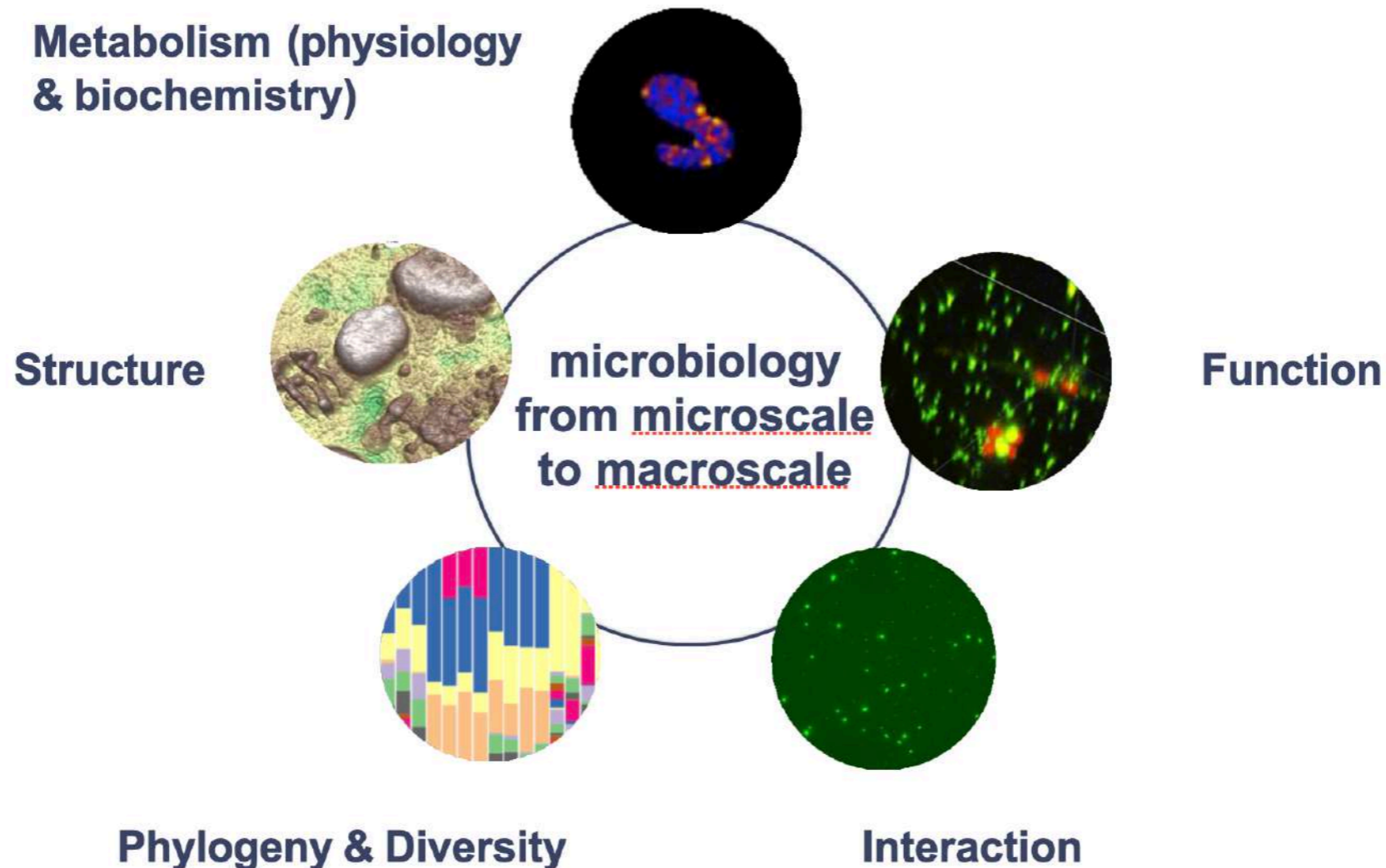


L07a

Microbial Ecology

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

Microbial Ecology



- Quantification of microbial abundance
- Identification of microbes—>microbial community diversity and structure
- Measuring activity rates
- Linking small scale to ecosystem scale microbial action

