L07b

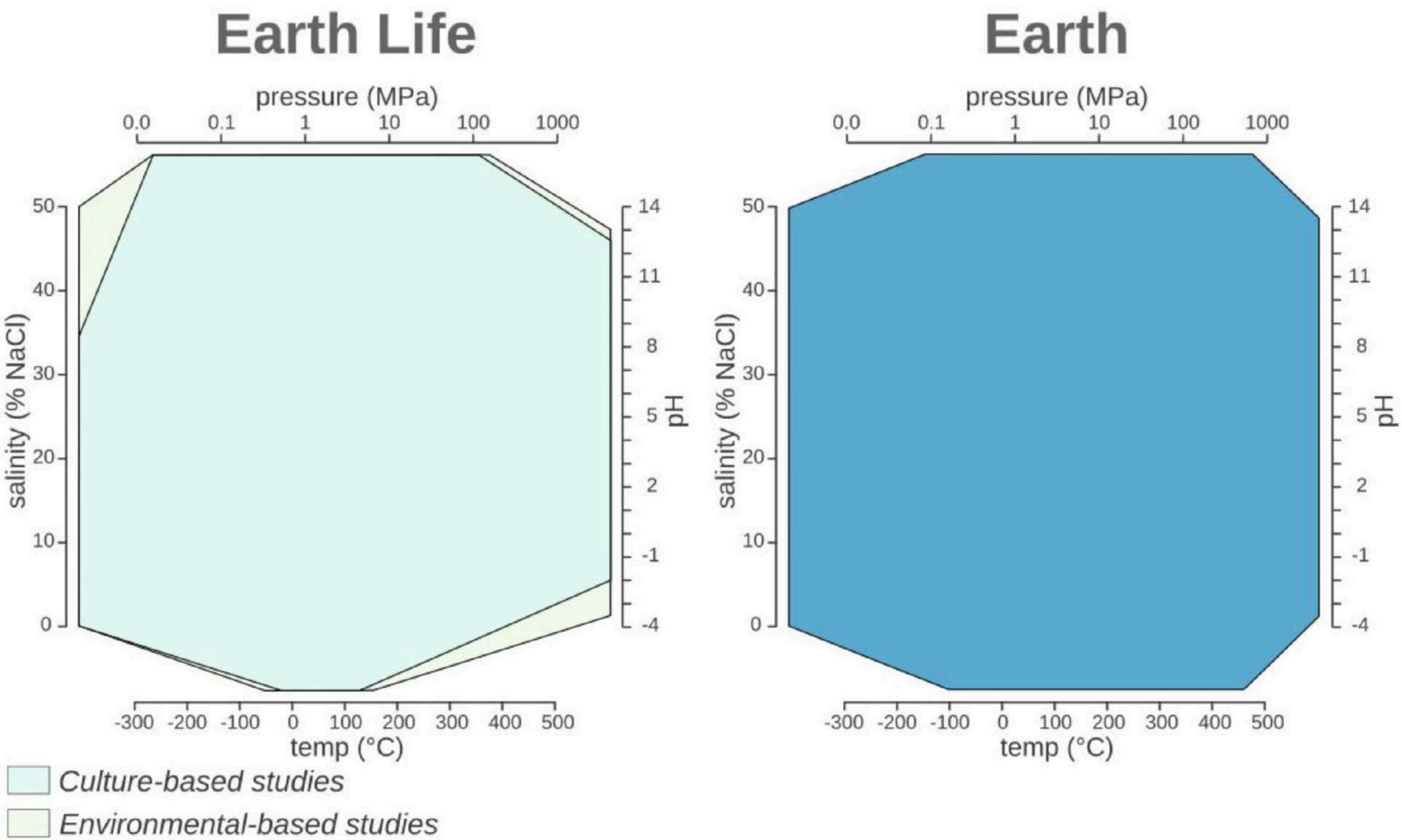
Microbial Ecology

- 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**

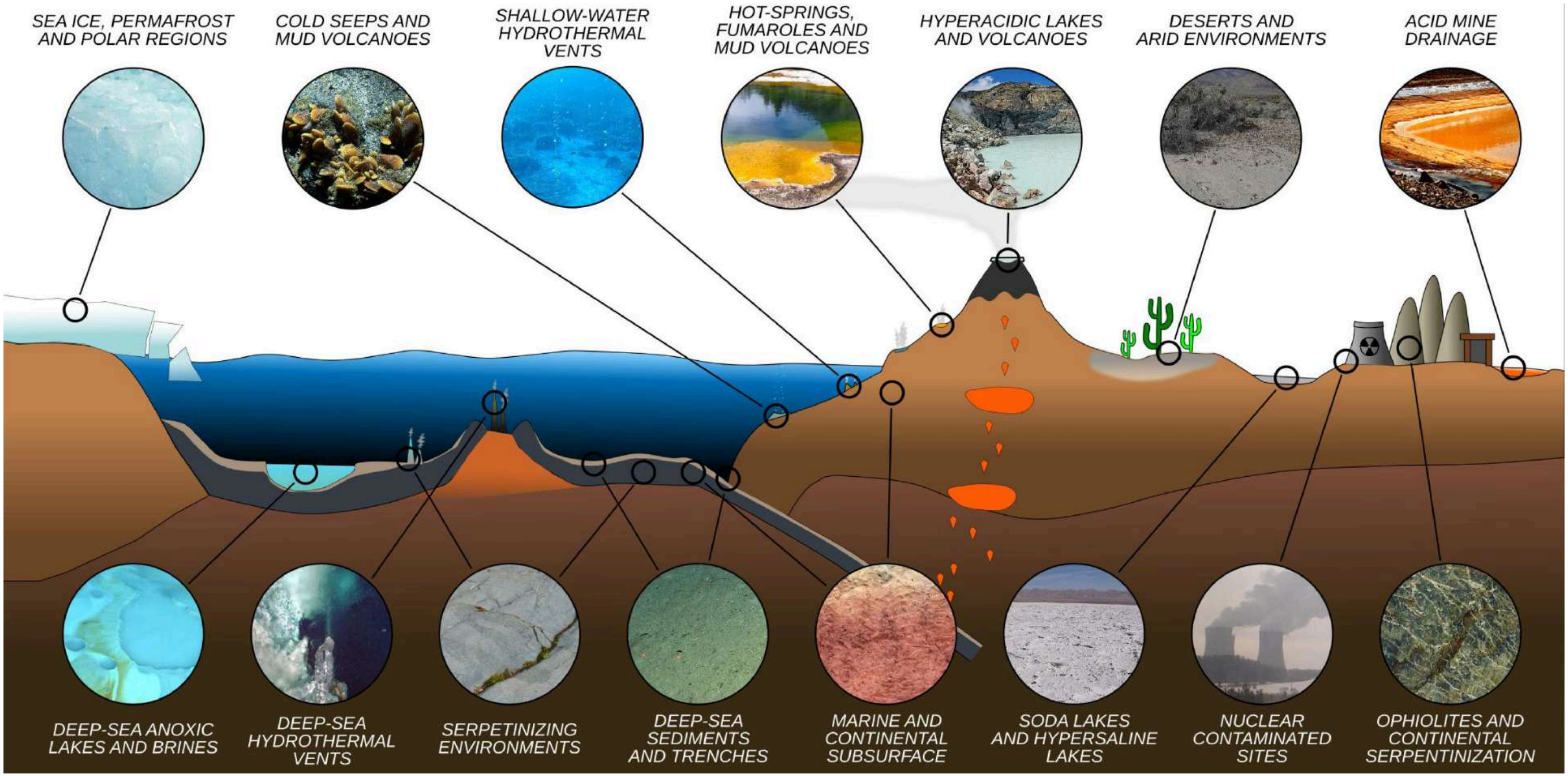
EXTREME ENVIRONMENT ECOSYSTEMS

Extreme microbial conditions



Merino et al. 2019

High diversity of extreme environments on Earth

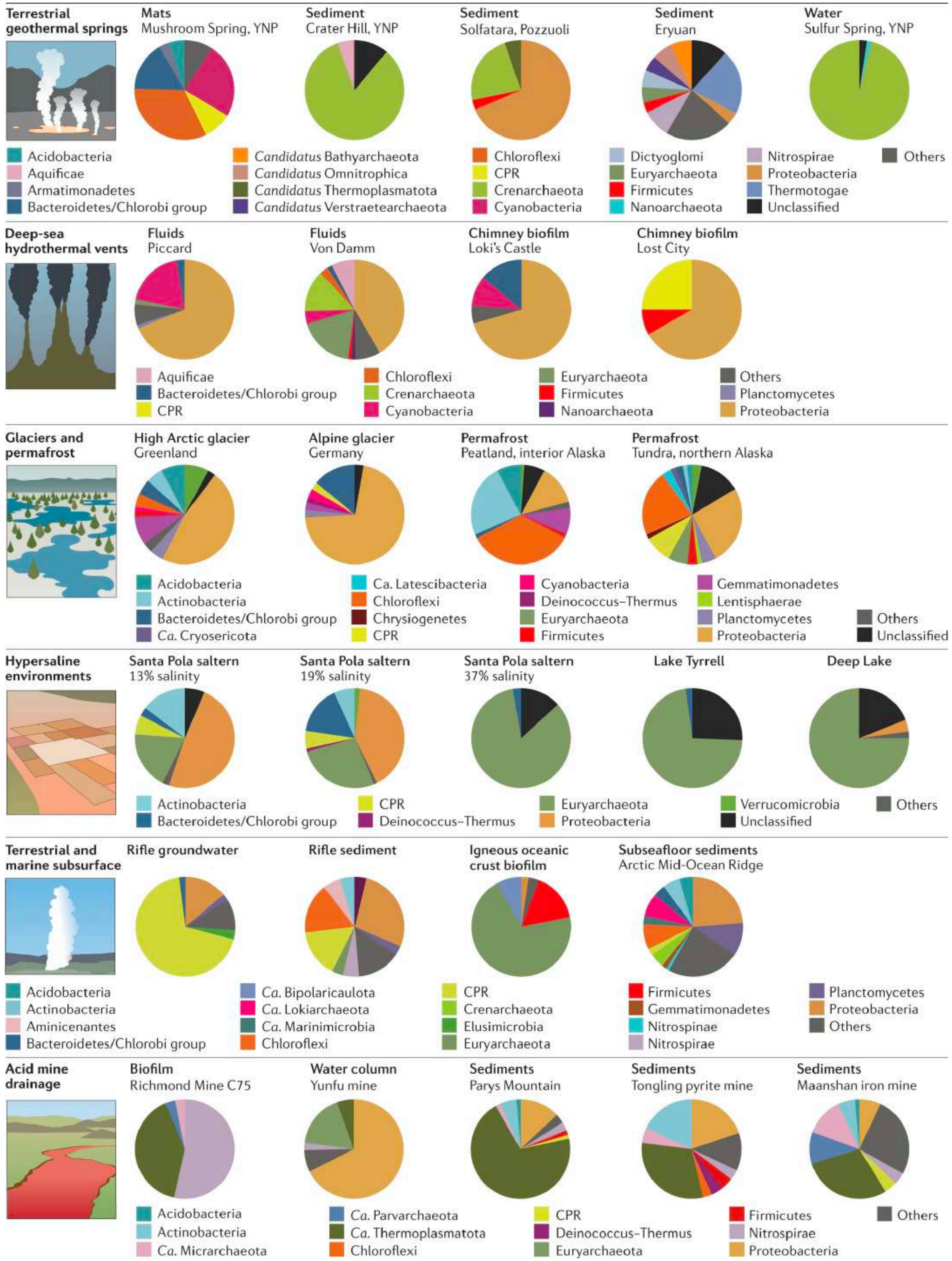


Merino et al. 2019

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
- Similar adaptation for living in harsh conditions
- 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, I

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, II

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)

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

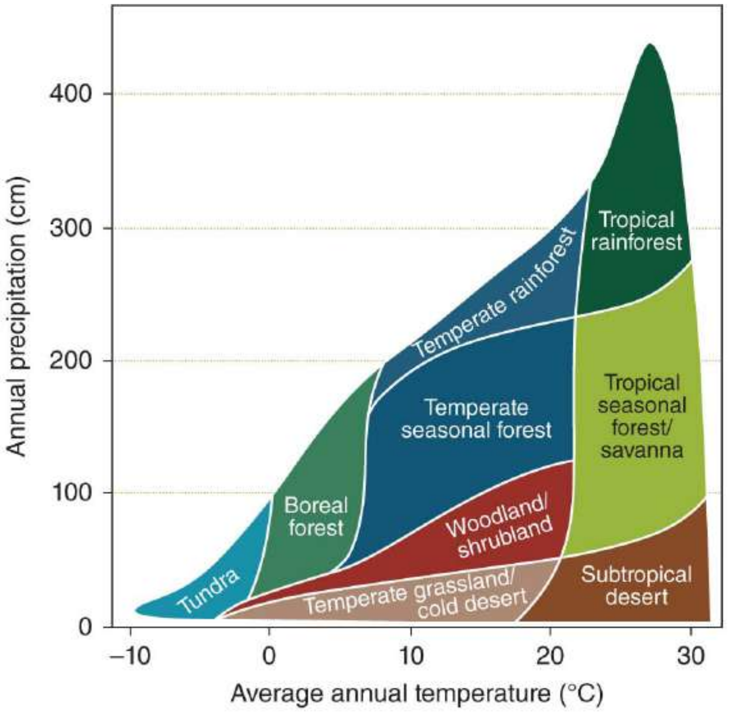


Figure 4.3 The pattern of plant biome types showing responses to annual habitat precipitation (vertical axis) and annual temperature (horizontal axis). Boundaries between the nine plant biome types are approximate–influenced by factors that include soil type, maritime versus continental climate, and 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.)

