fixation[f] |
| 1–15 | Fungal hyphal diam,[g] bacterial biofilm thickness in (0.12-mm-diameter) sand[h] | | Fungal mycelia reinforce aggregate tensile strength,[i] bacterial biofilm EPS production binds soil particles together[j] |
| 10–30 | Distance at which majority of bacterial cell interactions occur (<20 μm)[k] | Pores between soil microaggregates, can retain water against gravity for multiple days[e] | Denitrification,[l] quorum-sensing bacteria exhibit inhibited cell division[m] |

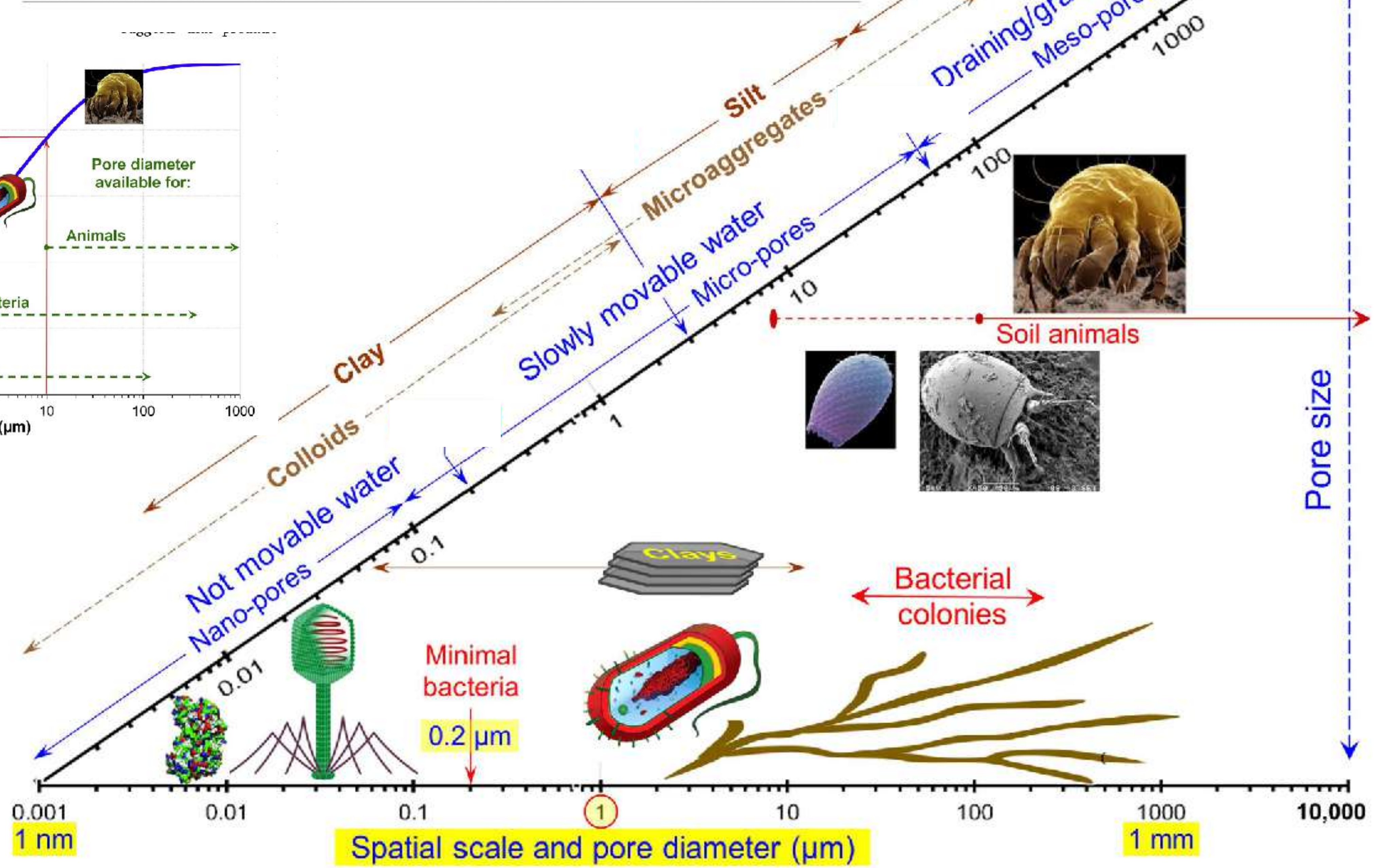


Wilpiszeski et al., 2019

# Soil structure defines niche

| | Bacteria | Virus | B:V Ratio |
|---|---|---|---|
| **Size**, µm | 0.2 - **2** - 5 | 0.03 - 0.08 | 25 - 70 |
| **Volume**, µm³ | 0.1 - **10** - 100 | 0.00003 - 0.0005 | **8000 - 125,000** |
| **C content**, fg | 20 - 100 | 0.05 - 0.2 | 100 - 2000 |