Microbial Ecology

- **Microbial Evolution**
- **Microbial Species**
- **Niche**
- **Microbial Diversity-Metabolic Diversity**
- **Ecosystem**
- **Carrying capacity**
- **Bottom-up and Top-down control**
- **Microbial roles in ecosystem functioning**

Evolution, I

- **Evolution** refers to the **heritable genetic changes** that a microbe accumulates during its life time, which can arise from **adaptations in response to environmental changes** (thus including the immune response of the host)
- Because of their **short generation times and large population sizes**, microbes can evolve rapidly
- **Allele: sequence variance of a gene**
- *Evolution is defined as a **change in allele frequencies** (= change in a sequence variance of a gene) in a population of organisms over time resulting in descent with modification*

Evolution, II

- **New alleles** are created through the processes of **mutation and recombination**
- Mutations occur at **random** and most mutations are neutral or deleterious, but some are beneficial
- **Natural selection and genetic drift** are two mechanisms that cause **allele frequencies to change in a population over time**
- ***Evolution occurs by four fundamental processes: mutation, recombination, natural selection, and genetic drift (results in a change in allele frequencies in a population as a result of random changes in # of offsprings from each individual over time)***

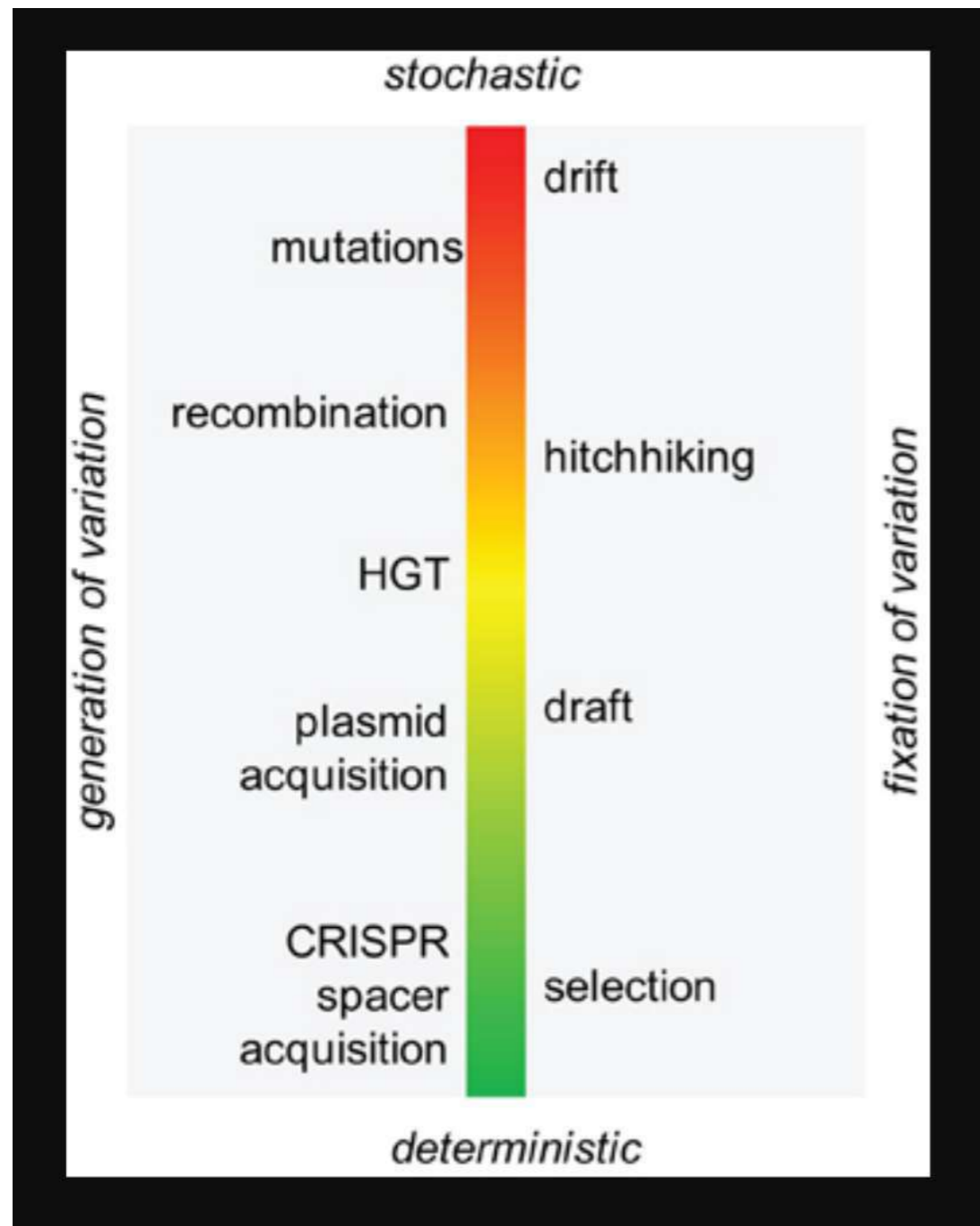
Evolution, III