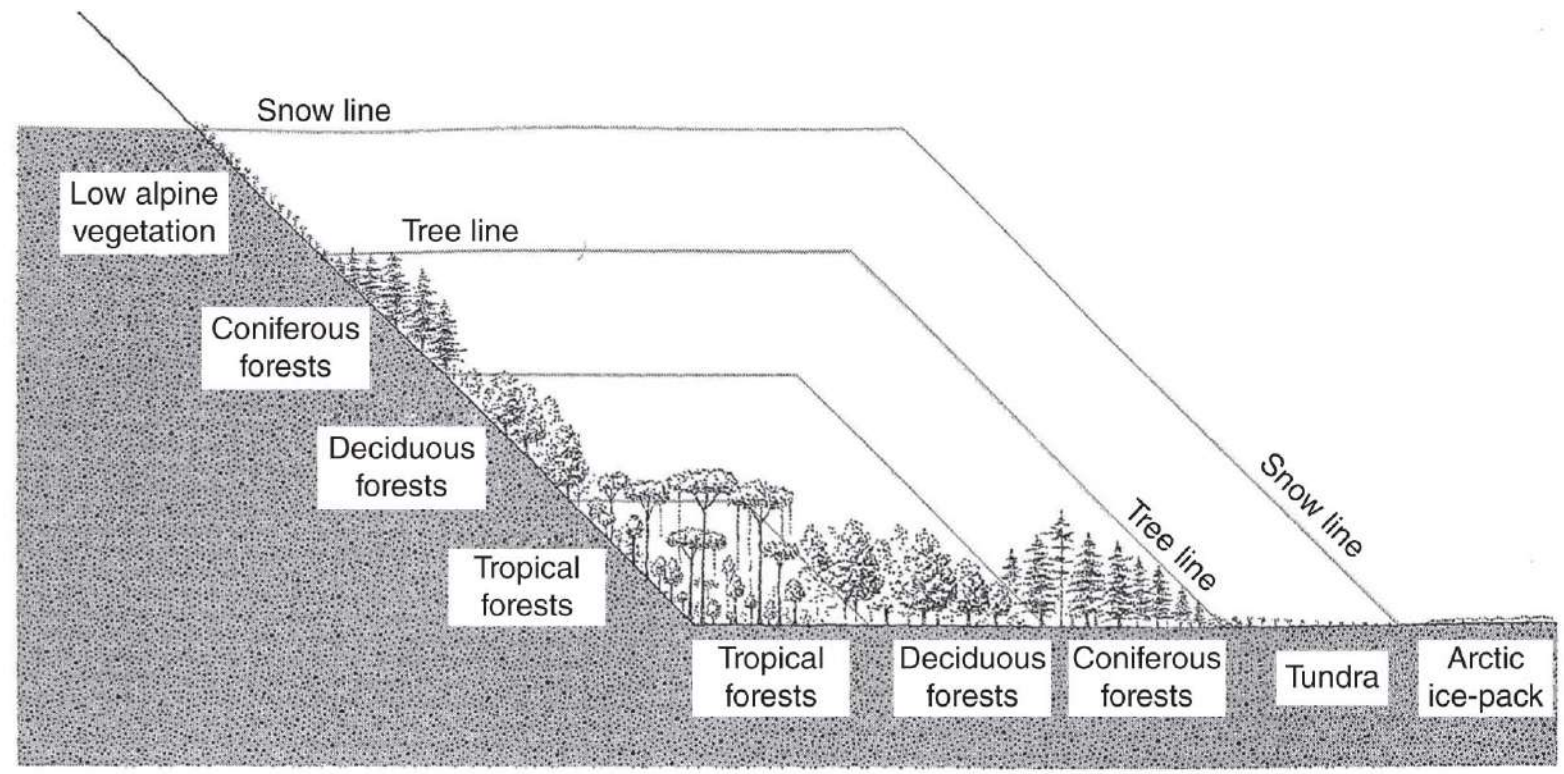


Figure 4.2 Examples of regional and altitudinal gradients of vegetation zones in North America. The south–north gradient (right side of diagram, horizontal line) primarily reflects gradually cooling temperature regimes that extend from the hot tropics (low latitudes) to the frigid arctic (high latitudes). 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

Biomes and Soils connectivity

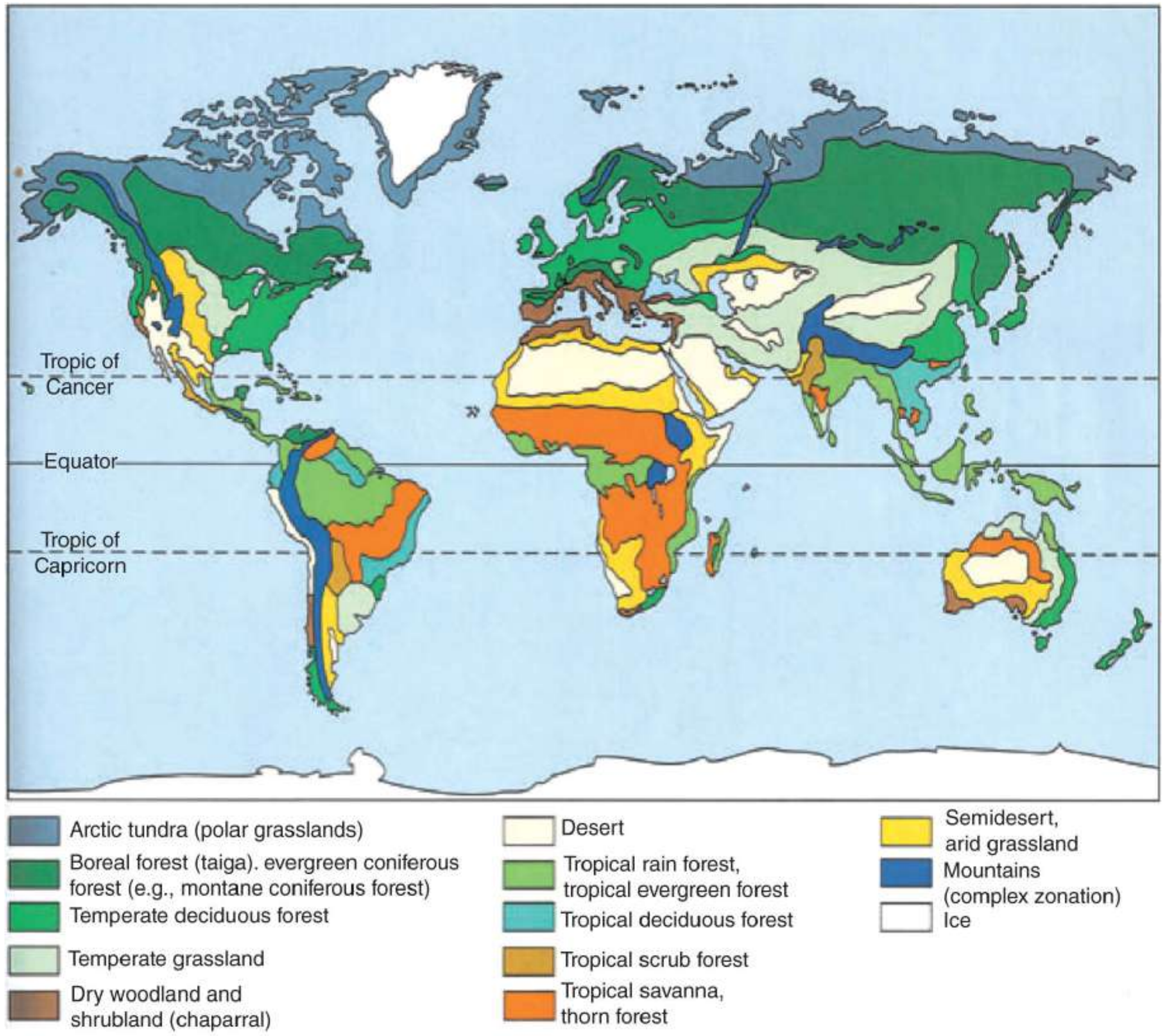


Figure 4.1 Global map of terrestrial biomes. (Republished with permission of Brooks/Cole, a division of Thomson Learning. From Miller, G.T. 2004. *Living in the Environment*, 13th edn. Permission conveyed through Copyright Clearance Center, Inc.)

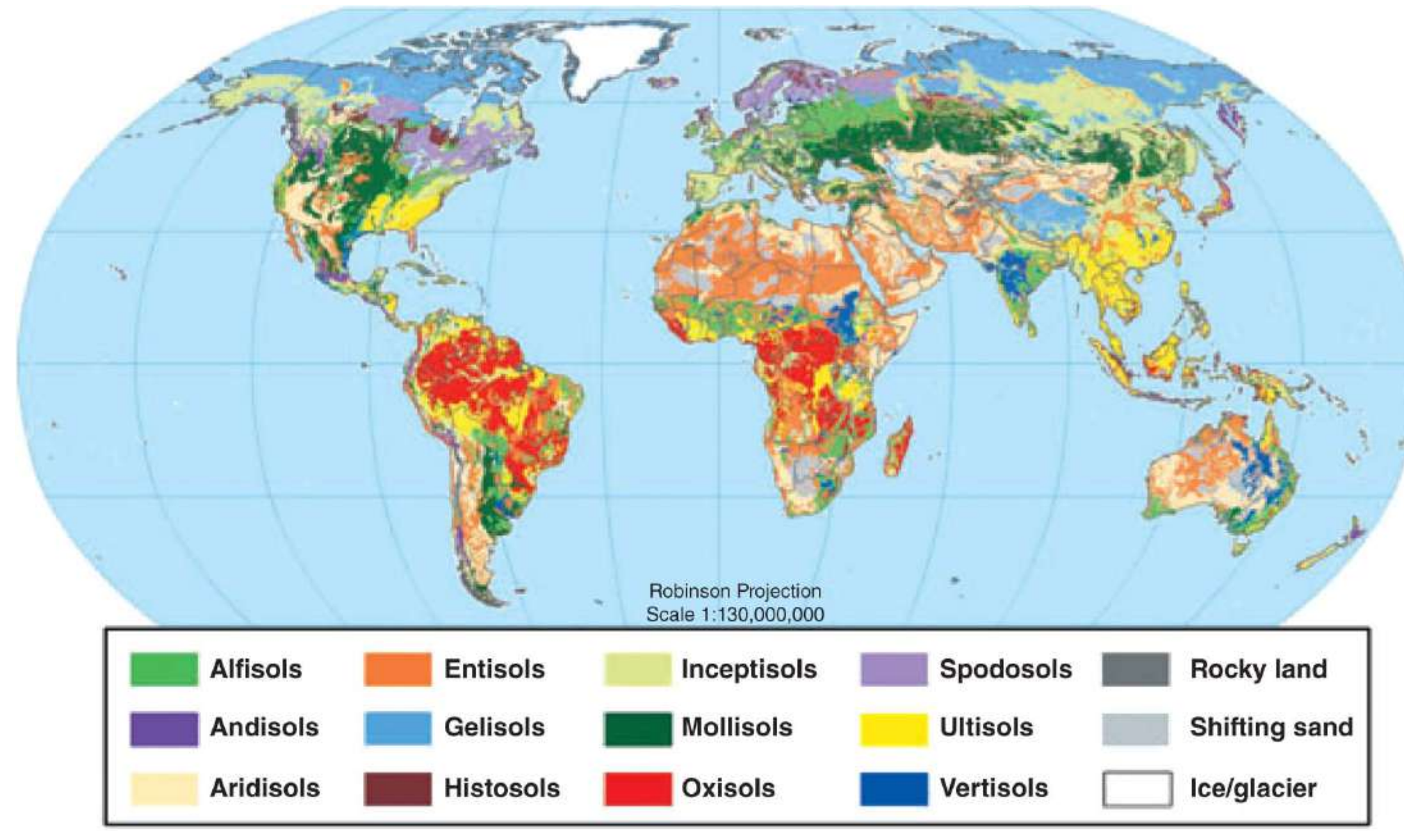


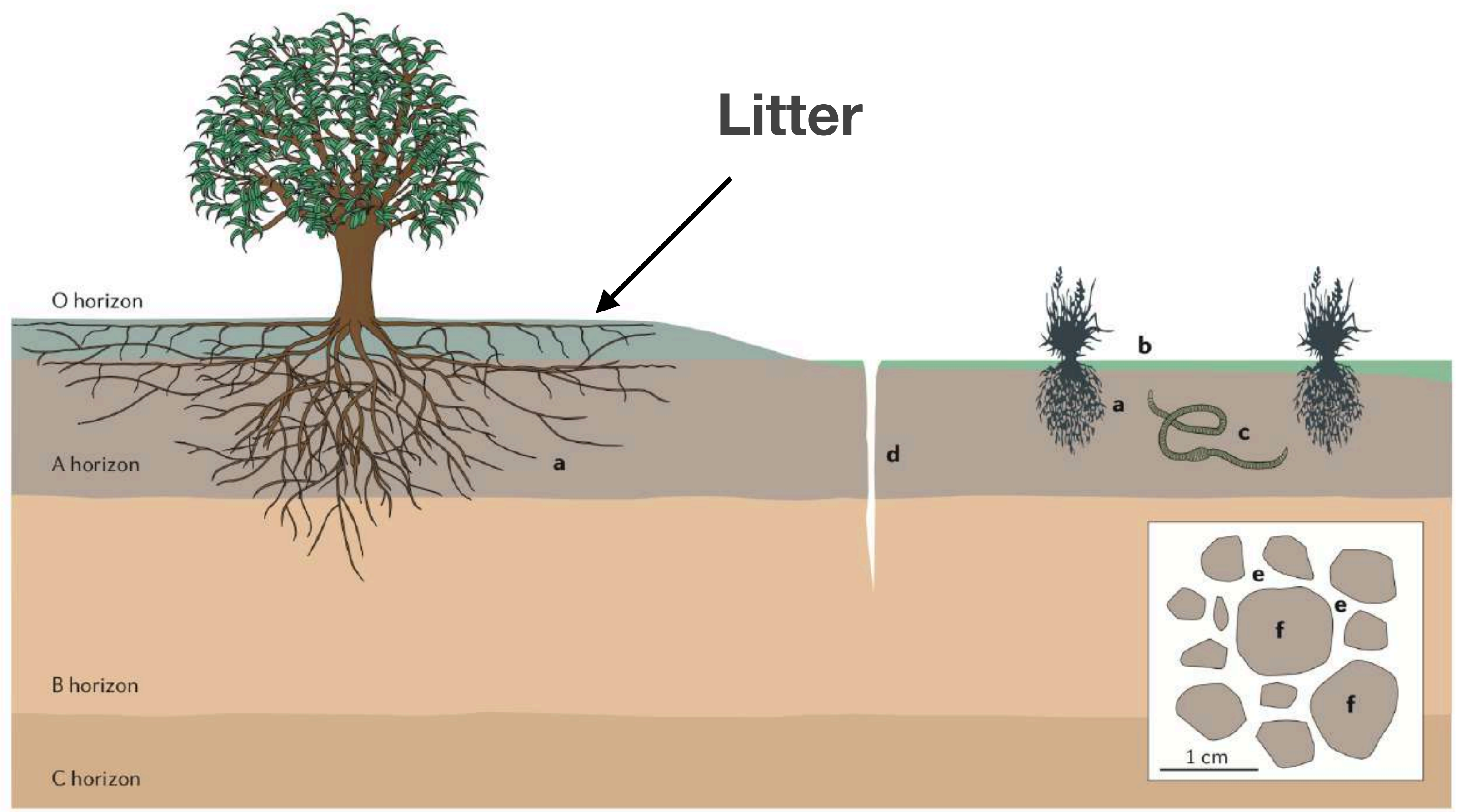
Figure 4.4 Distribution of 12 major soil orders throughout the world. (Reprinted with permission from USDA Natural Resources Conservation Service, Soil Survey Division, World Soil Resources, Washington, DC.)

Madsen, 2016

- 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)

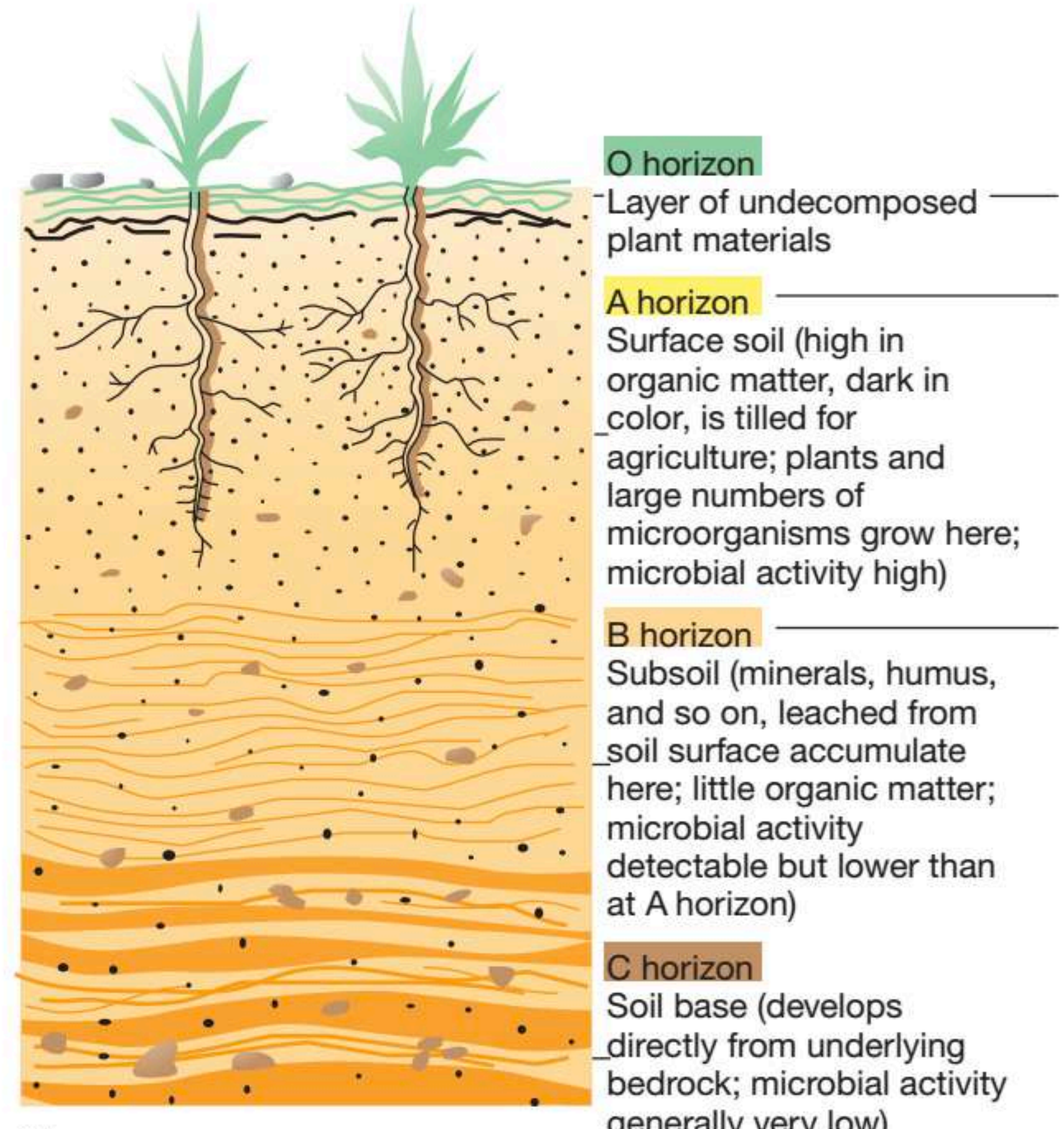
  b. Surface layers that are exposed to light (the photic zone)