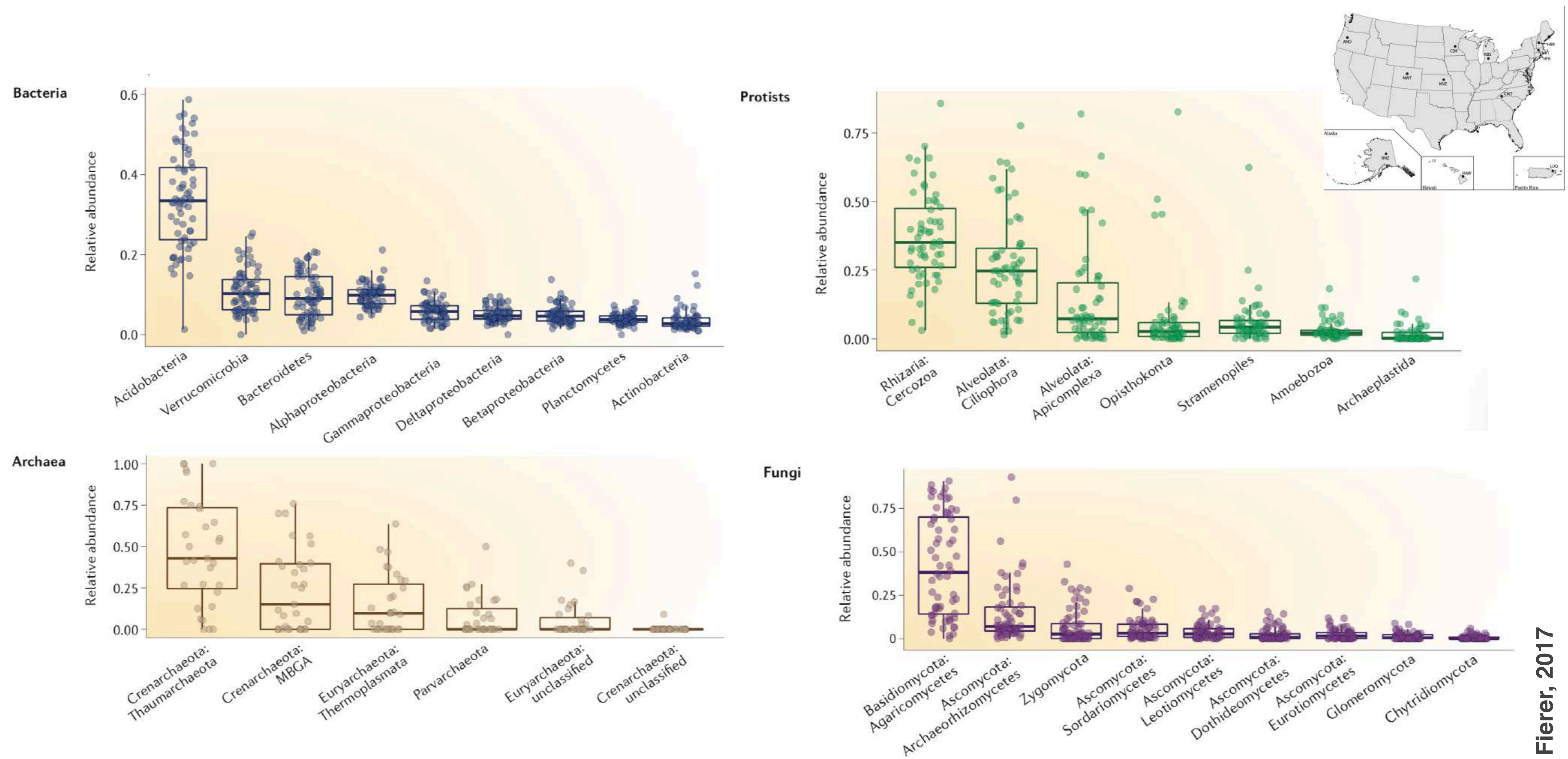



**Argilla**
**Limo**
**Sabbia**

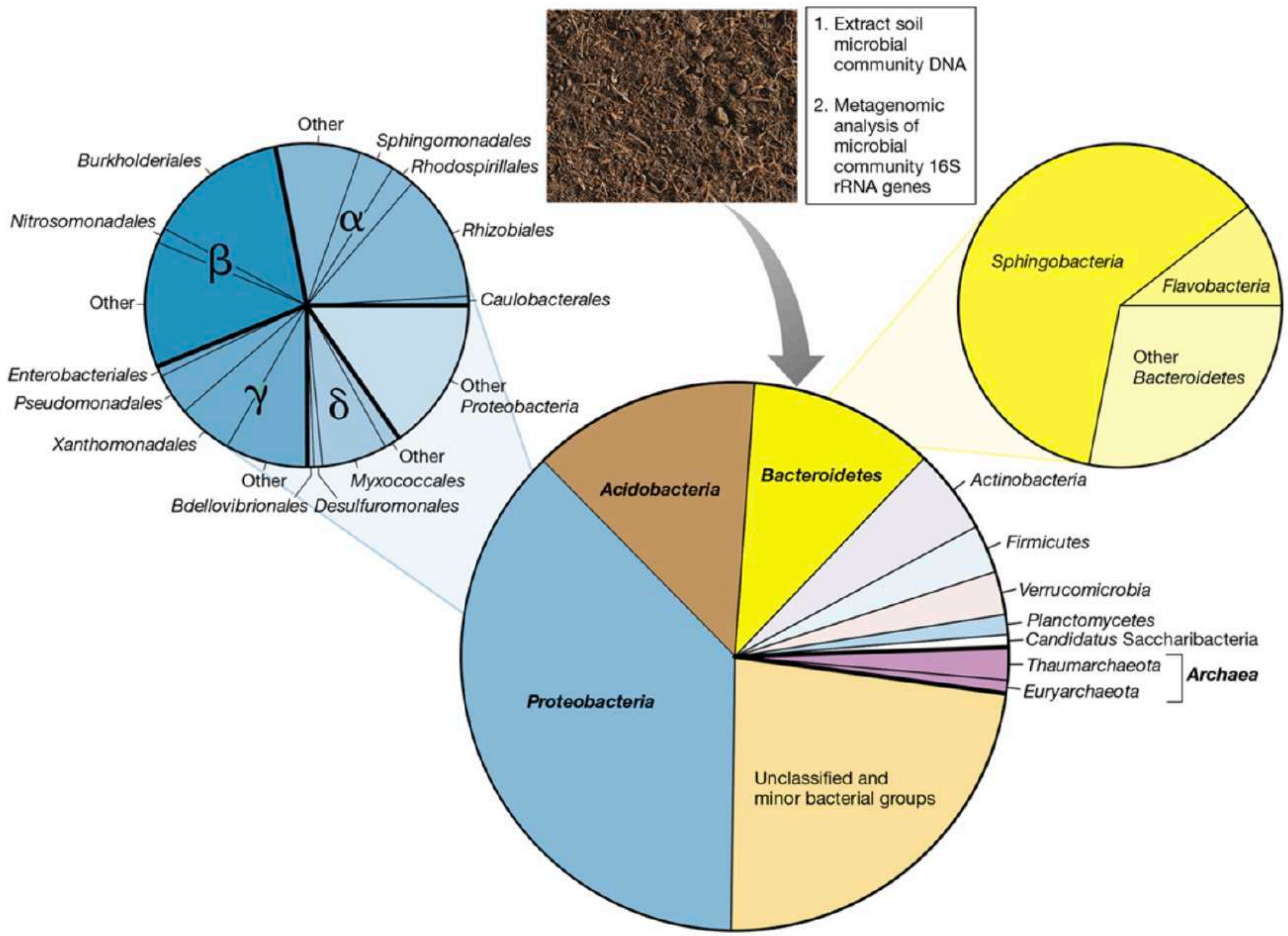
# Soil ecosystem structure

- Across diverse soil types the relative abundance of Bacteria, Archaea, Protist and Fungi diversity (66 samples)




Fierer, 2017

# Soil microbial diversity

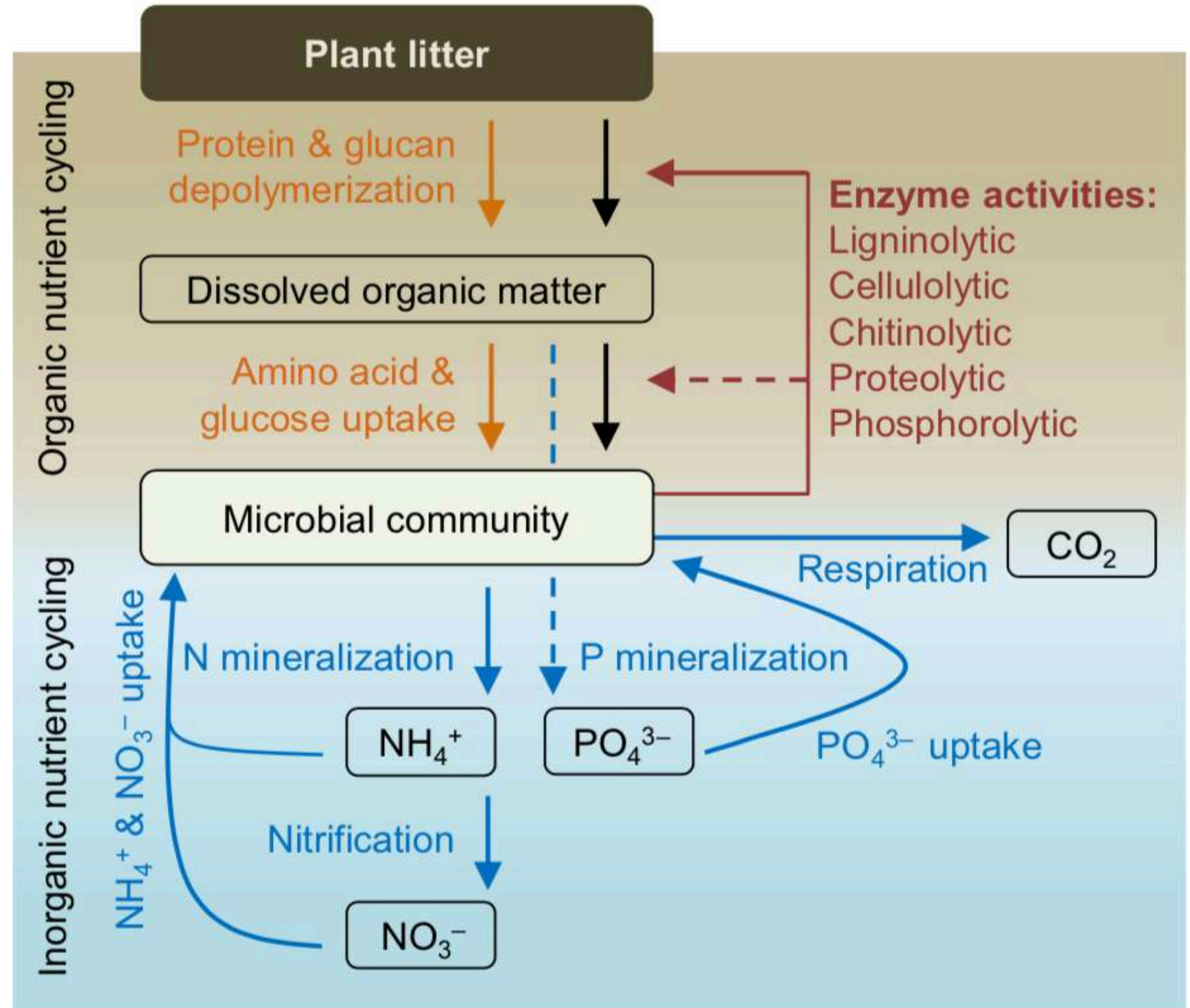



- 16SrRNA gene based diversity

Madigan, 2020

# Interconnected inorganic and organic nutrient cycling

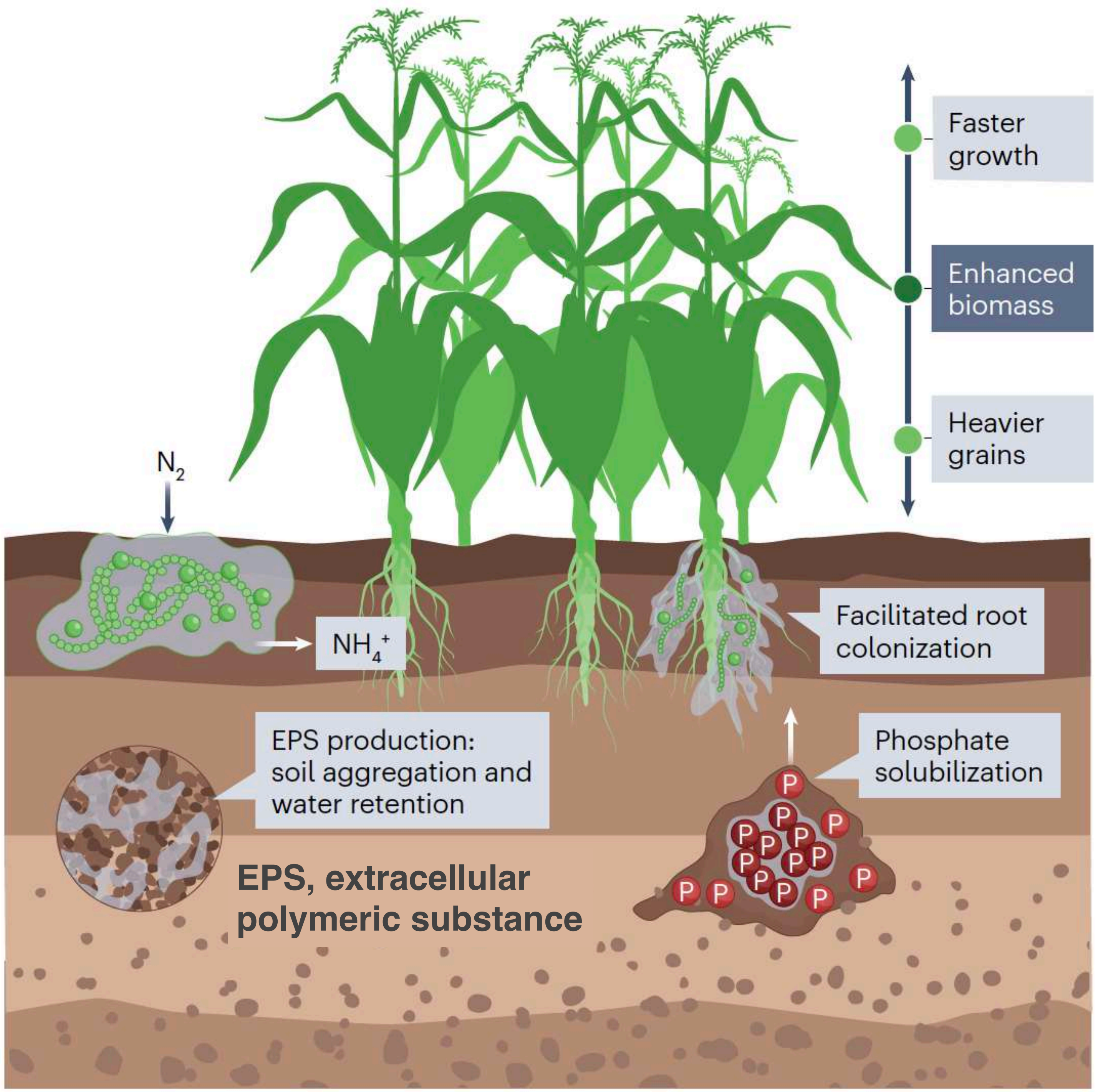
- Biogeochemical complexity within the soil community
- Coupling between primary production and organic matter decomposition
- Coupling organic matter decomposition and nutrient cycling