- **Mutation, recombination** (gene flow, interspecific hybridization, and horizontal gene transfer are special forms of recombination. The first describes the movement of genes across a **spatial landscape**; the second and third involve genes moving between species and microbial lineages, respectively) produce **genetic variation**
- Natural selection, and genetic drift **govern the fate of variants**

Evolution, IV

- **Mutation, recombination and genetic drift are stochastic** in the sense that the specific variants produced or lost in a given generation are (or appear to be) **a matter of chance (whether any specific event happens is unknowable** or, at the least, impossible to incorporate into a mathematically efficient and useful theory of evolution)
- **Natural selection is a deterministic process** that reflects systematic differences in the propensity of alternative genotypes to survive and reproduce, **depending on their fit to the environment**

The continuum of evolutionary processes, from stochasticity to determinism



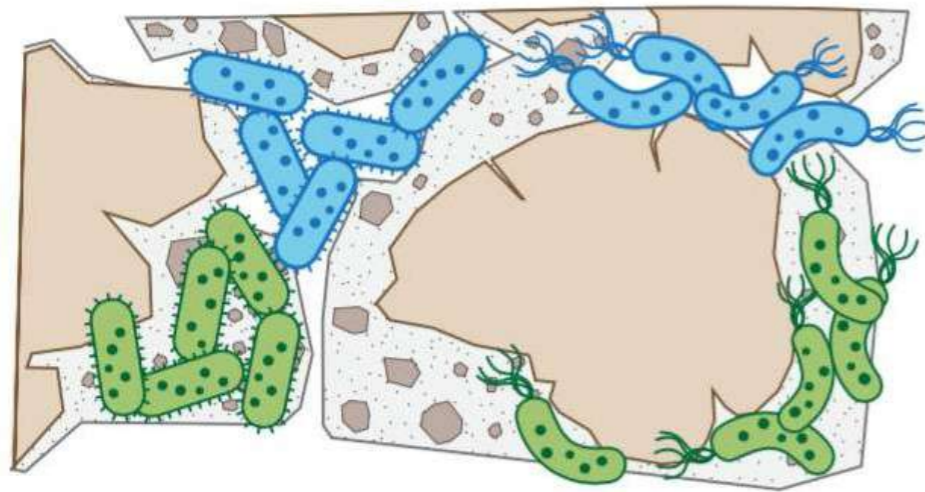
The **Modern Synthesis** of evolutionary biology emphasizes the **randomness of mutations** that provide the **starting material for selection** which engenders **survival of the fittest under the given conditions** and hence constitutes the adaptive, deterministic component of evolution





- **Lamarck**
- **CRISPR-Cas immune system responds to an environmental cue**
- **HGT depends on gene present in environment**
- **Stress-induced mutagenesis (error prone repair, SOS system) depends on environmental conditions**

From theory to practice

Where?