  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)



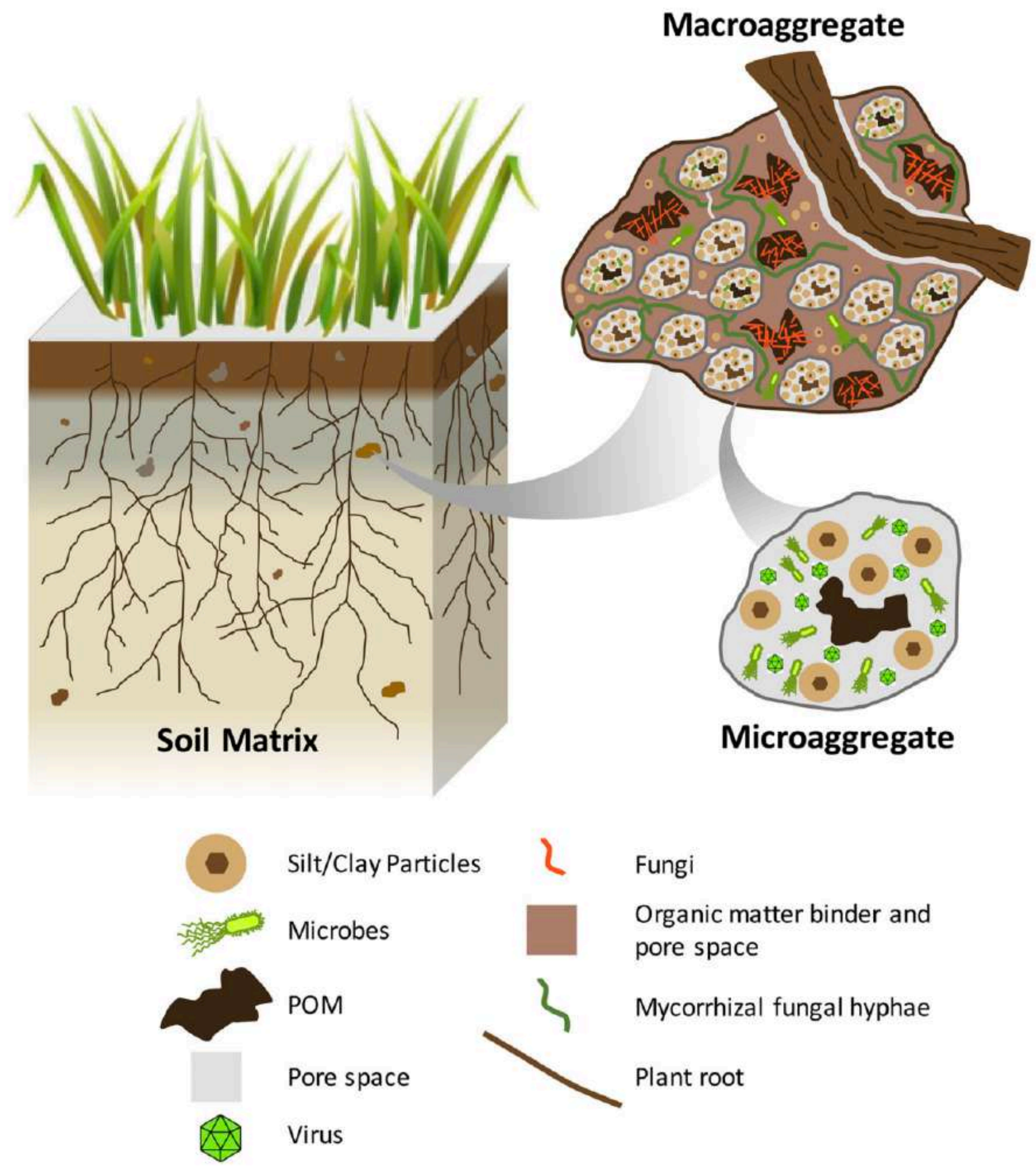
(a)

Madigan et al. 2018

- 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**

Soil ecosystem structure

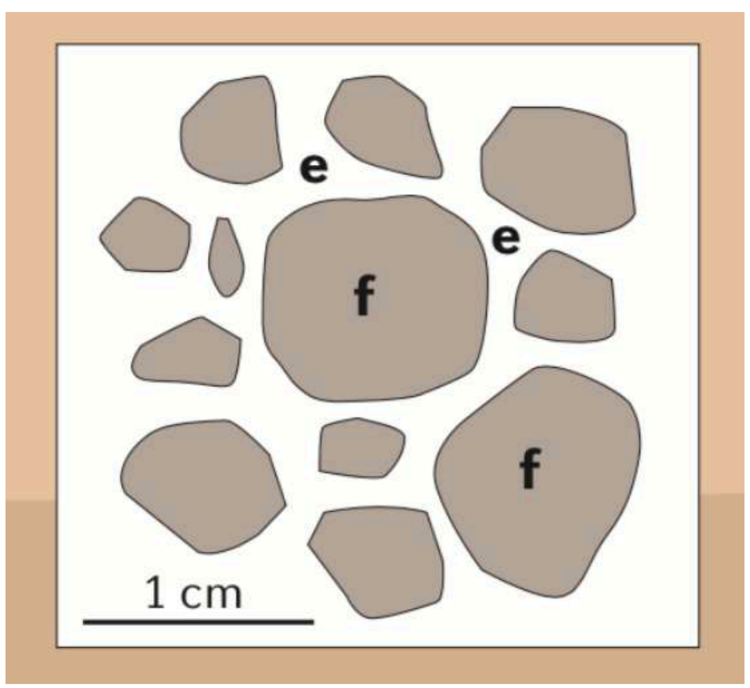
- Soils are primarily composed of **microaggregates** (<250 µm), which bind soil organic carbon and protect it from removal by erosion
- **Macroaggregates** (0.25 to 2 mm), which limit oxygen diffusion and regulate water flow
- These length scales are particularly important in **shaping microbial interactions 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

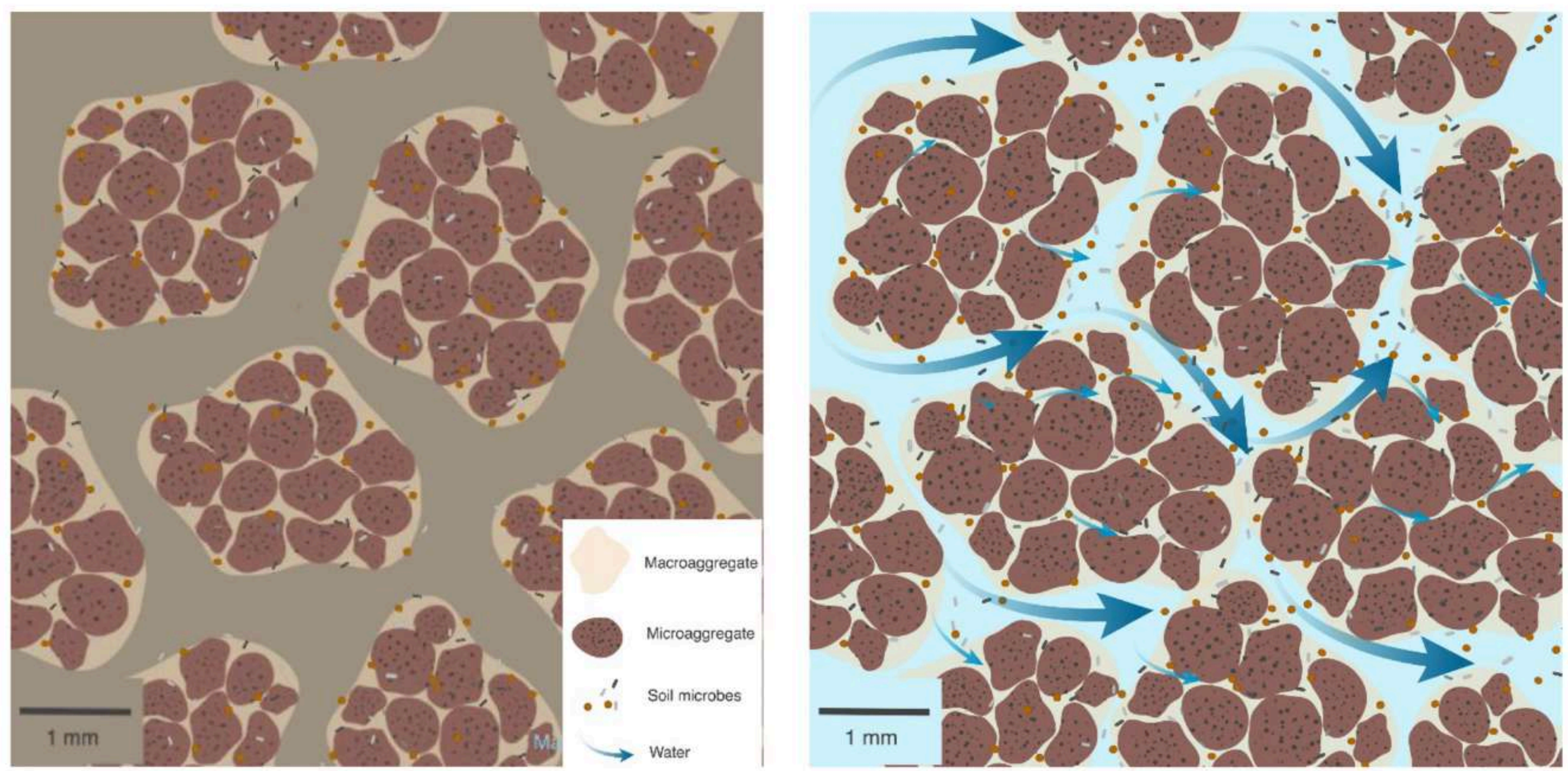
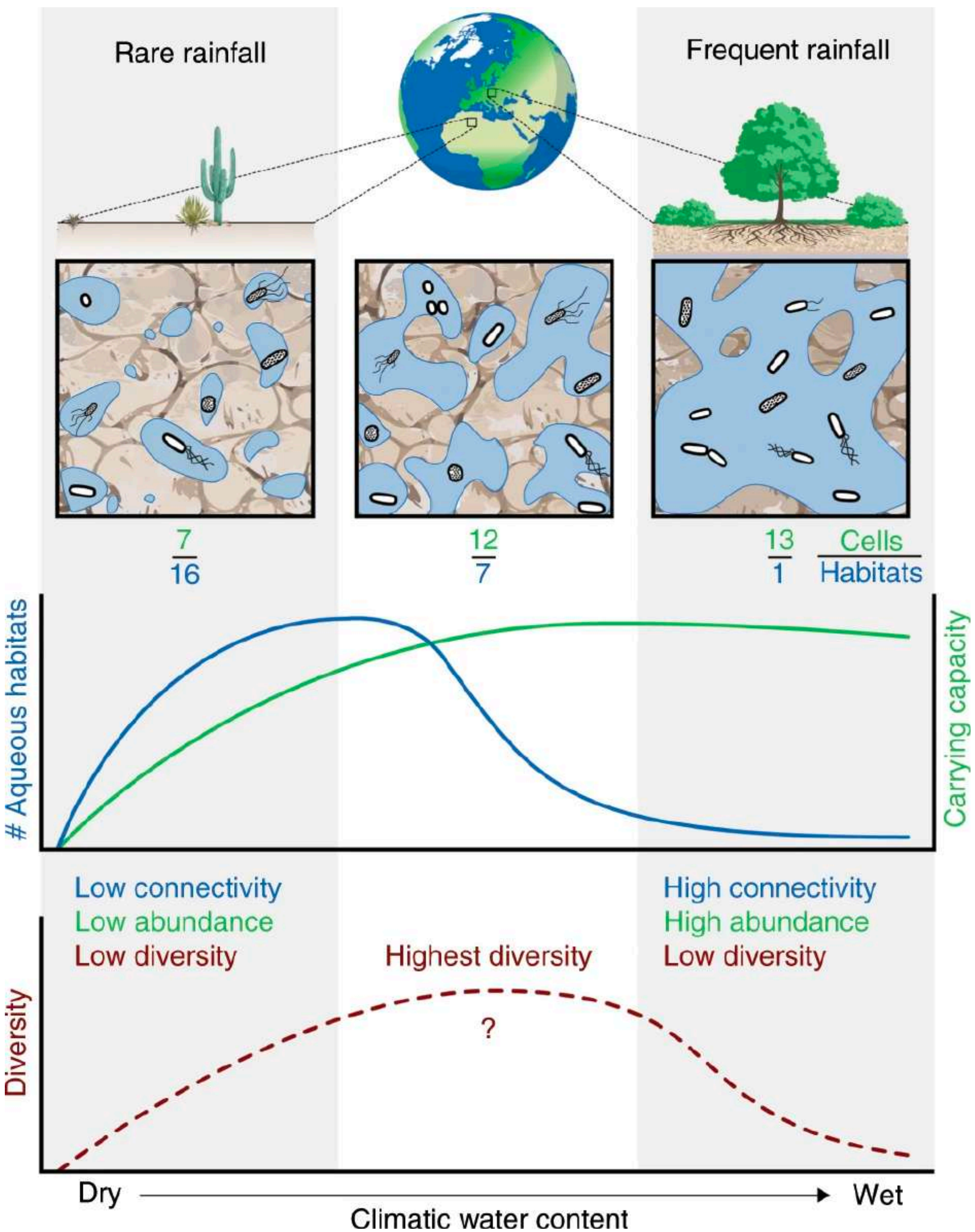


FIG 2 Conceptual drawing of isolated micro- and macroaggregates during (left) dry conditions and (right) wet conditions. Wet conditions would allow for nutritional, microbial, viral and metabolite dispersal.