Mooshammer et al., 2020

# Wild Soil *vs* Agricultural soil




Philipp et al., 2024

**Customizing agriculture:**

Biofilms increase the water-binding capacity of the soil, and support the supply of nitrogen compounds, phosphorus and carbon

Biofilms facilitate the colonization of the rhizosphere by other, symbiotic microorganisms

Plant biomass is enhanced, growth is accelerated and grain weight is enhanced

**Symbiotic community that protects crops**

**Microbial fertilisation** instead of chemical one

# Soil microbiome in agroecosystems

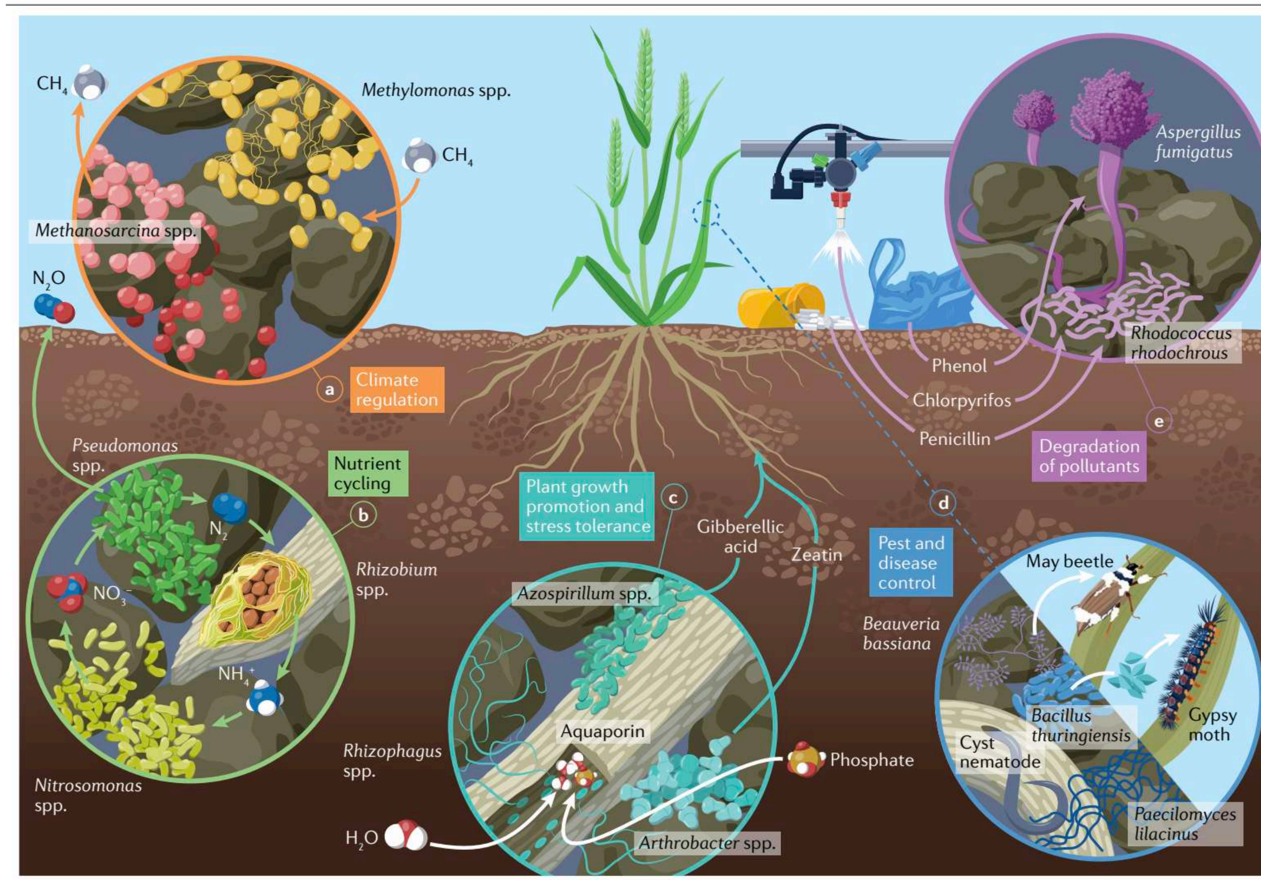
**Agroecosystems: sites or integrated regions that support food production while conserving biotic and abiotic resources and providing a balanced supply of ecosystem services**

Soil microbiomes drive key functions in agroecosystems:

- determining soil fertility
- crop productivity
- stress tolerance

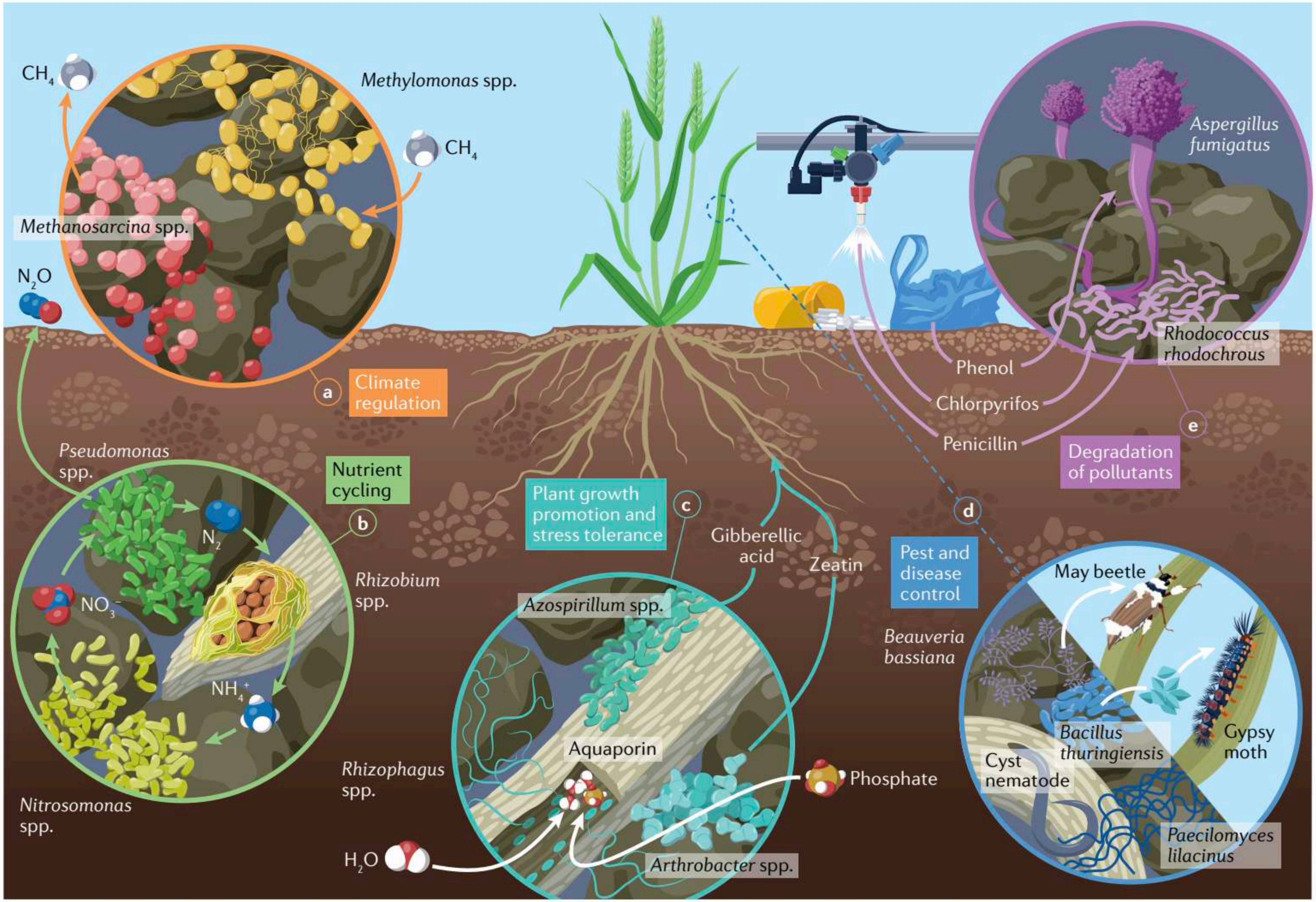
The microbiome is intricately linked with soil structure, such as aggregation and pore connectivity, because this structure regulates through the system:

- flow of water
- oxygen
- nutrients




Hartman and Six, 2023

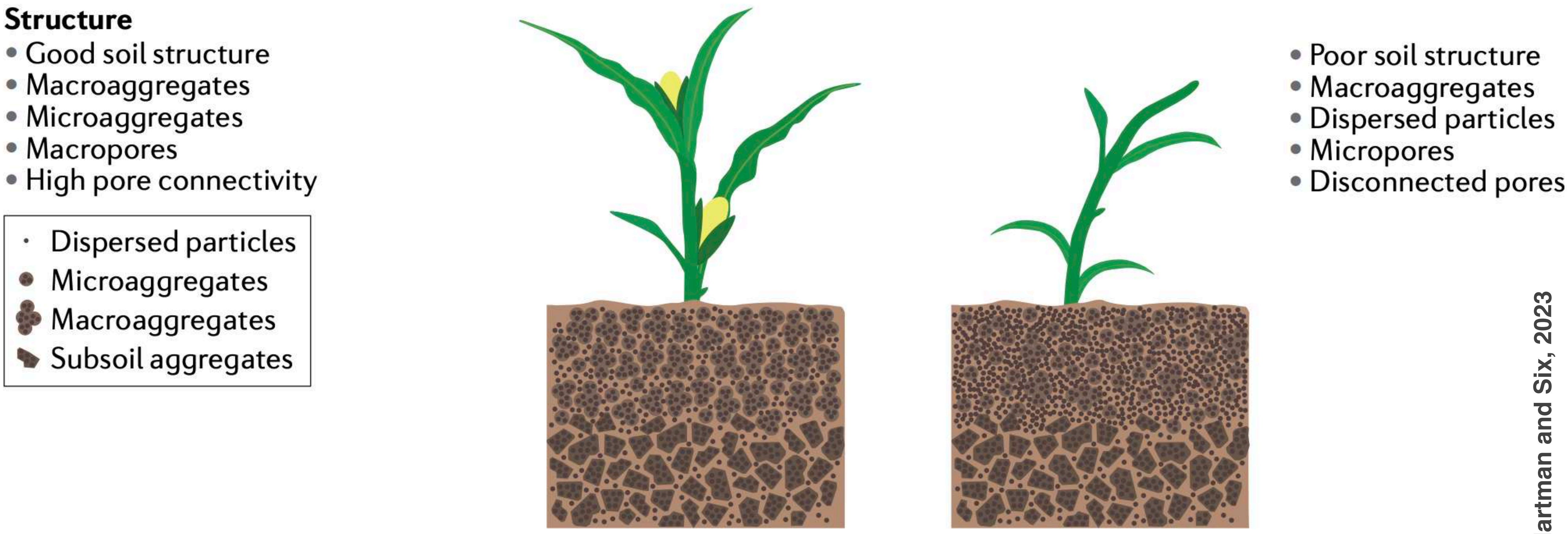
# Microbial key functions in the plant–soil system




Hartman and Six, 2023

a, Climate regulation. b, Microbial nutrient cycling. c, Plant growth promotion and abiotic stress tolerance. d, Pest and disease control. e, Toxin and pollutant degradation