Microscale environment where the gene flow and speciation take place



	genetic similarity	ecological overlap	gene flow
	+++	+++	+++
	+++	+	++
	+	+++	++
	+	+	+

The magnitude of **gene flow between microbial populations** is shaped predominantly by the **genetic similarity and ecological overlap** of the individual strains that make up those populations

While the **efficiency of homologous recombination decreases exponentially with sequence divergence**, the **likelihood of transfer increases** with greater **physical contact** between strains that occupy similar physical niches

**How to work with a prokaryotic
species/taxon/organism ?**

**Only 1 - 10% microbes are cultivable
on Earth**

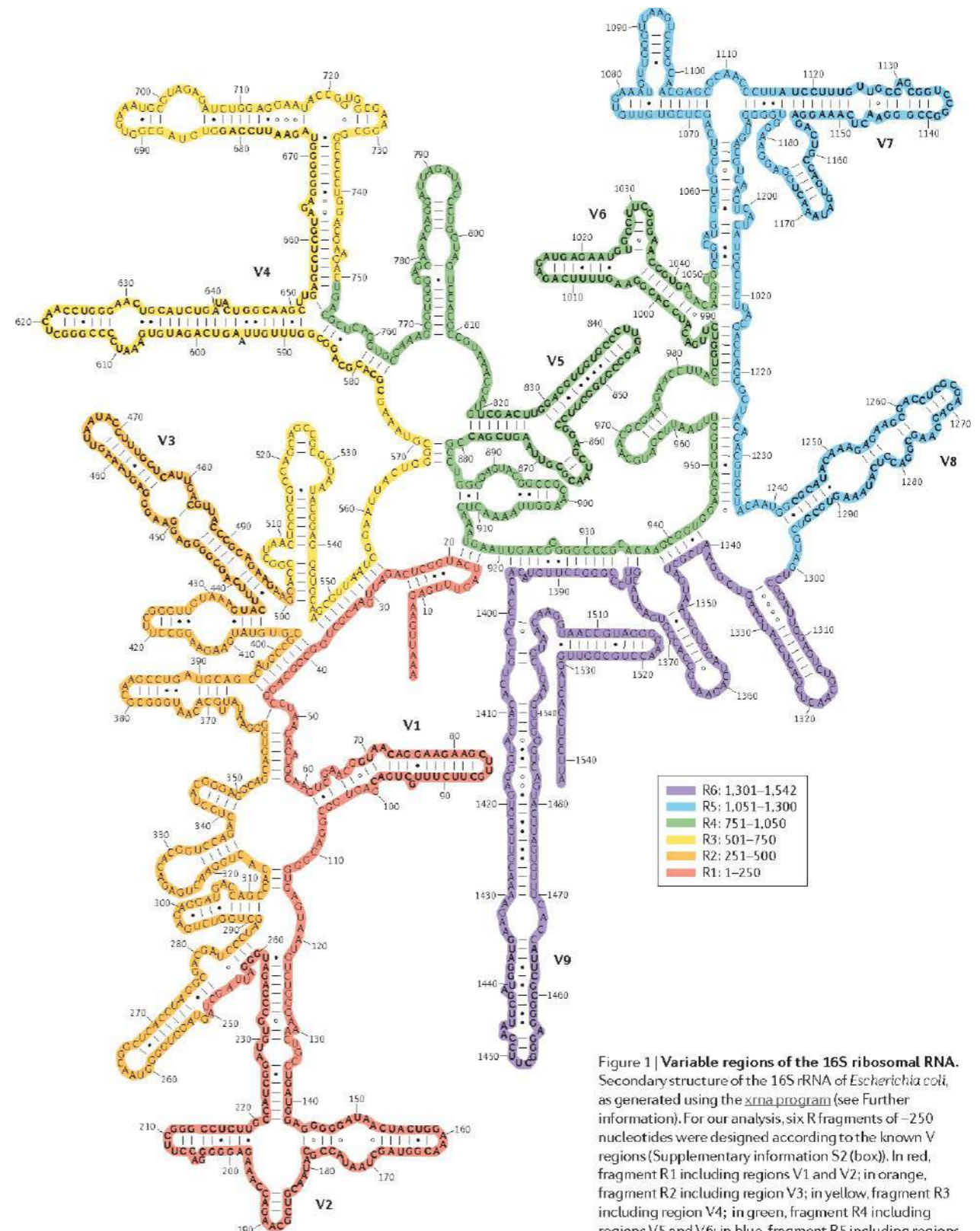
—>DNA only

Woese



Ribosomal RNAs are components of ribosomes, the structures that synthesize new proteins in the process of translation.