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

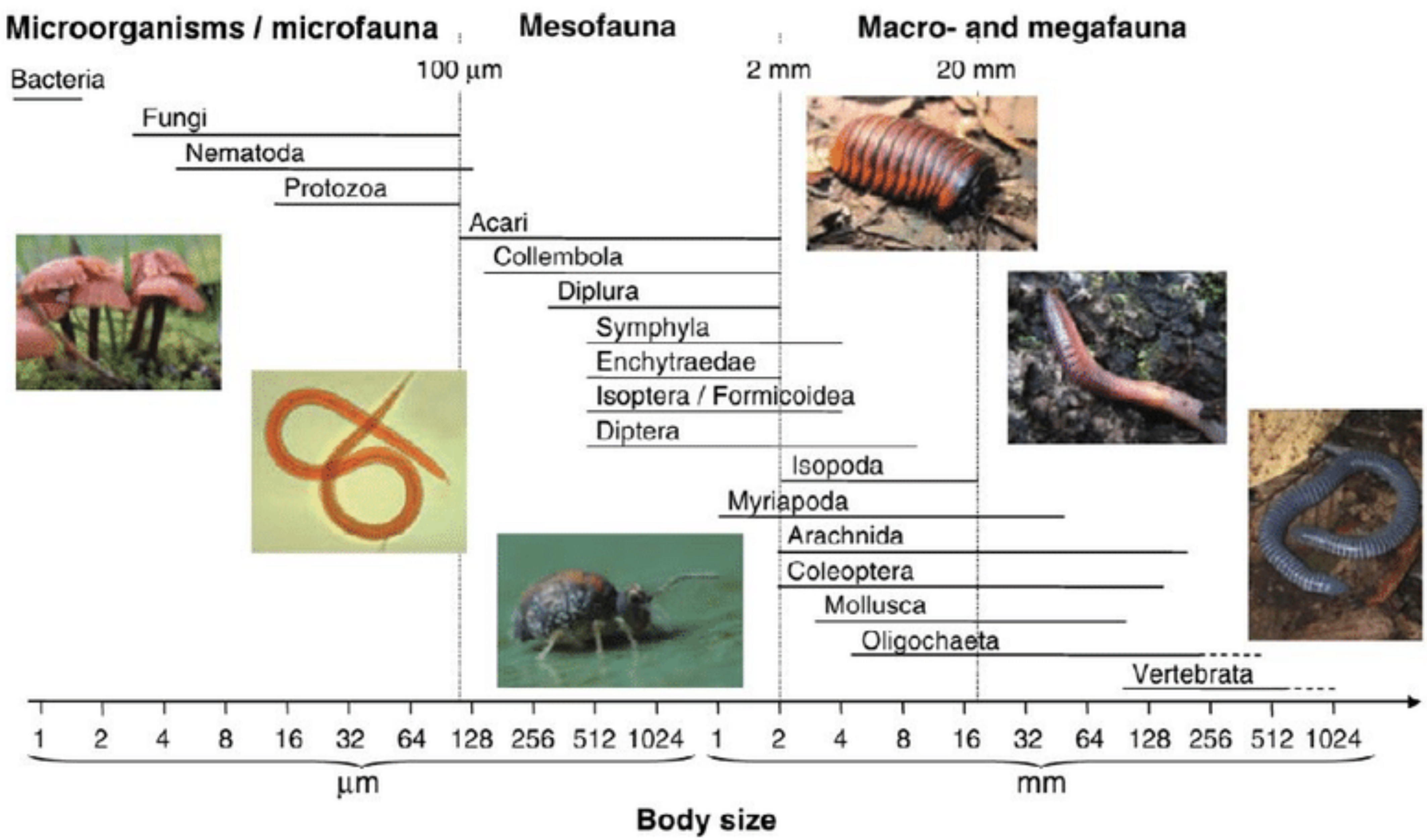
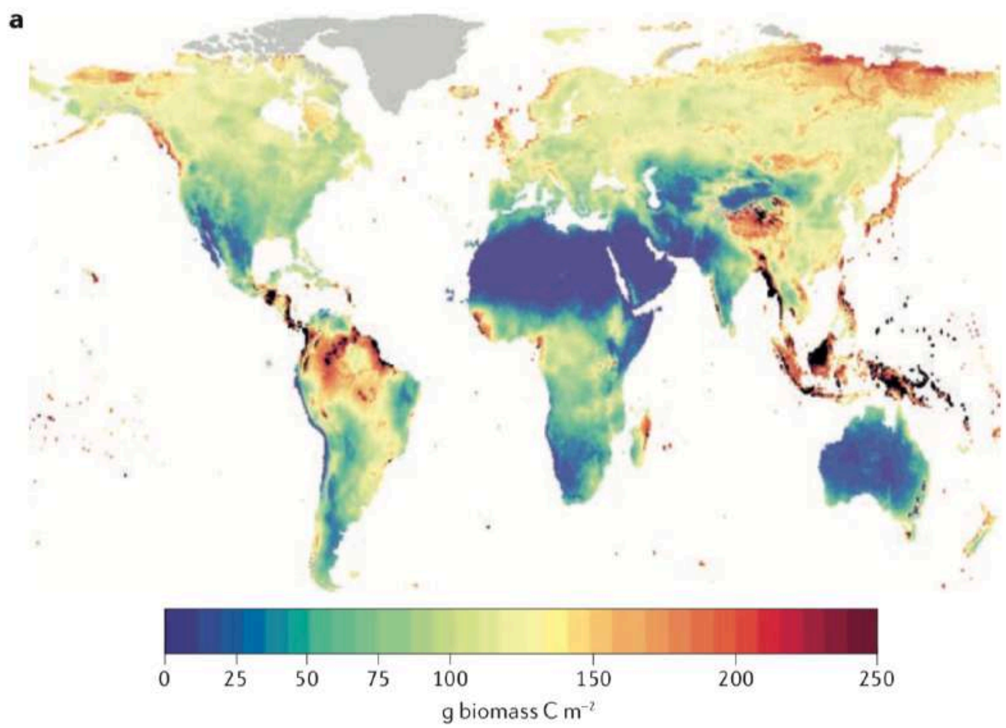
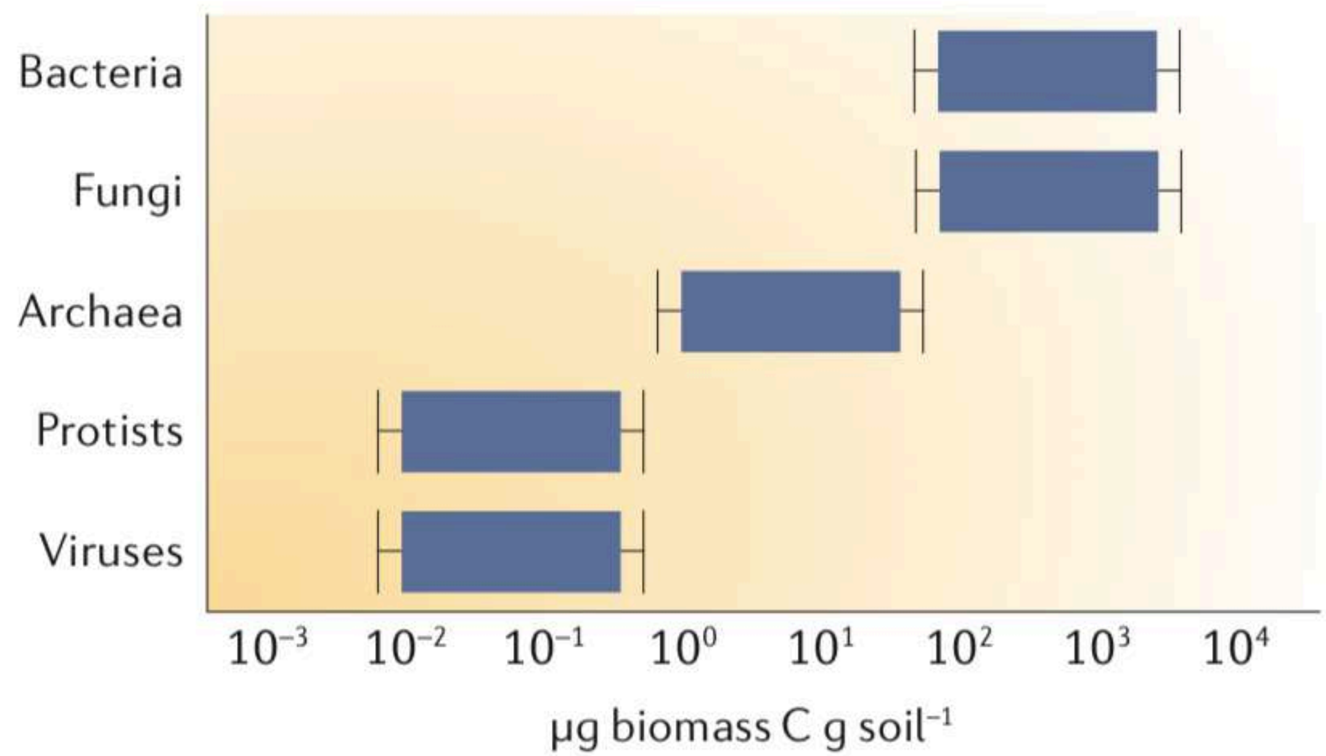


Figure 1: Representation of the main taxonomic groups of soil organisms on a body-width basis (Reprinted with permission from John Wiley and Sons after Swift et al., 1979) from Decaens (2010) and Barrios (2007) (all photo credits: Flickr, http://www.flickr.com/)