# Differences in soil properties between structurally intact versus *degraded soils, I*

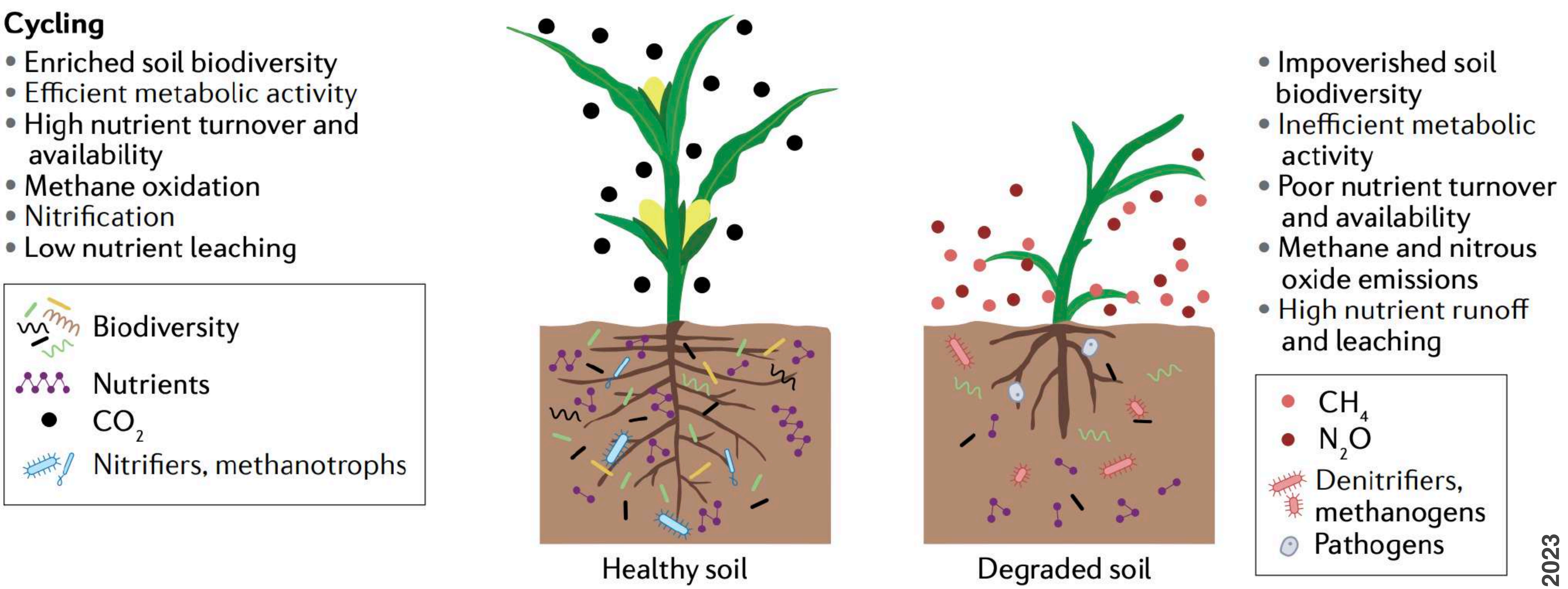



Hartman and Six, 2023

# Differences in soil properties between structurally intact versus *degraded soils, II*

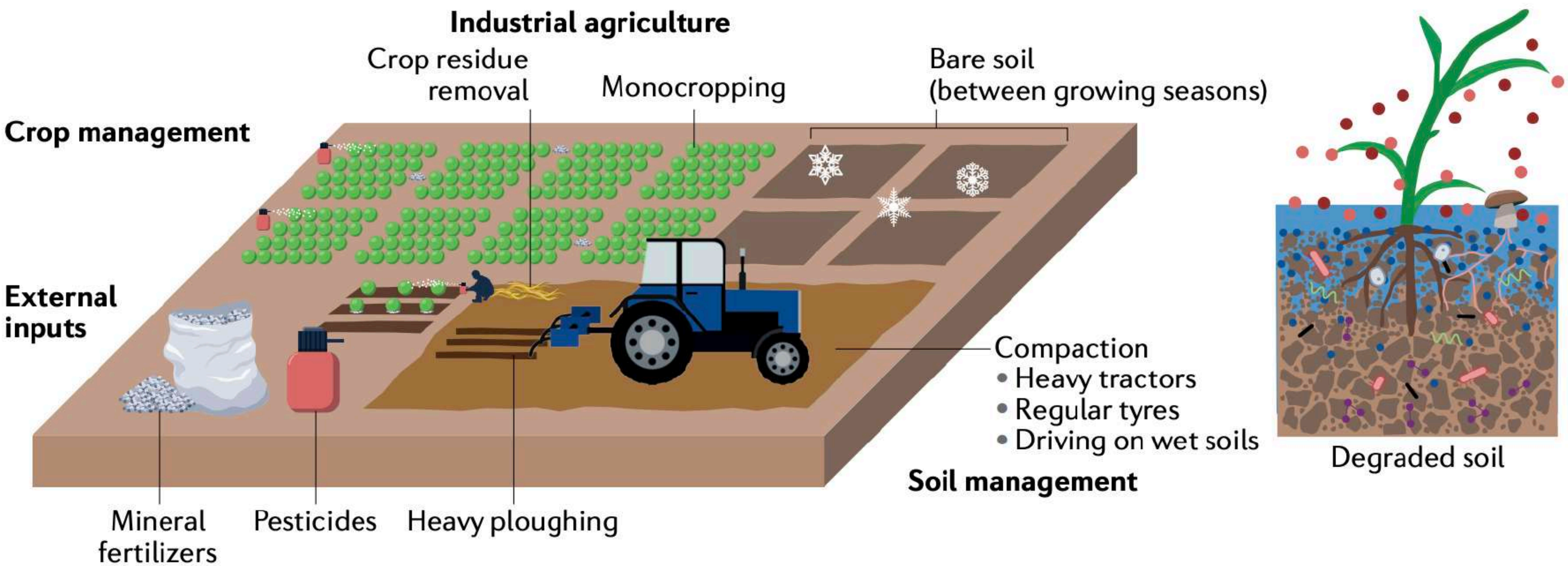

Hartman and Six, 2023

# Differences in soil properties between structurally intact versus *degraded soils, III*




Hartman and Six, 2023

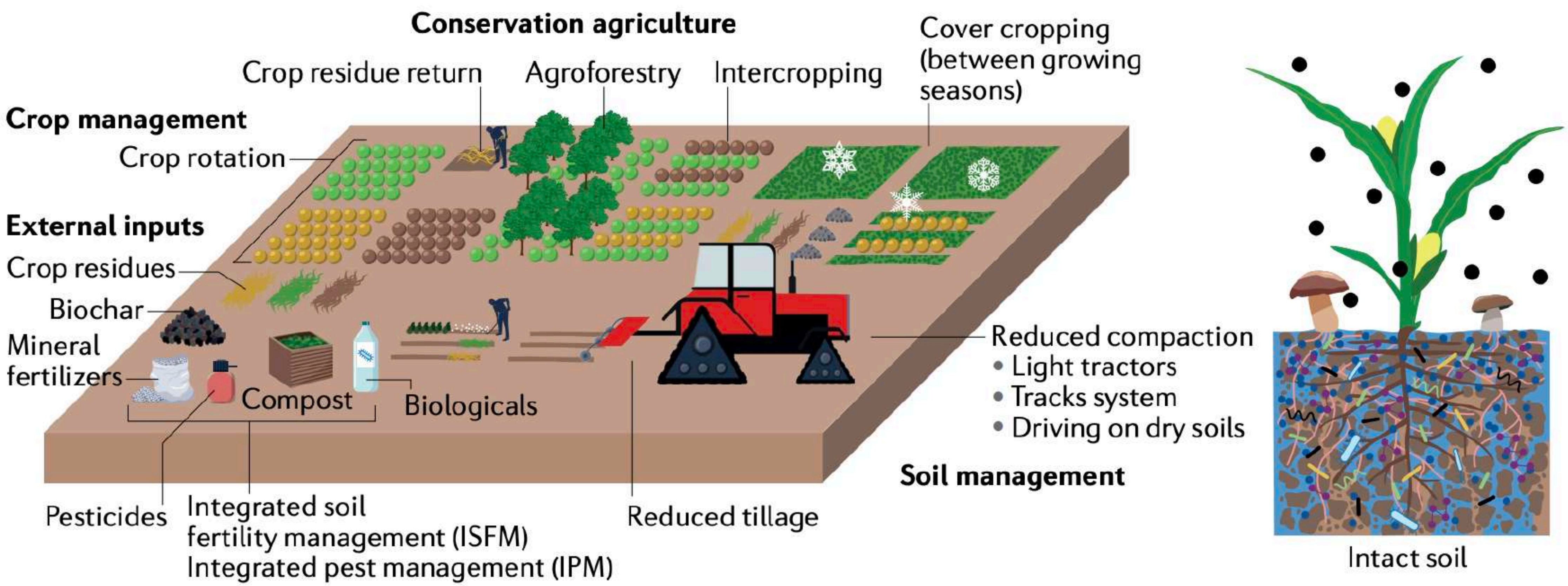
# INDUSTRIAL AGRICULTURE




Hartman and Six, 2023

**Industrial** agriculture focuses on **maximizing yields** and often relies on **intensive** soil management, **chemical fertilizers** and **pesticides**, and the use of highly productive plant material in **simple** cropping systems —> **Soil is degraded** as a result

# CONSERVATION AGRICULTURE

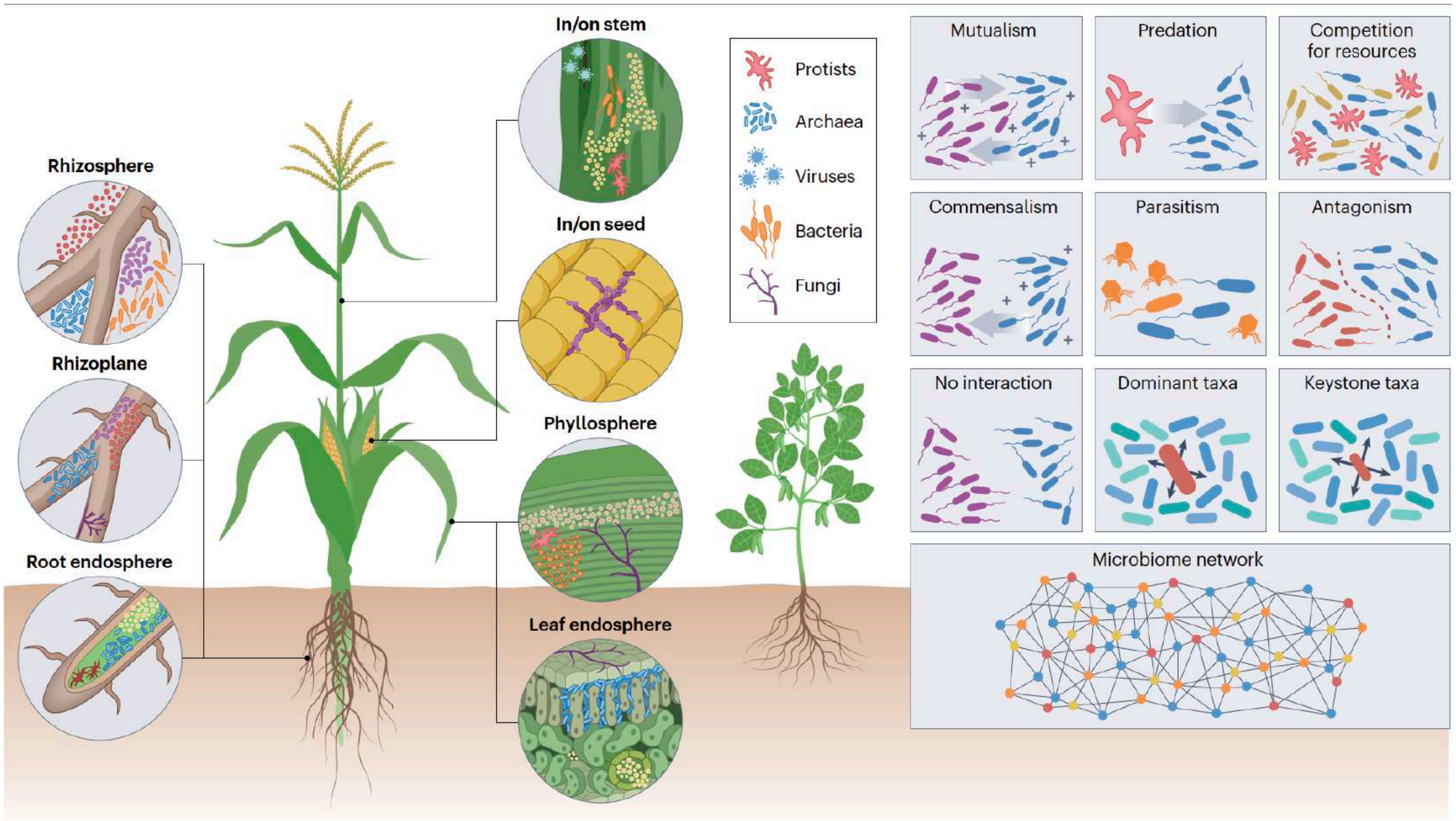



Hartman and Six, 2023

**Conservation** agriculture features protective approaches in terms of soil management (reduced or no tillage, agricultural vehicles better protecting the soil), crop management (crop diversification, cover cropping) and external inputs (organic fertilizers and amendments, biologicals).

**Integrated soil fertility management and integrated pest management** use beneficial use of targeted and microdosed application of agrochemicals with the application of organic fertilizers and other soil amendments, the use of **biocontrol strategies**, and the development of resource-efficient and disease-resistant plant germplasm —> healthy, intact soil

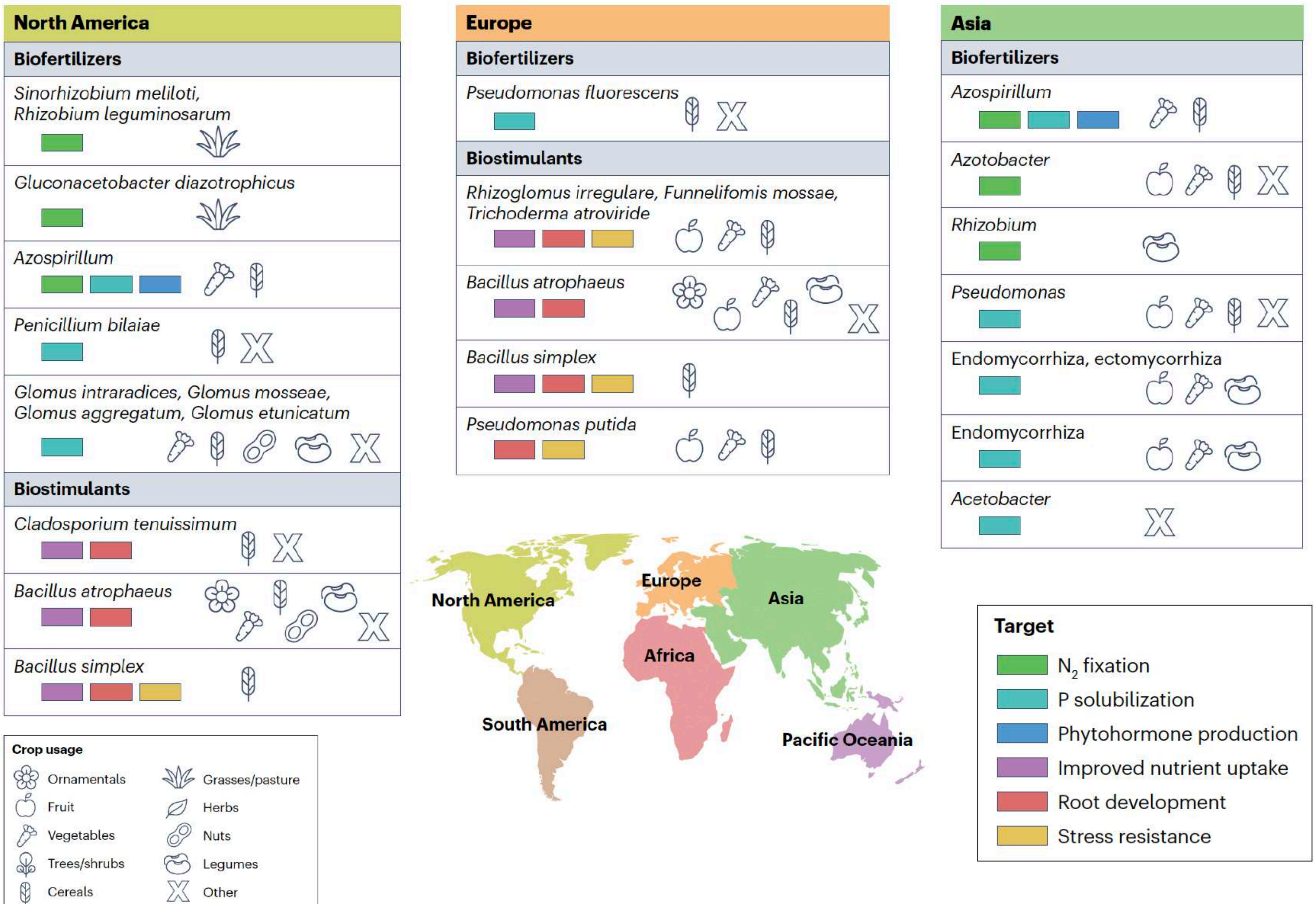
# The plant microbiome and microbial interactions