16S ribosomal RNA gene



**16S ribosomal RNA gene
identification for defining
the “invisible microbes”**

Microbial species I

Variation generation

↑ Mutations

- DNA replication errors
- DNA repair errors
- Mutagens



↑↓ Gene flow

- Horizontal gene transfer
- Homologous recombination
- Plasmid acquisition
- Dispersal



Variation shaping

↑↓ Genetic drift

↑↓ Selective pressure

Multiple environments

- Geographic location
- pH
- Xenobiotics
- Nutrient availability
- Ecological interactions
- O₂ concentration

• Antibiotics

Ocean

- Temperature
- Salinity
- CO₂ concentration

Soil

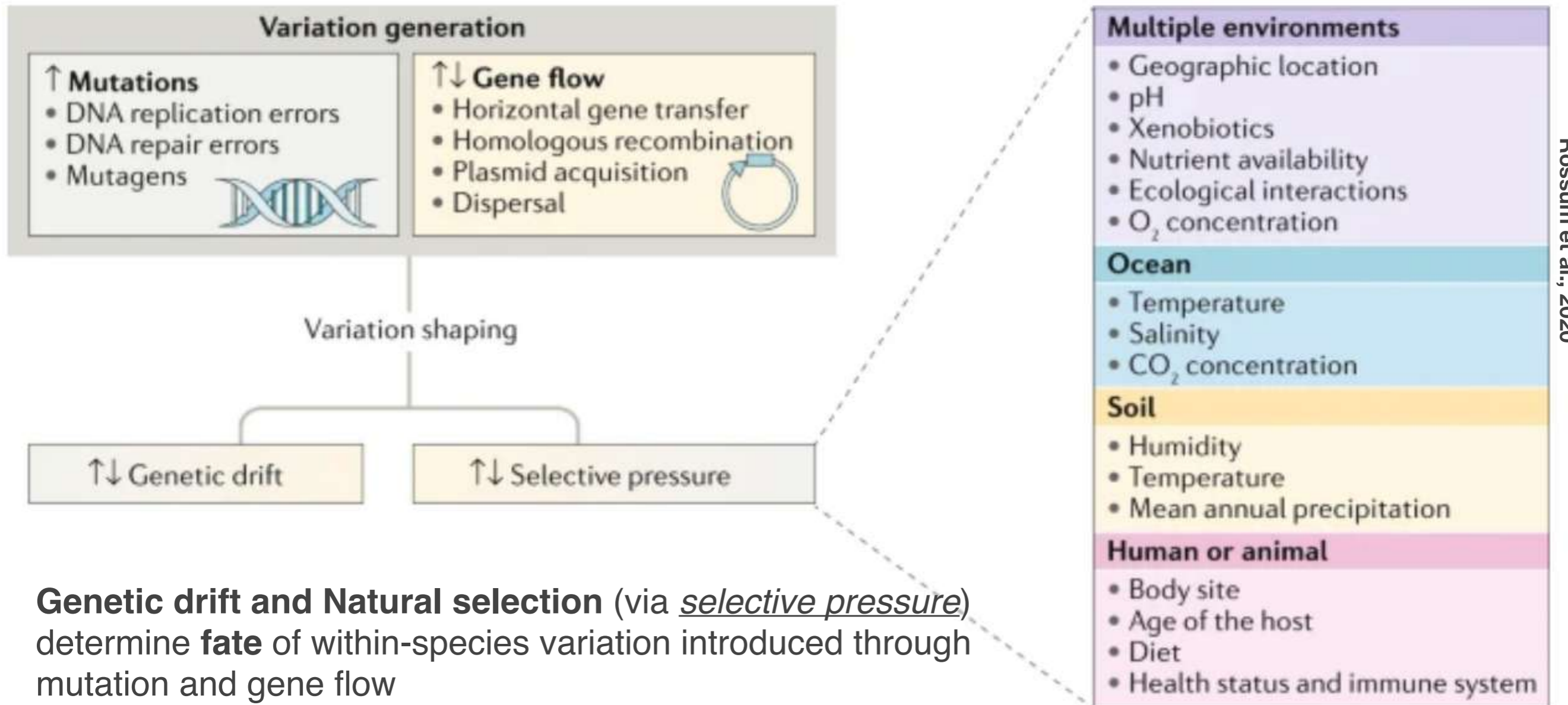
- Humidity
- Temperature
- Mean annual precipitation