Soil microbial biomass





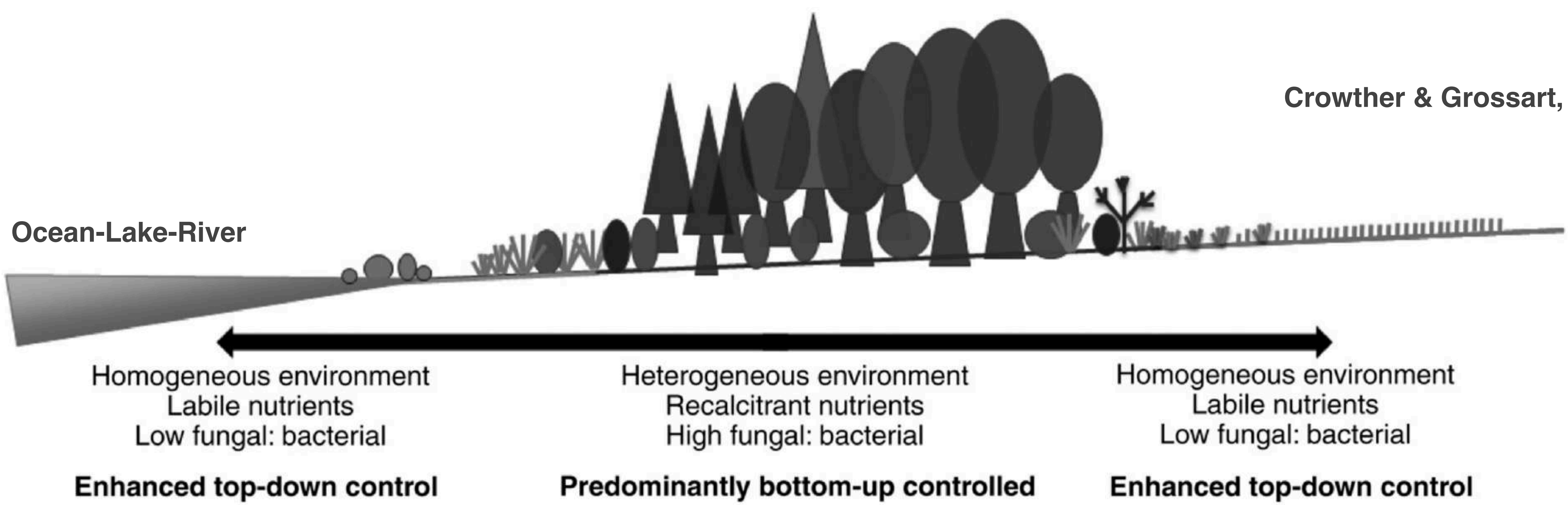
Fierer, 2017

- 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

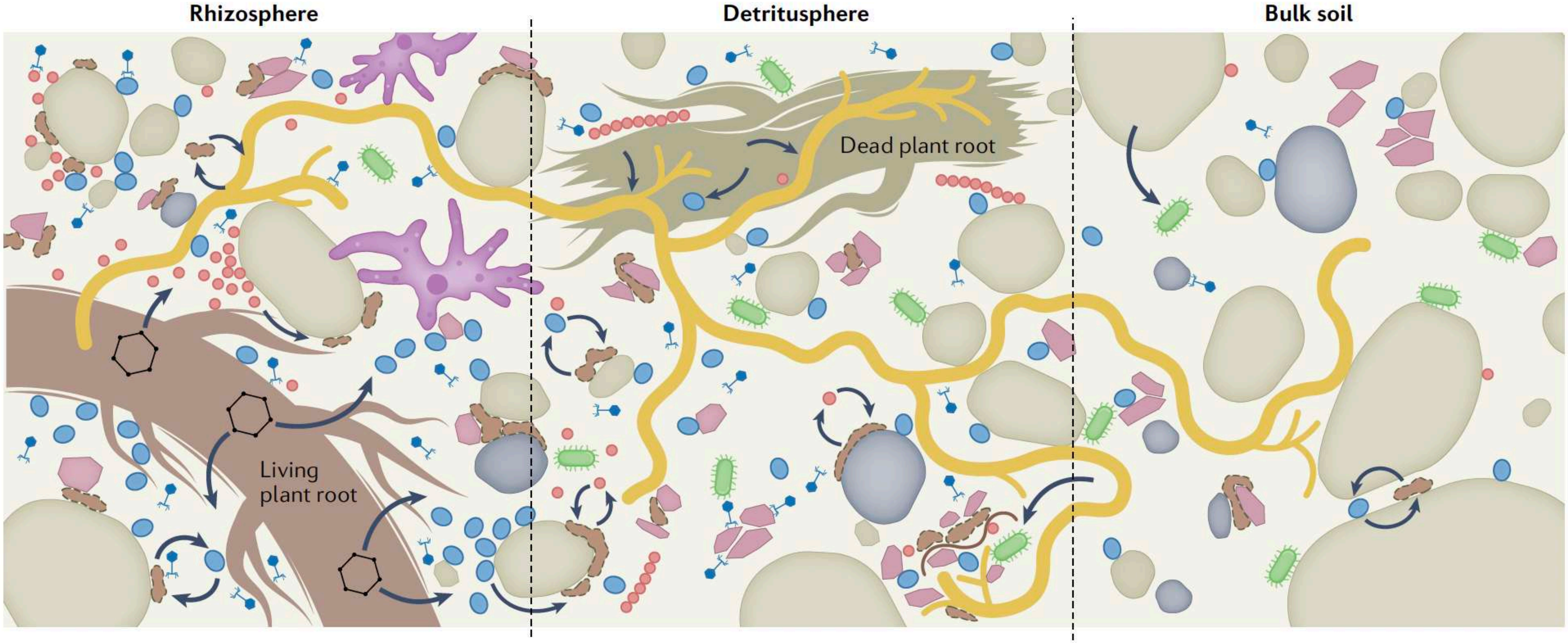
Soil microbial communities

- **< 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



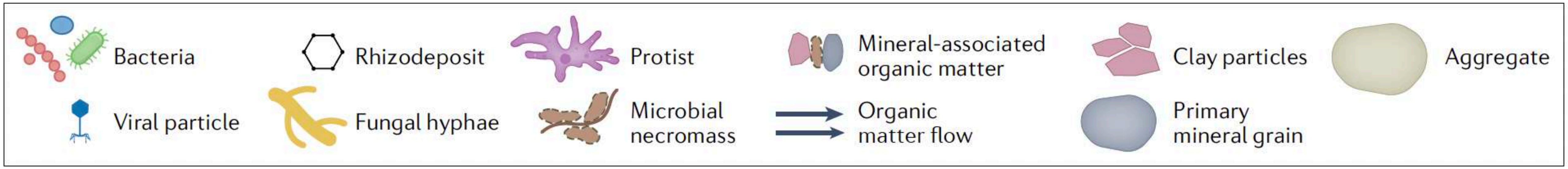
Soil microbiome



- 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

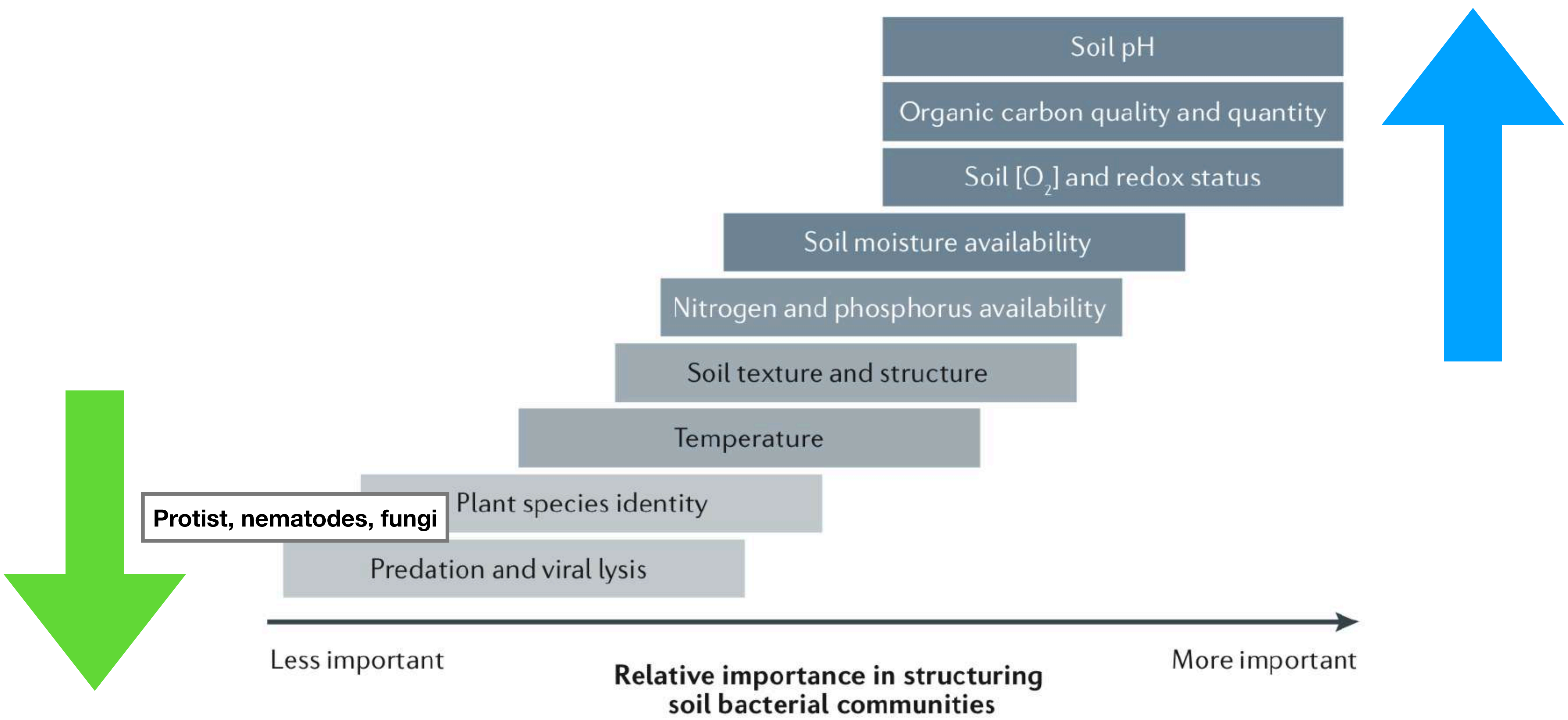
- Lower microbial biomass and activity
- Higher microbial diversity
- Slower biomass turnover and rates of organic matter flow



Sokol, 2022

Soil: Top-down & Bottom-up

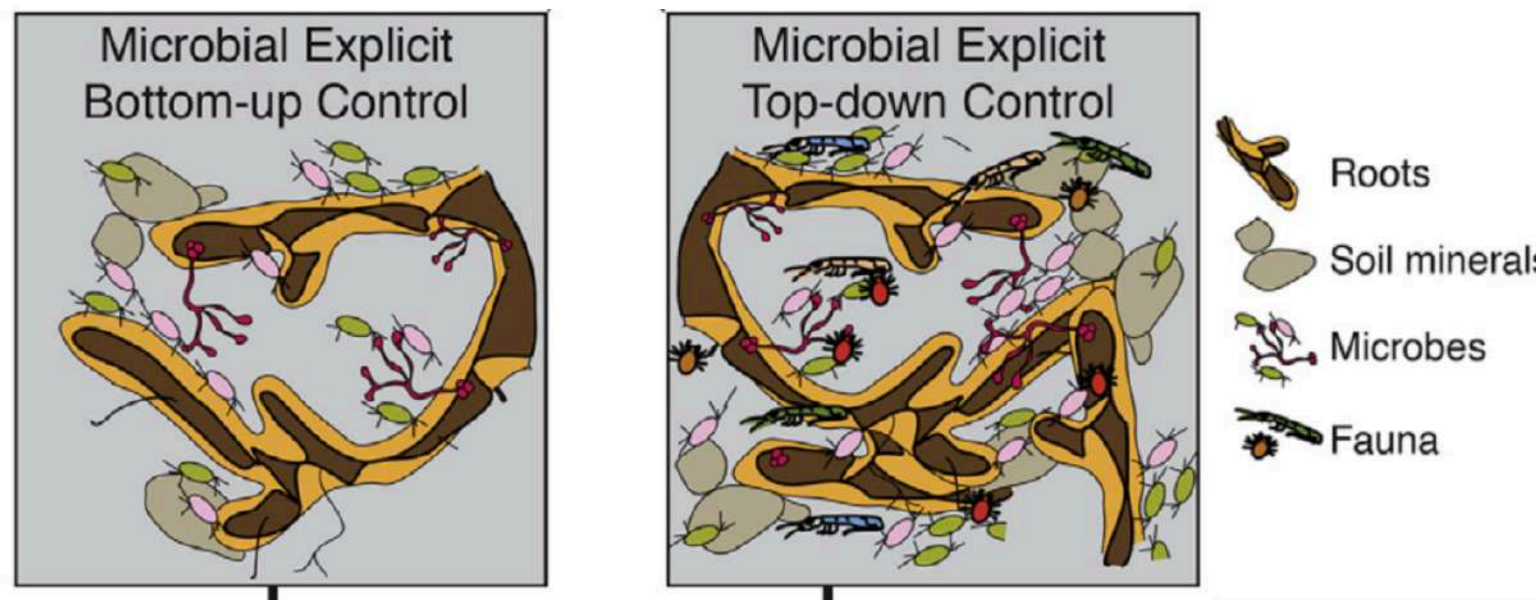
- Biotic and abiotic factors that can **influence** the composition of **soil bacterial** communities
- The shading of each box qualitatively indicates how well we understand the specific effects of each factor on bacterial communities; darker shades highlight factors that have been reasonably well-studied



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

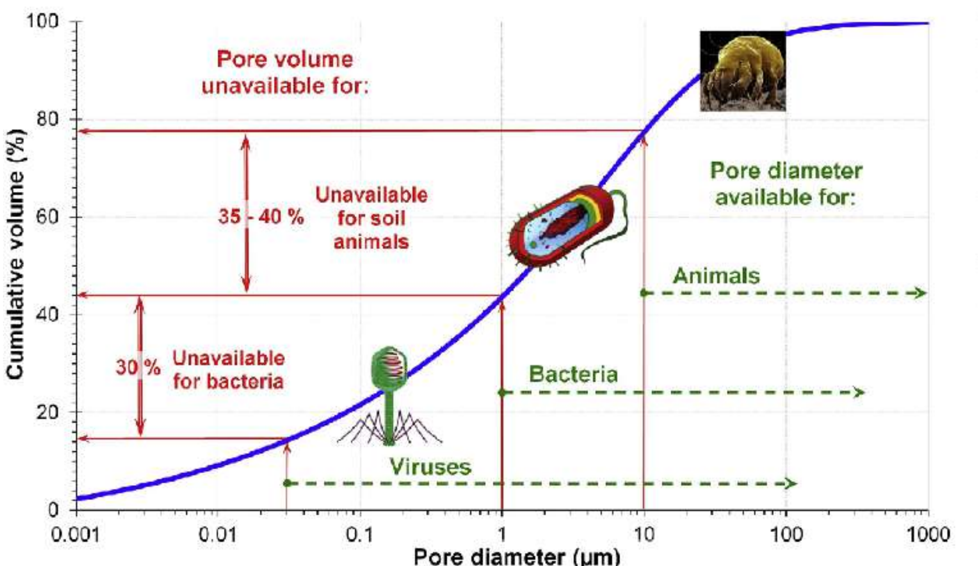
TABLE 1 Length scales relevant for interactions between soil particles and microbes

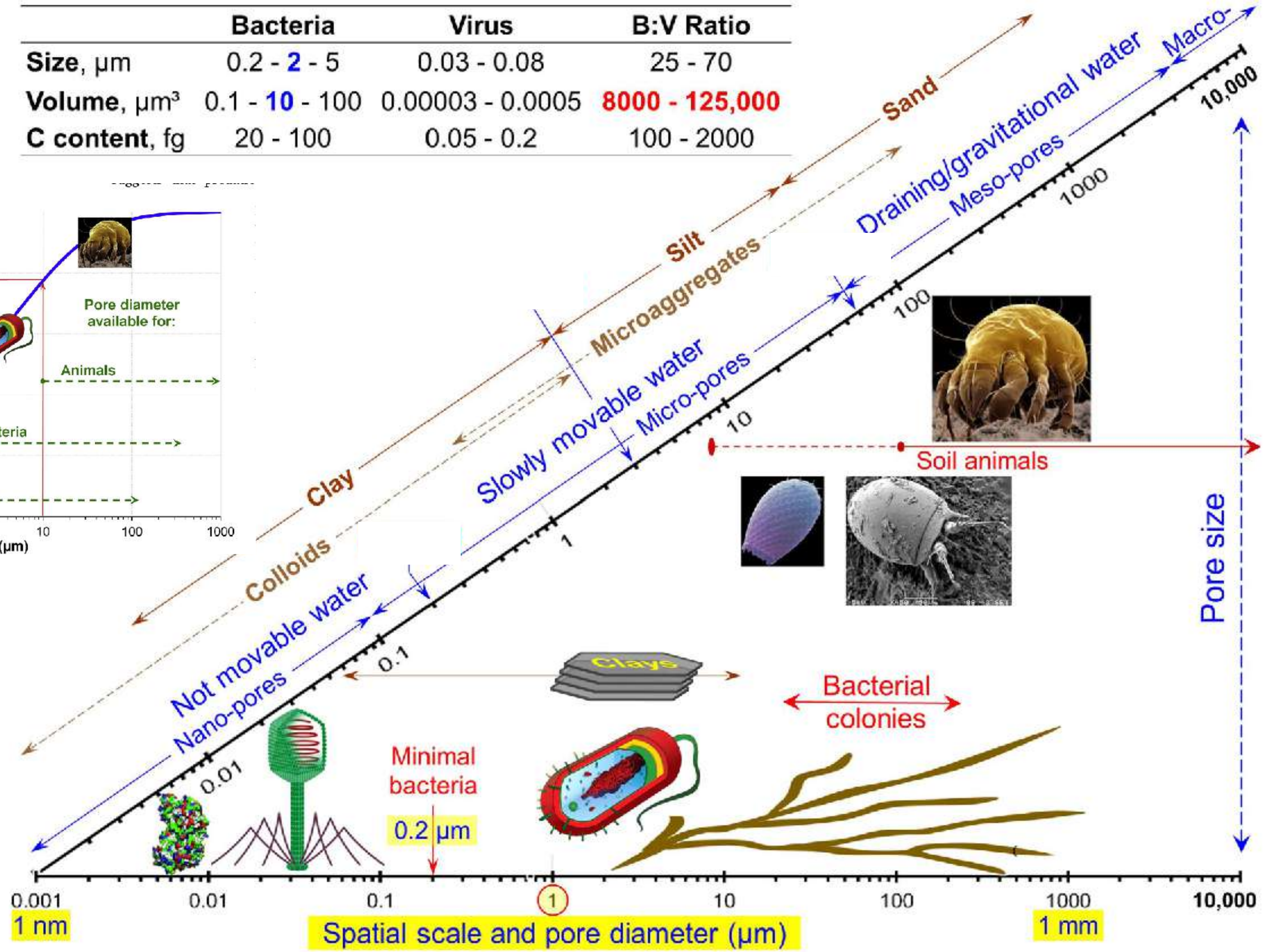
Size (μm)	Biological relevance	Soil relevance	Interaction
<1	Viral particle sizes,[a] *E. coli* cells deform (300 nm)[b]	Particle surface roughness promotes selective adhesion of specific bacterial species (10–100 nm)[c]	Lysogeny and gene transfer,[d] bacterial shape deformation,[b] surface attachment[c]
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