Compant et al., 2024

- The plant microbiome consists of bacteria, viruses, archaea, fungi and protists, each performing important community functions
- Microbial intervention is a fruitful strategy for promoting plant health and augmenting C storage/sequestration

# Major microbial biofertilizers and biostimulants

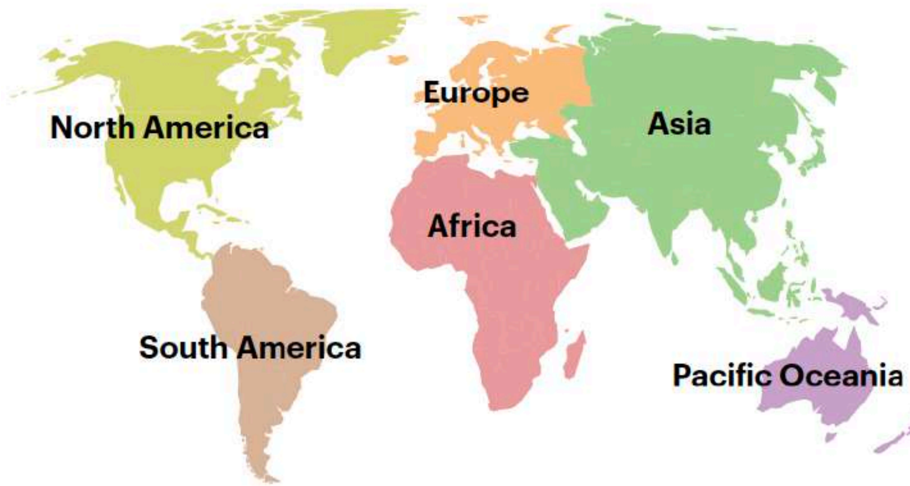



Compant et al., 2024

# Major microbial biofertilizers and biostimulants

**Target**
- $N_2$ fixation
- P solubilization
- Phytohormone production
- Improved nutrient uptake
- Root development
- Stress resistance

**Crop usage**
- Ornamentals
- Fruit
- Vegetables
- Trees/shrubs
- Cereals
- Grasses/pasture
- Herbs
- Nuts
- Legumes
- Other



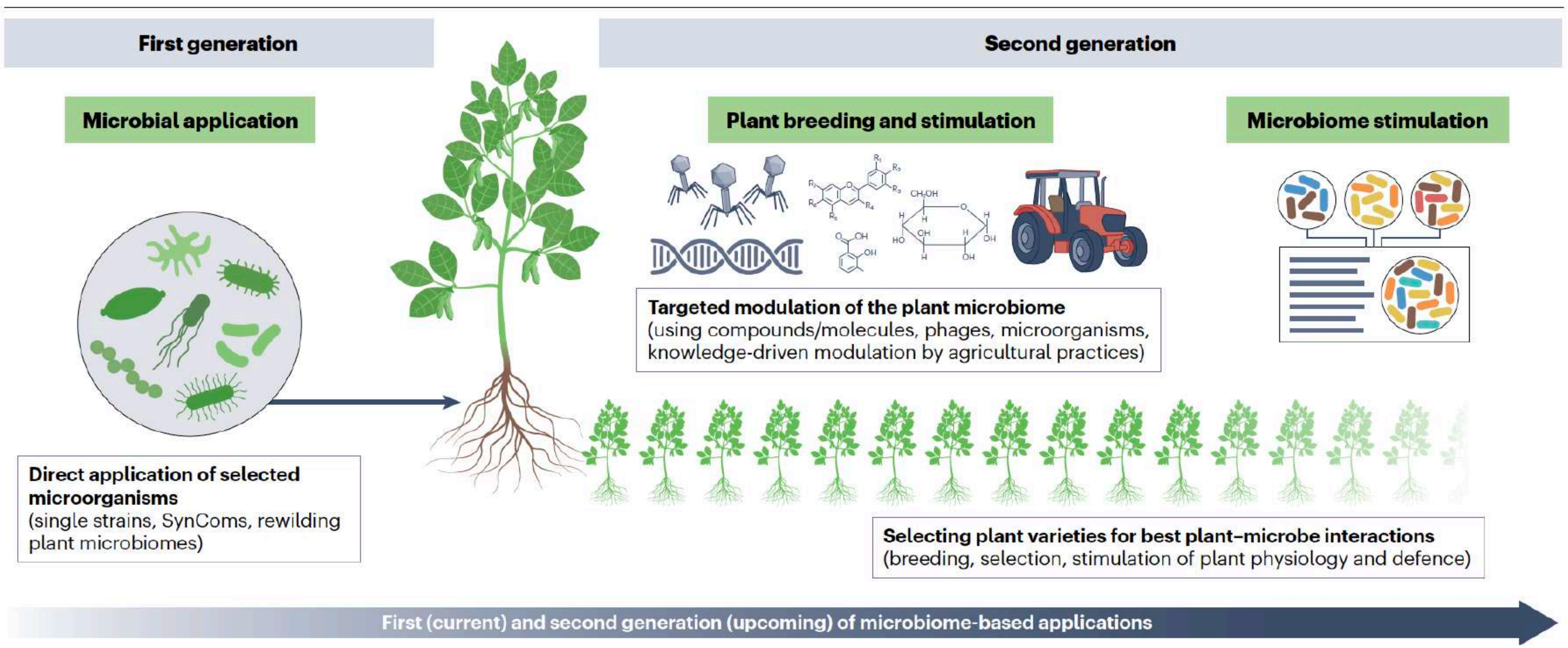

| South America |
|---|
| **Biofertilizers** |
| *Azospirillum* |
| *Azospirillum brasilense* |
| *Pseudomonas fluorescens* |
| *Bacillus amyloliquefaciens, Trichoderma* |
| **Biostimulants** |
| *Bacillus simplex* |
| *Pseudomonas putida* |

| Pacific Oceania |
|---|
| **Biofertilizers** |
| *Penicillium bilaiae* |
| *Bradyrhizobium japonicum, Penicillium bilaiae* |
| Endomycorrhiza, ectomycorrhiza |
| Endomycorrhiza |
| **Biostimulants** |
| *Bacillus velezensis* |

| Africa |
|---|
| **Biofertilizers** |
| *Bradyrhizobium* |
| *Azospirillum brasilense* |
| *Bradyrhizobium japonicum* |
| *Bradyrhizobium japonicum, Bacillus subtilis* |
| *Rhizobium meliloti* |
| *Bradyrhizobium japonicum* strain WB74 |
| **Biostimulants** |
| *Pseudomonas putida* |