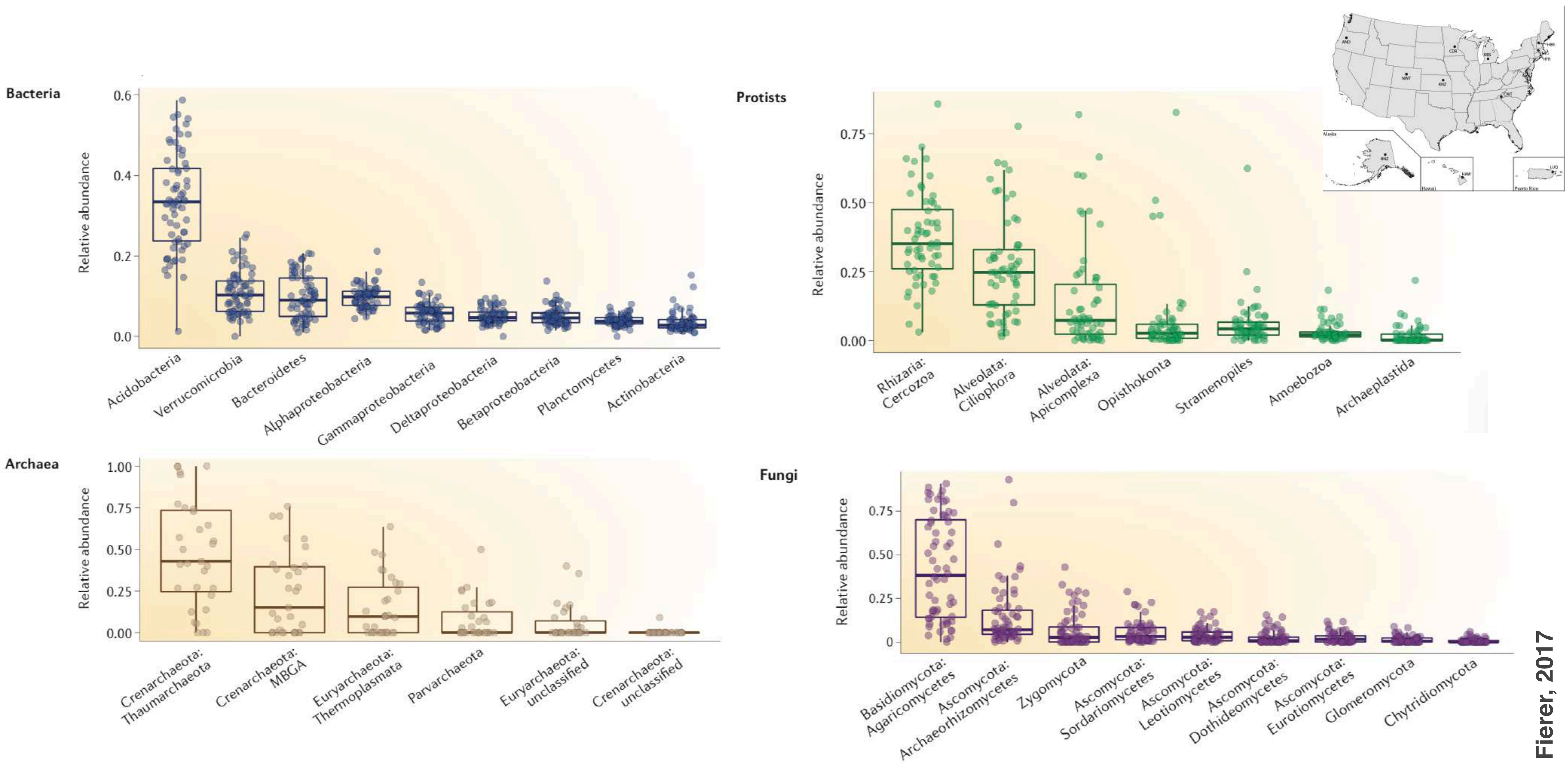




Argilla
Limo
Sabbia

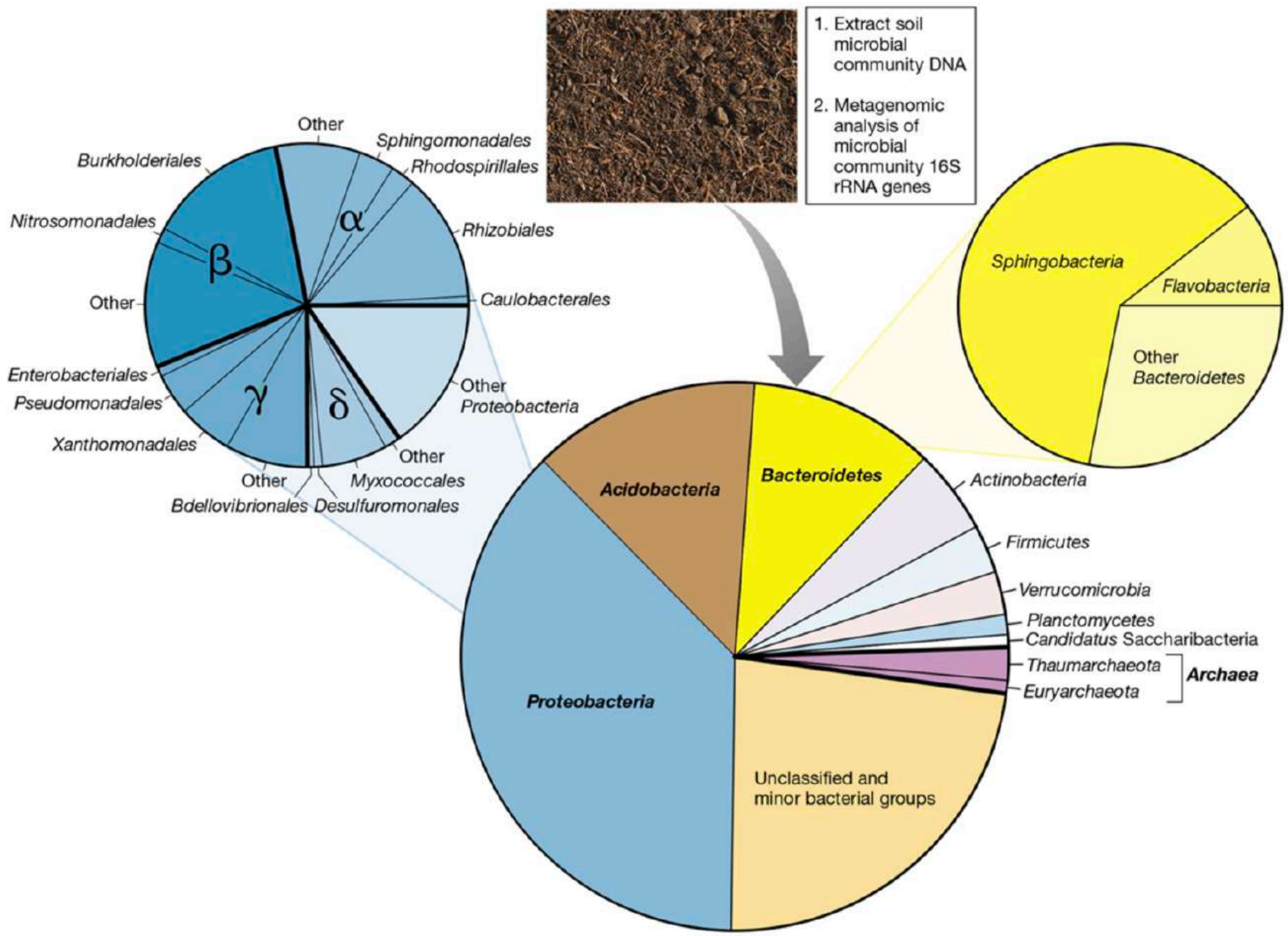
Soil ecosystem structure

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



Fierer, 2017

Soil microbial diversity

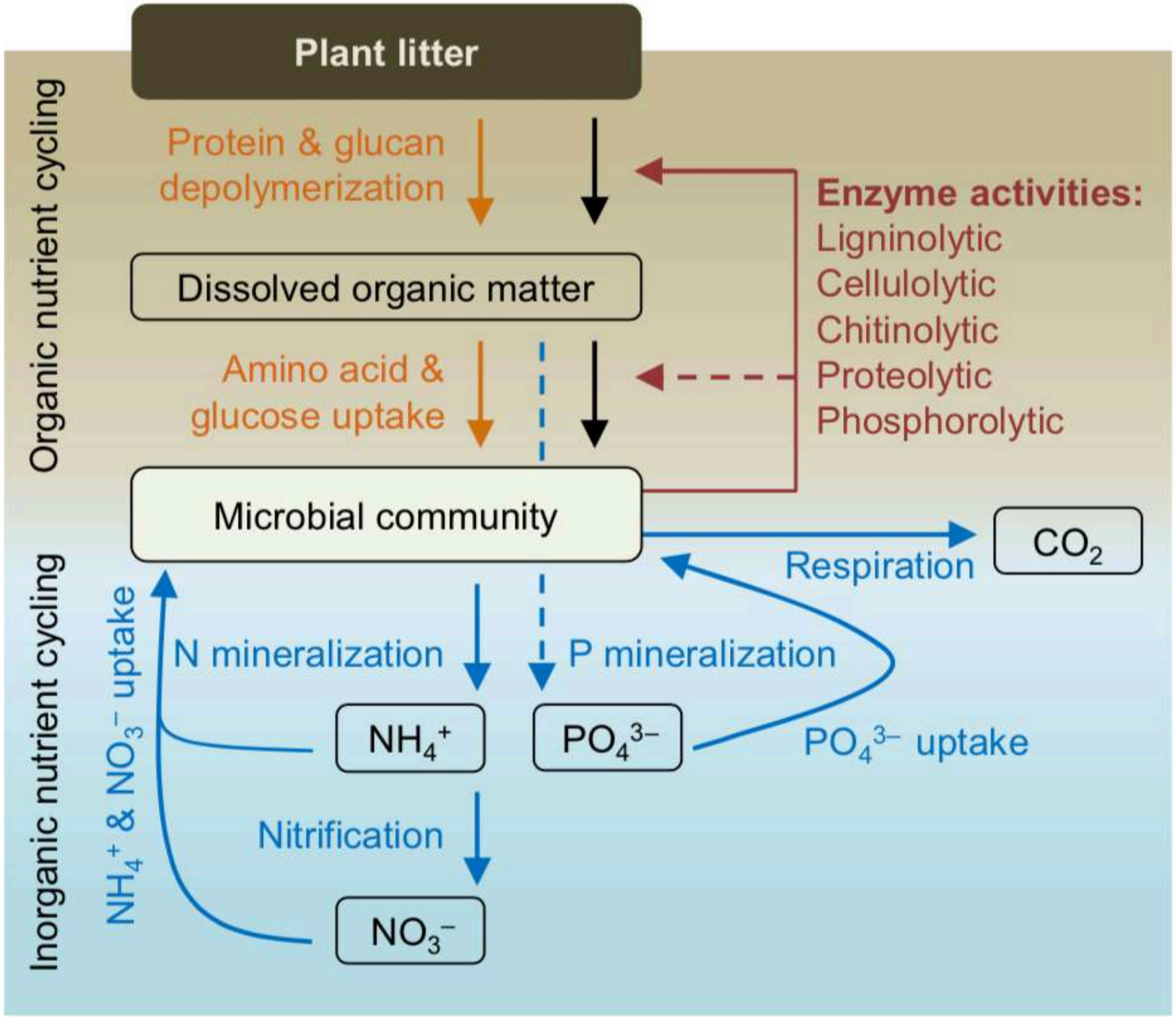


- 16SrRNA gene based diversity

Madigan, 2020

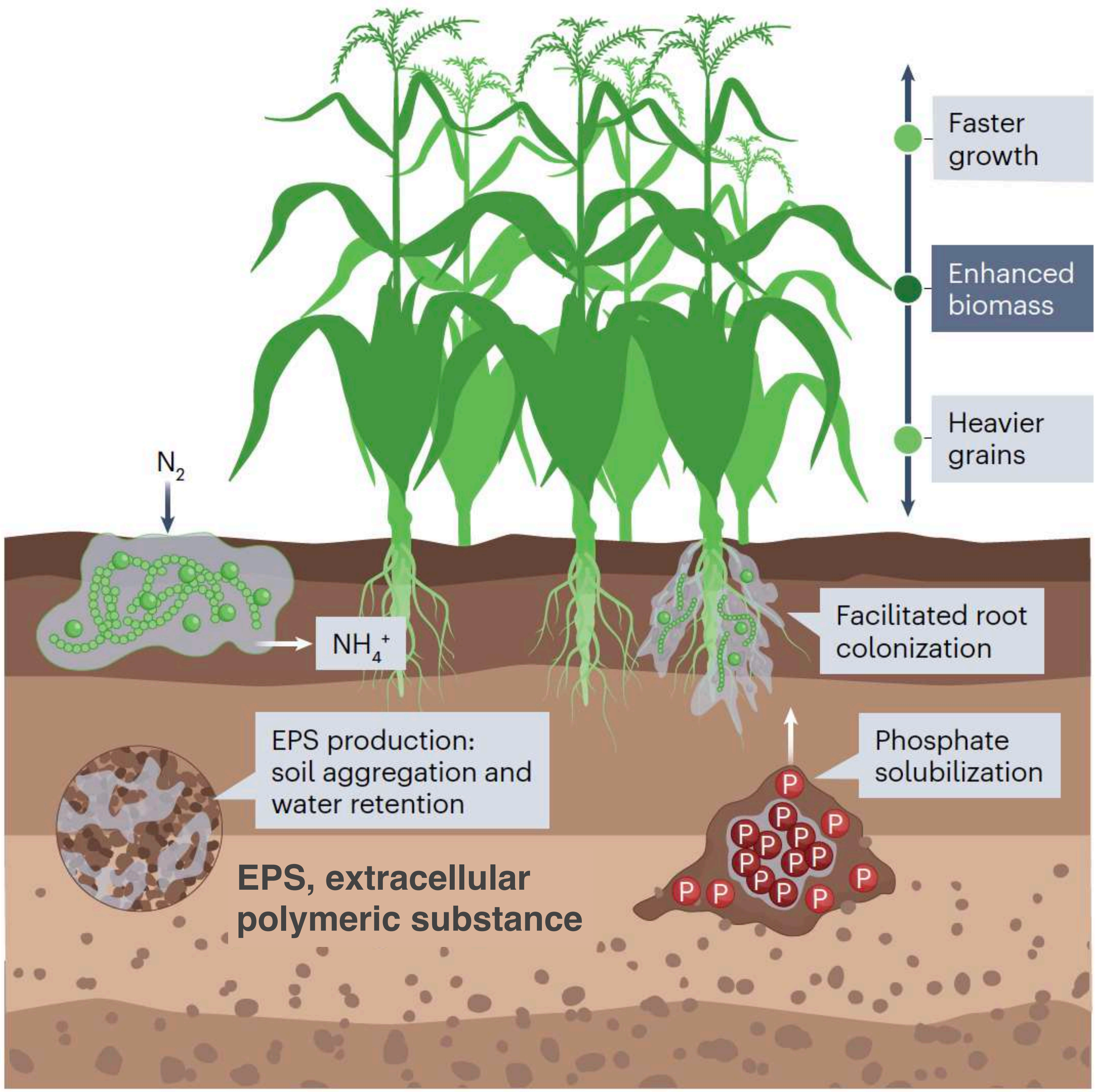
Interconnected inorganic and organic nutrient cycling

- 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

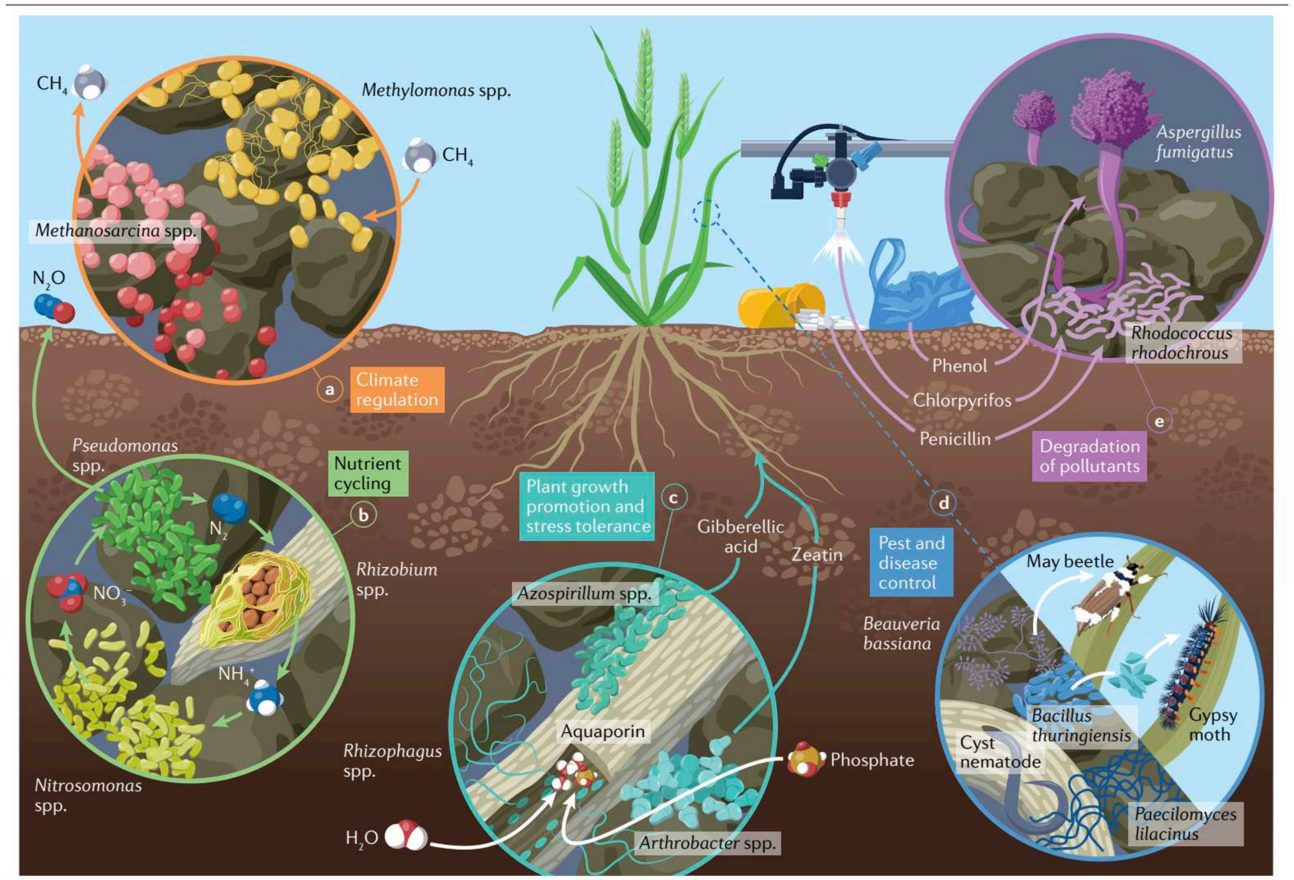
Agroecosystems: sites or integrated regions that support food production while conserving biotic and abiotic resources and providing a balanced supply of ecosystem services

Soil microbiomes drive key functions in agroecosystems:

- determining soil fertility
- crop productivity
- stress tolerance

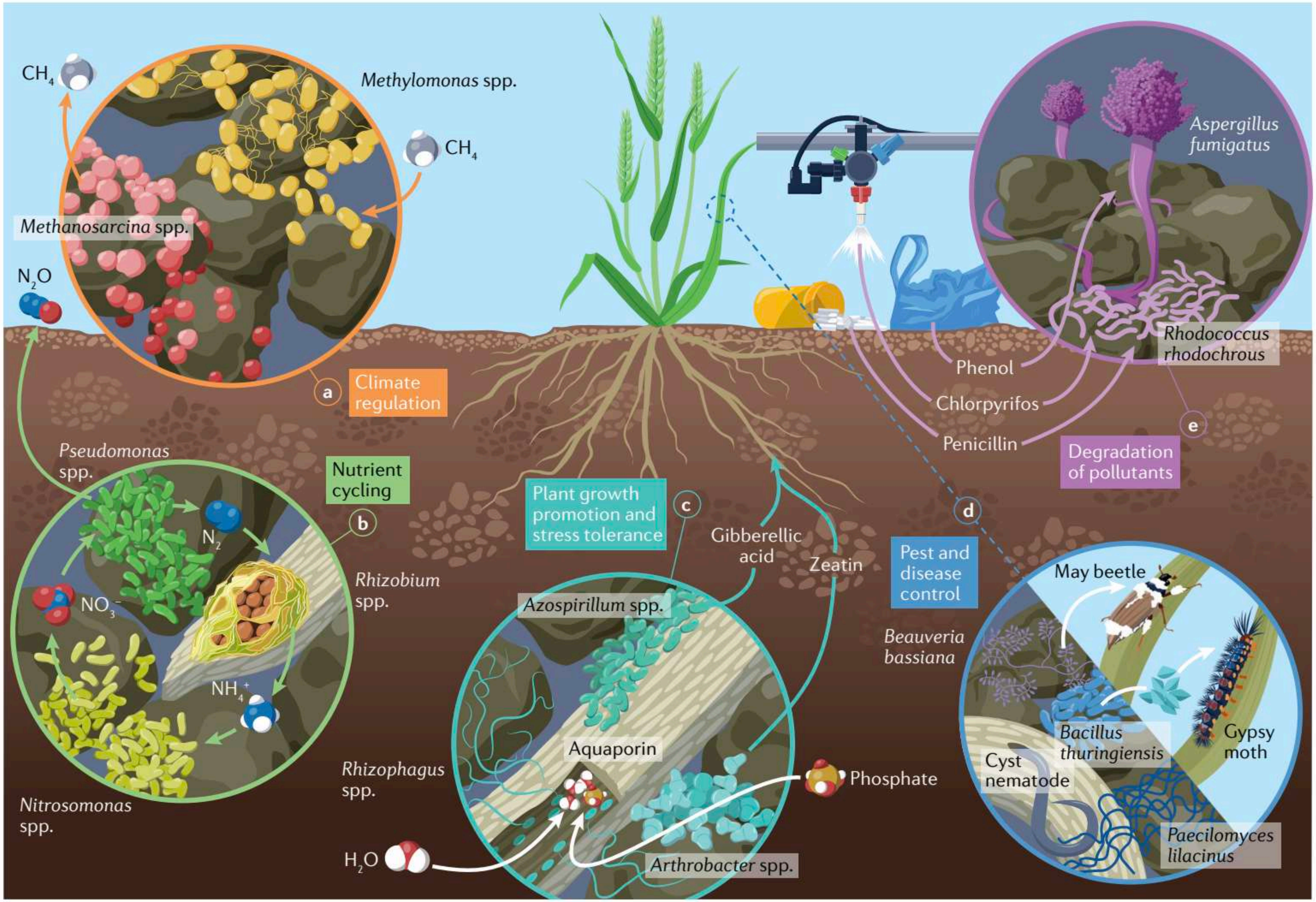
The microbiome is intricately linked with soil structure, such as aggregation and pore connectivity, because this structure regulates through the system:

- flow of water
- oxygen
- nutrients



Hartman and Six, 2023

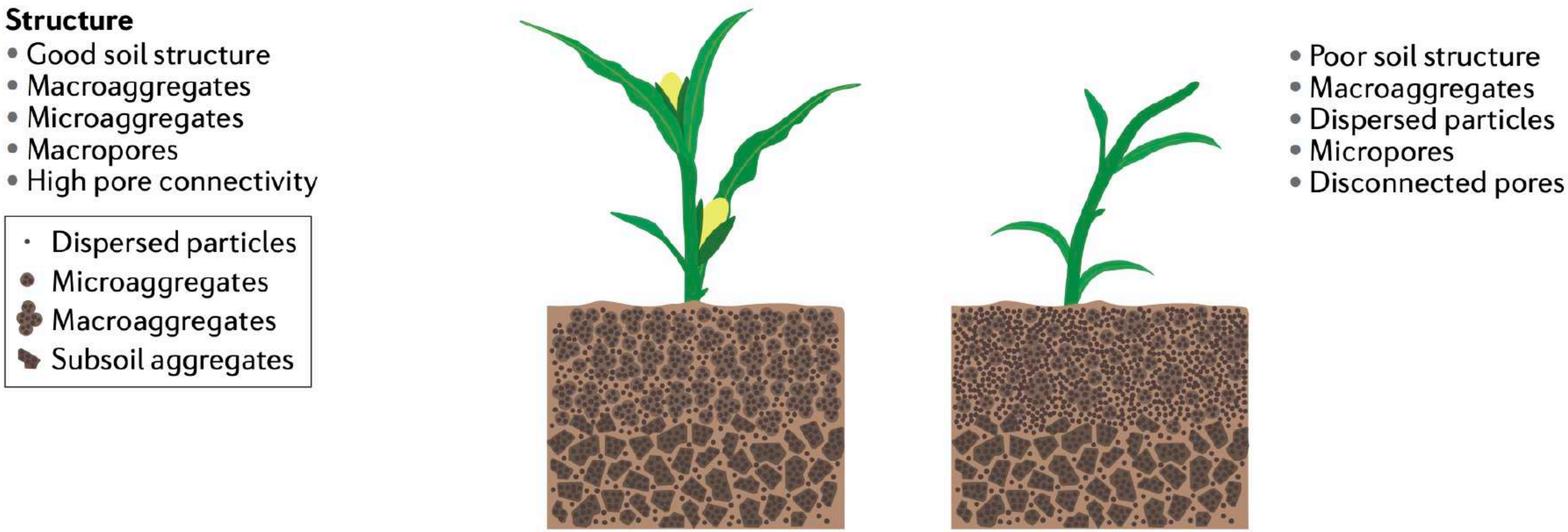
Microbial key functions in the plant–soil system



Hartman and Six, 2023

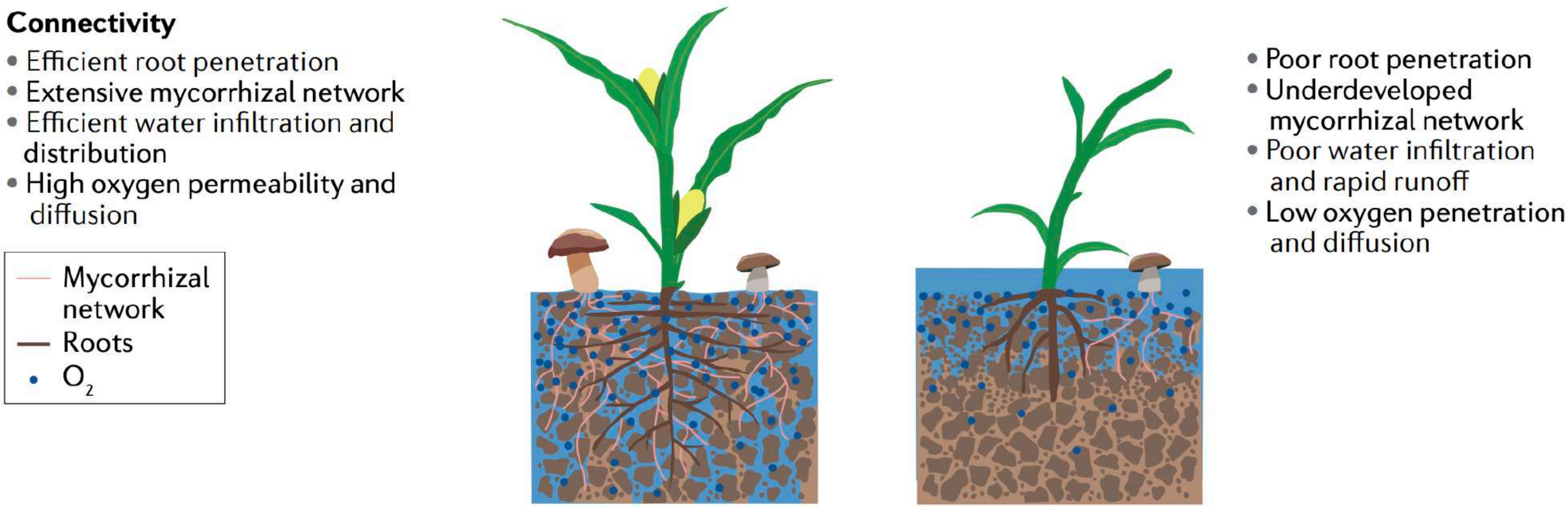
a, Climate regulation. b, Microbial nutrient cycling. c, Plant growth promotion and abiotic stress tolerance. d, Pest and disease control. e, Toxin and pollutant degradation

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



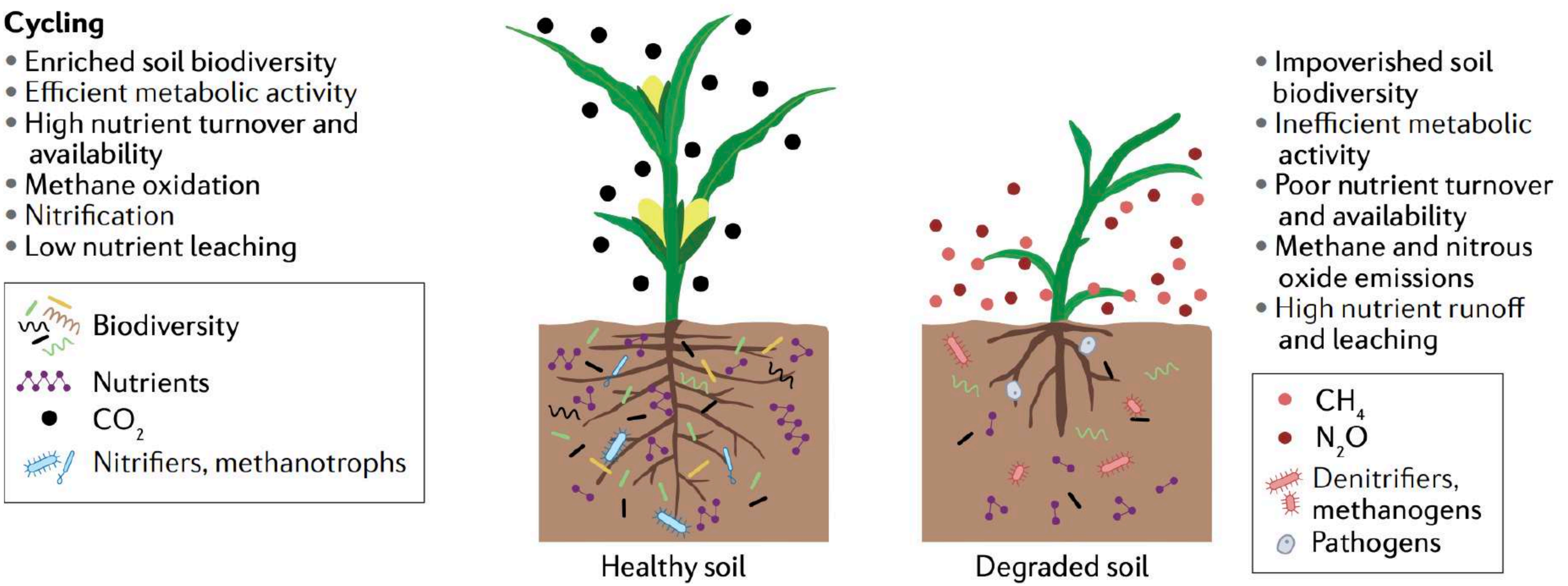
Hartman and Six, 2023

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



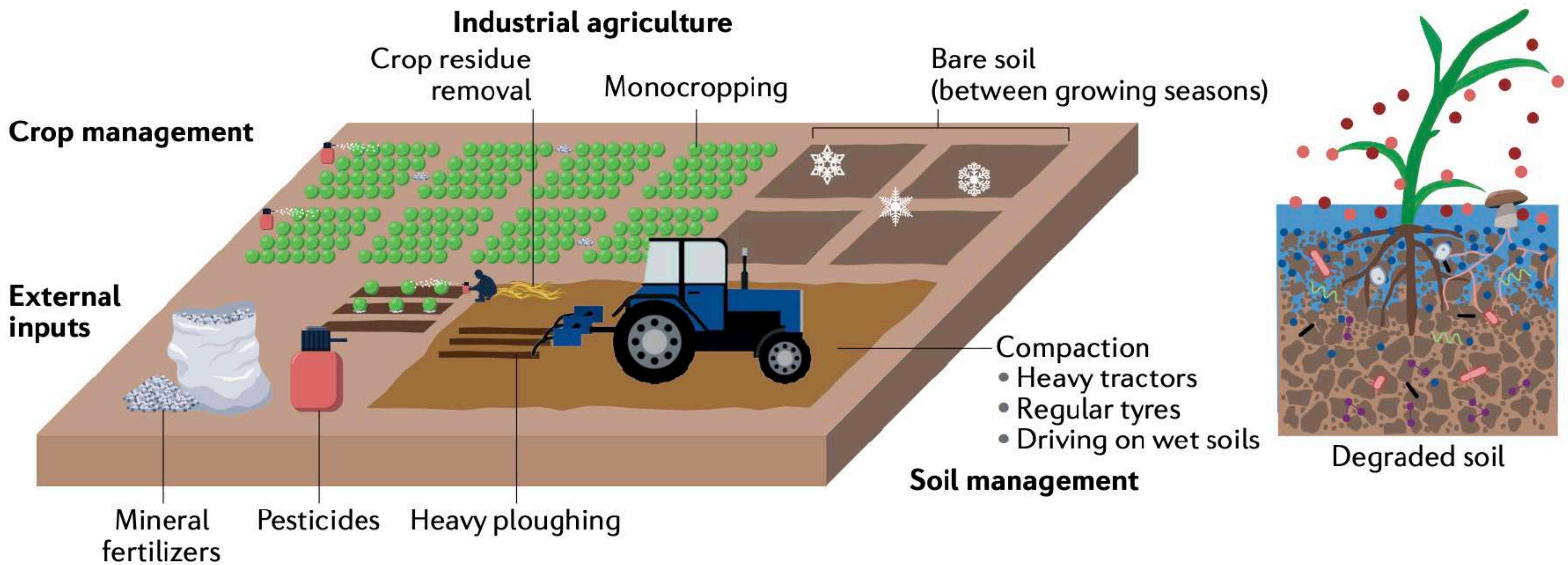
Hartman and Six, 2023

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



Hartman and Six, 2023

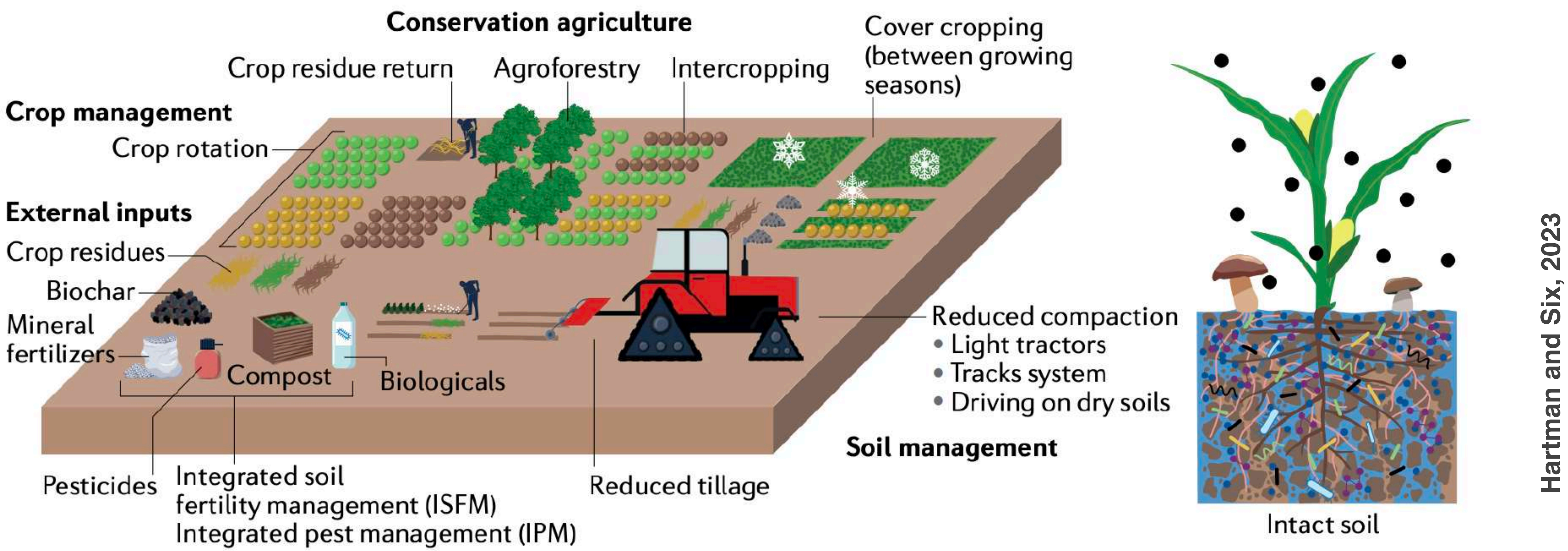
INDUSTRIAL AGRICULTURE



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

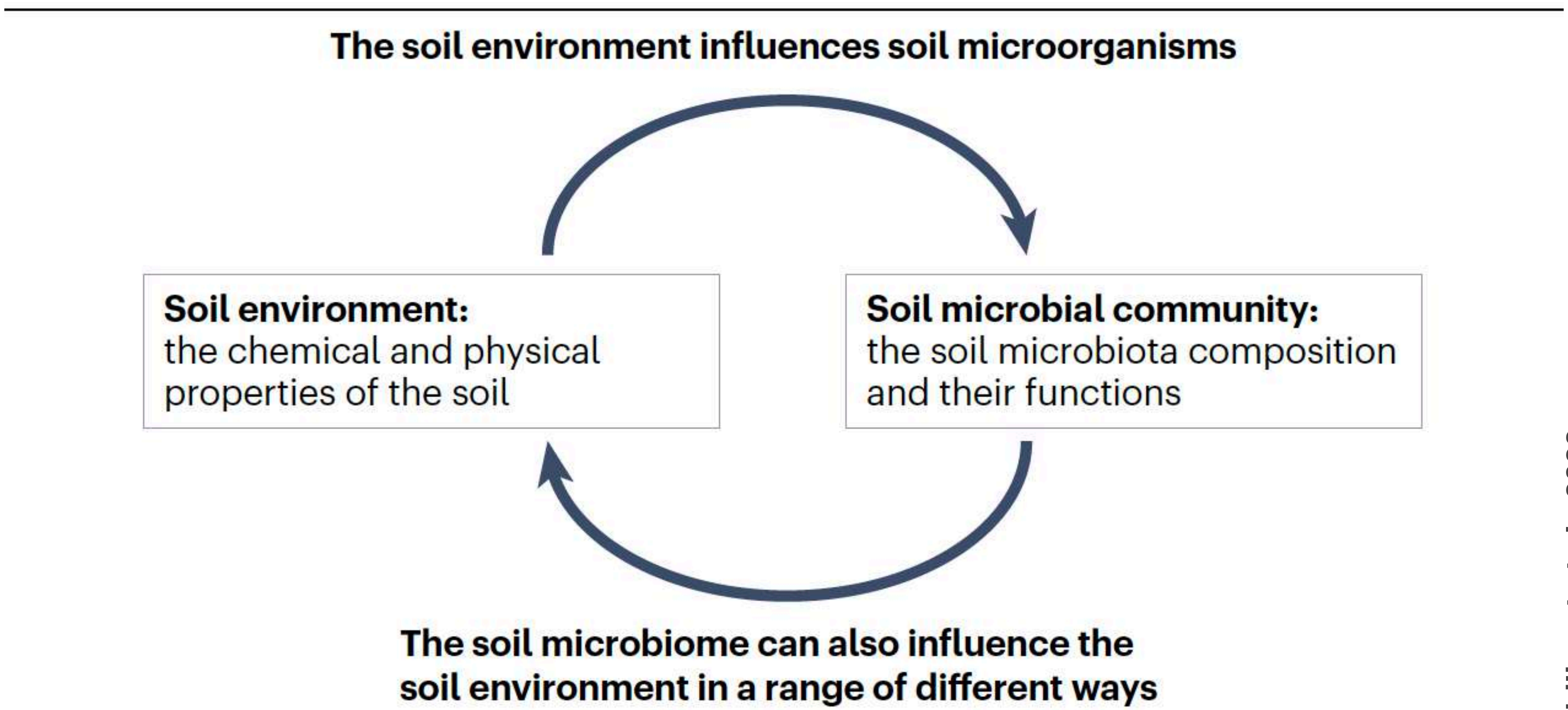
CONSERVATION AGRICULTURE



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

Tight interacting network



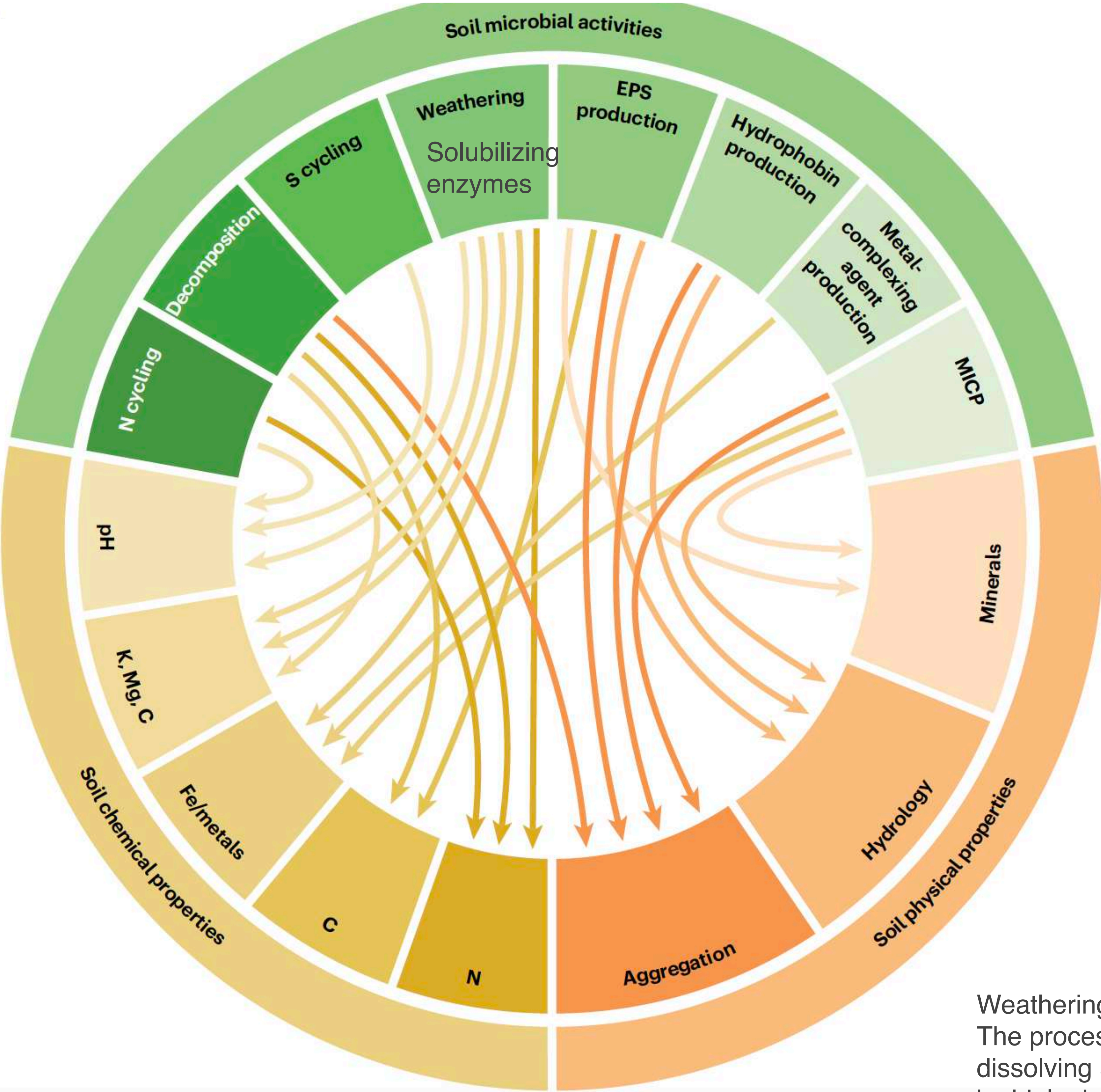
Philippot et al., 2023

- 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

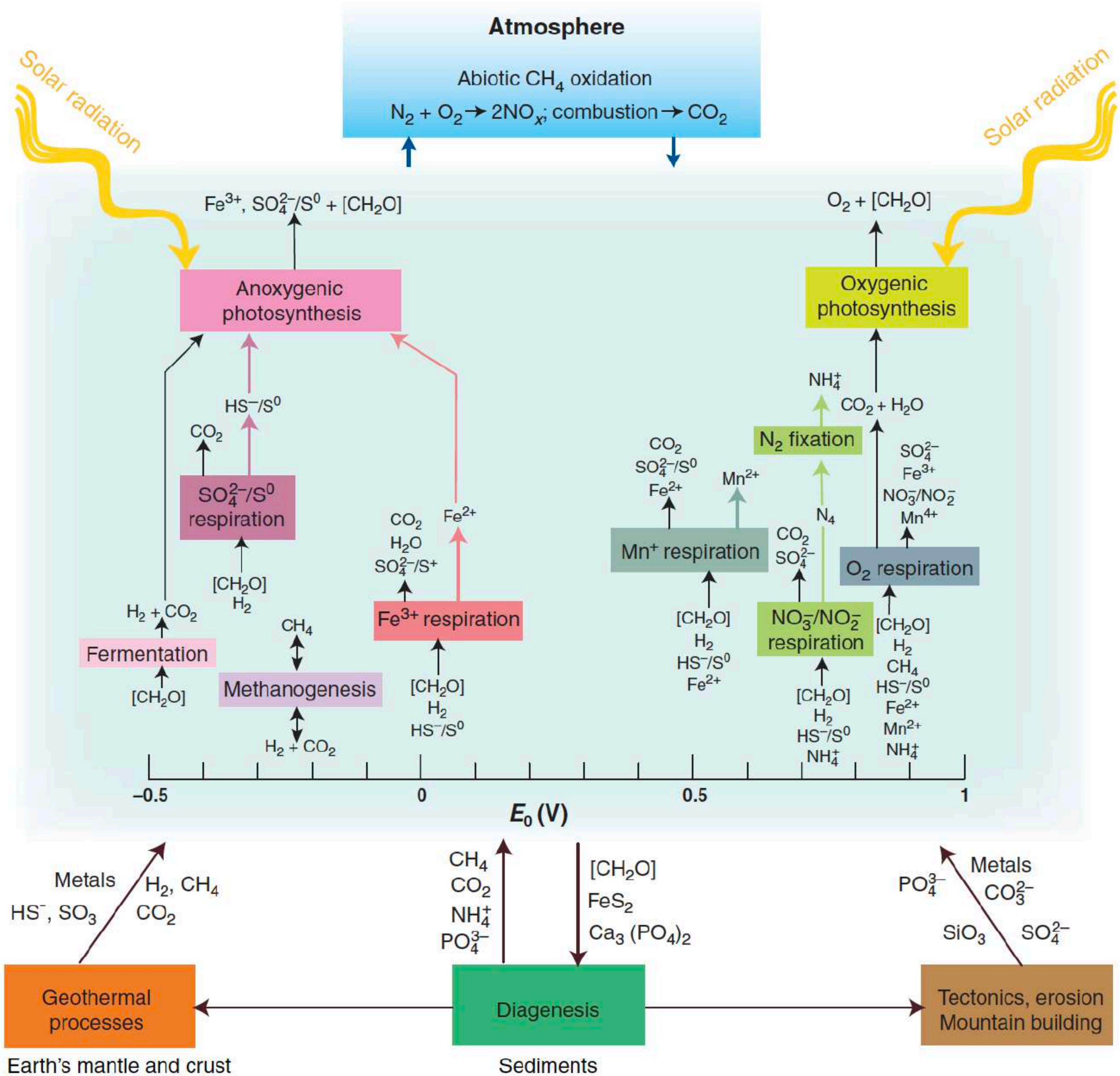
As, arsenic; C, carbon; CH_4, methane; CO_2, carbon dioxide; Fe, iron; FeS, iron sulphide; Fw, freshwater; FwS, freshwater sediment; Gw, groundwater; H_2, hydrogen; Hg, mercury; Hg^{2+}, mercuric ion; MTBE, methyl tertiary butyl ether; N_2, nitrogen; NH_3, ammonia; NH_4^+, ammonium; NO_2^-, nitrite; 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

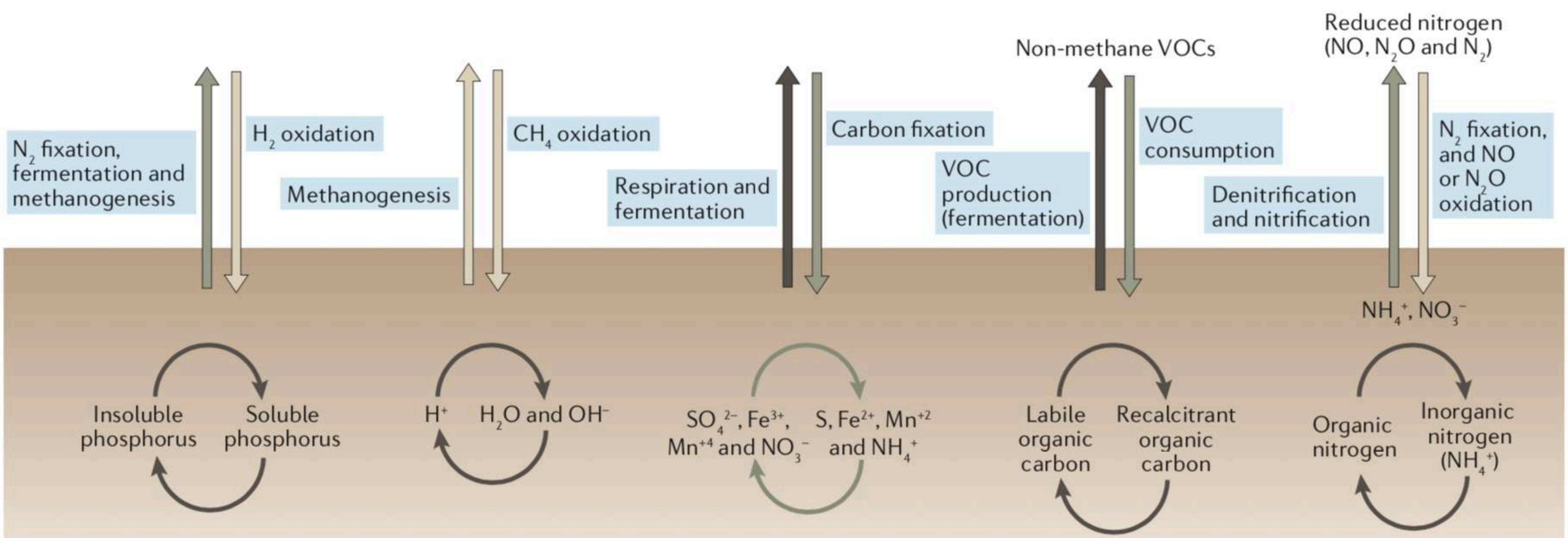
Soil biogeochemical processes that can be **modulated by the soil microbiome that are interrelated**

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