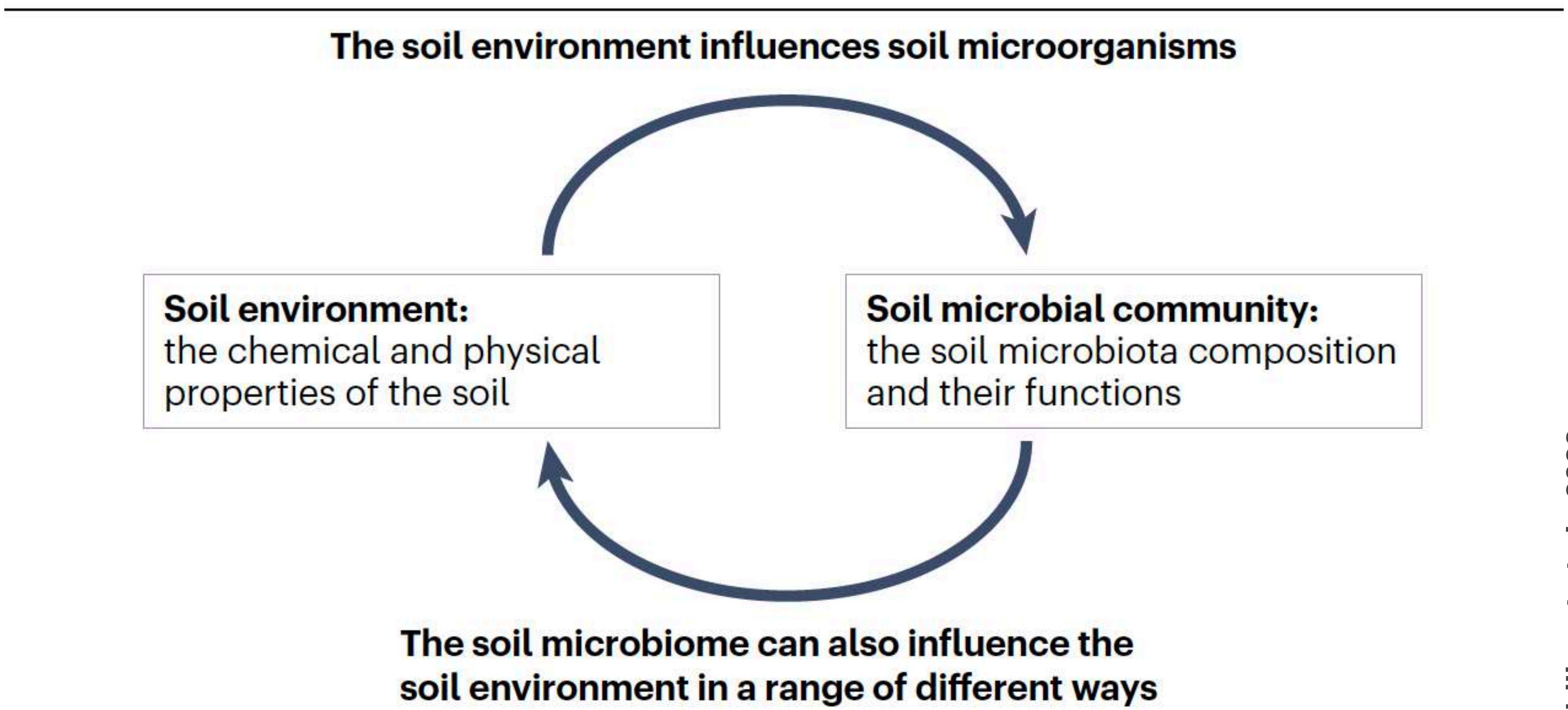
Compant et al., 2024

# Current and emerging microbiome-based applications for sustainable crop production




Compant et al., 2024

# Tight interacting network



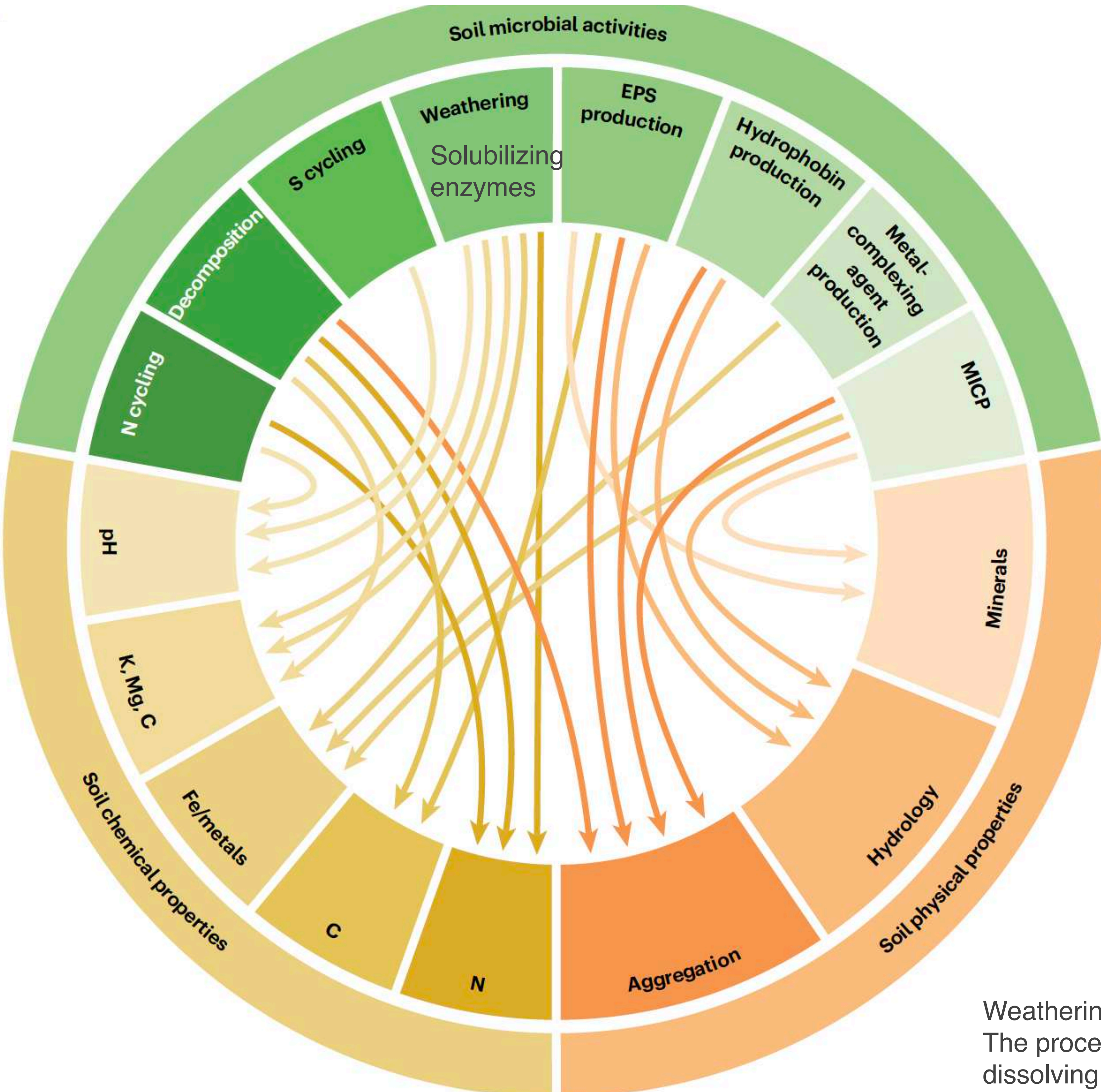

Philippot et al., 2023

- Soil properties, such as pH, soil organic carbon and oxygen partial pressure, are shaping the soil microbiome composition and function

- Soil microorganisms also exert an effect on their habitat through various biogeochemical and biophysical mechanisms

# The interplay between soil environmental conditions and the soil microbiome

Hydrophobins: small proteins produced by filamentous fungi that can spontaneously self-assemble and change the polarity of a surface, they are amphiphilic compounds




Philippot et al., 2023

Microbially induced carbonate precipitation (MICP) can affect many physical and mechanical properties of soils, which results in reduced hydraulic conductivity and increased shear strength

Some of the relevant microbial metabolisms involved in MICP are ureolysis, denitrification and photosynthesis

$CO_2$ dissolution after respiration produce protons

Nitrification
Aerobic oxidation of ammonium to nitrite and then to nitrate to generate energy (produce protons)

Denitrification
The respiratory reduction of nitrogen oxides to $N_2O$ and $N_2$ when oxygen is limiting (consume protons)

Ammonification
The respiratory reduction of nitrate to ammonium when oxygen is limiting (consume protons)

Weathering
The process of breaking down or dissolving solids (minerals and rocks) by biological, chemical or physical processes

# Biogeochemical processes

Table 1 | **Examples of physiological processes catalysed by microorganisms in biosphere habitats**

| Process | Nature of process | Typical habitat |
|---|---|---|
| ***Carbon cycle*** | | |
| Photosynthesis | Light-driven $CO_2$ fixation into biomass | Ow, Fw, FwS, Os |
| C respiration | Oxidation of organic C to $CO_2$ | All |
| Cellulose decomposition | Depolymerization, respiration | Sl |
| Methanogenesis | $CH_4$ production | Sw, FwS, Os |
| Aerobic $CH_4$ oxidation | $CH_4$ becomes $CO_2$ | All |
| Anaerobic $CH_4$ oxidation | $CH_4$ becomes $CO_2$ | Os |
| ***Biodegradation*** | | |
| Synthetic organic compounds | Decomposition, $CO_2$ formation | All |
| Petroleum hydrocarbons | Decomposition, $CO_2$ formation | All |
| Fuel additives (MTBE) | Decomposition, $CO_2$ formation | Sl, Sw, Gw |
| Nitroaromatics | Decomposition, $CO_2$ formation | Sl, Sw, Gw |
| Pharmaceuticals, personal care products | Decomposition | Sl, Sw, Gw |
| Chlorinated solvents | Compounds are dechlorinated through respiration in anaerobic habitats | Sl, Sw, Gw |

Madsen, 2005

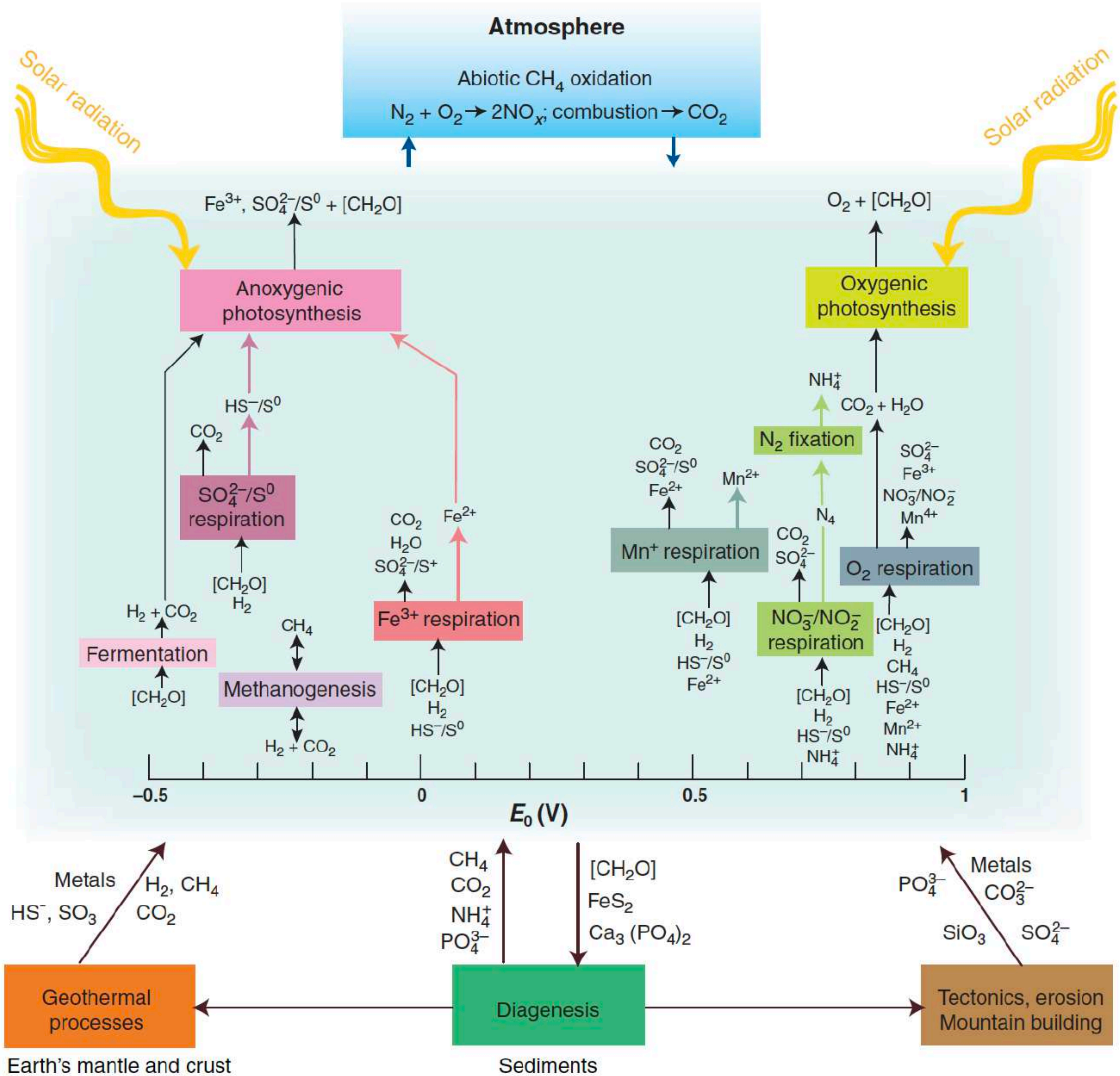
As, arsenic; C, carbon; $CH_4$, methane; $CO_2$, carbon dioxide; Fe, iron; FeS, iron sulphide; Fw, freshwater; FwS, freshwater sediment; Gw, groundwater; $H_2$, hydrogen; Hg, mercury; $Hg^{2+}$, mercuric ion; MTBE, methyl tertiary butyl ether; $N_2$, nitrogen; $NH_3$, ammonia; $NH_4^+$, ammonium; $NO_2^-$, nitrite; $NO_3^-$, nitrate; Os, ocean sediments; Ow, ocean waters; $S^0$, elemental sulphur; $S^{2-}$, sulphide; Sl, soil; $SO_4^{2-}$, sulphate; Sw, sewage; U, uranium.

| | | |
|---|---|---|
| ***Nitrogen cycle*** | | |
| $N_2$ fixation | $N_2$ gas becomes $NH_3$ | Sl, Ow |
| $NH_4^+$ oxidation | $NH_3$ becomes $NO_2^-$, $NO_3^-$ | Sl, Sw |
| Anaerobic $NH_4^+$ oxidation | $NO_2^-$ and $NH_3$ become $N_2$ gas | Sw, Os |
| Denitrification | $NO_3^-$ is used as an electron acceptor and converted to $N_2$ gas | Sl, Sw |
| ***Sulphur cycle*** | | |
| $S_2$ oxidation | $S^{2-}$ and $S^0$ become $SO_4^{2-}$ | Os, FwS |
| $SO_4^{2-}$ reduction | $SO_4^{2-}$ is used as an electron acceptor and converted to $S^0$ and $S^{2-}$ | Os, Sw, Gw |
| ***Other elements*** | | |
| $H_2$ oxidation | $H_2$ is oxidized to $H^+$, electrons reduce other substances | Sw, Sl, Os, FwS |
| Hg methylation and reduction | Organic Hg is formed and $Hg^{2+}$ is converted to Hg | FwS, Os |
| (per)chlorate reduction | Oxidants in rocket fuel and other sources are converted to chloride | Gw |
| U reduction | U oxyanion is used as an electron acceptor; therefore immobilized | Gw |
| As reduction | As oxyanion is used as an electron acceptor; therefore toxicity is diminished | FwS, Gw |
| Fe oxidation, acid mine drainage | FeS ores are oxidized, strong acidity is generated | FwS, Gw |

Madsen, 2005

As, arsenic; C, carbon; $CH_4$, methane; $CO_2$, carbon dioxide; Fe, iron; FeS, iron sulphide; Fw, freshwater; FwS, freshwater sediment; Gw, groundwater; $H_2$, hydrogen; Hg, mercury; $Hg^{2+}$, mercuric ion; MTBE, methyl tertiary butyl ether; $N_2$, nitrogen; $NH_3$, ammonia; $NH_4^+$, ammonium; $NO_2^-$, nitrite; $NO_3^-$, nitrate; Os, ocean sediments; Ow, ocean waters; $S^0$, elemental sulphur; $S^{2-}$, sulphide; Sl, soil; $SO_4^{2-}$, sulphate; Sw, sewage; U, uranium.

# Biosphere model




Falkowski et al., 2008

# Soil biogeochemical processes

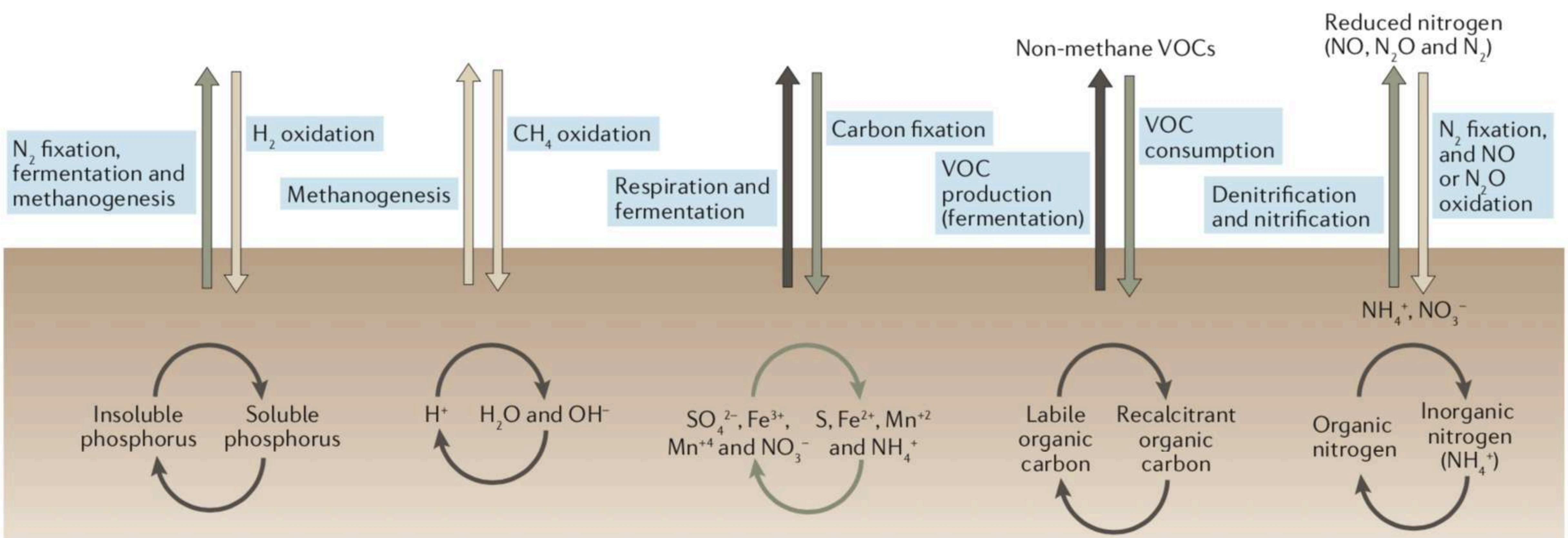
Soil biogeochemical processes that can be **modulated by the soil microbiome that are interrelated**

The vertical arrows indicate microbial processes that are responsible for the production or consumption of trace gases at the soil–atmosphere interface

The curved arrows indicate some of the key **microbial processes** that can occur within soil thus regulating, **soil acidity, the availability of nitrogen, phosphorus or other nutrients, and the lability (ease of consumption by microorganisms) of soil organic carbon pools**

**Non-methane volatile organic compounds (VOCs)** include acetone, methanol, formaldehyde, isoprene and other organic compounds with low molecular weight

Small subset of microbial taxa (light grey; 'narrow' processes), by an intermediate number of taxa (dark grey) and by a broad diversity of taxa (black; 'broad' processes)




Fierer, 2017