Human or animal

- Body site
- Age of the host
- Diet
- Health status and immune system

Xenobiotics are foreign chemical substances found within an organism that are not naturally produced or expected to be present, such as drugs, environmental pollutants, food additives, and pesticides

Microbial species I



Rossum et al., 2020

Genetic drift and Natural selection (via *selective pressure*) determine **fate** of within-species variation introduced through mutation and gene flow

Genetic drift randomly eliminates **genetic variations within a population**, whereas **natural selection maintains or eliminates** variations that respectively confer a **fitness** advantage or disadvantage

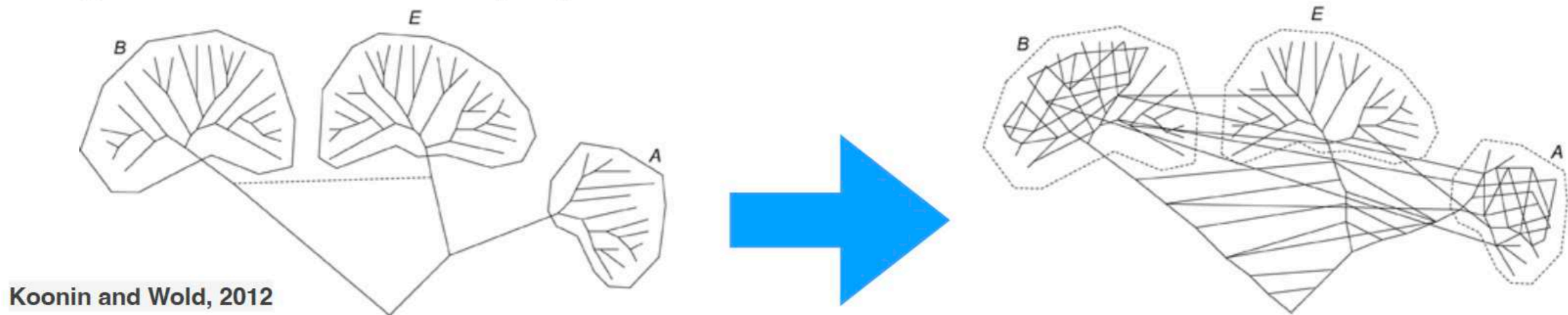
Effect of natural selection is limited by the background noise of genetic drift —> **Natural selection is driven by a multitude of biotic and abiotic factors** that *differentially influence the survival and replicative capability of species subpopulations*

Pangenome= core genome and accessory genome of a species (also cloud genome)

Bacterial genome is thought to consist of two distinct parts, the **core** genome and the **accessory** genome

The **core** genome comprises genes that are **essential** in most circumstances and might form the basis for Mayrian species that maintain **coherence** through homologous recombination.

The **accessory** genome encodes **special ecological adaptations** in genes that are readily gained and lost within the pangenome



Bacterial gene-transfer processes, which are erratic and transfer only a small part of the genome

Not clear if there are more changes in core vs accessory genomes

Recombination is an important process driving the evolution of bacterial genomes **homologous and not-homologous kind** (i.e., **HGT**)

Mutations are the ultimate source of heritable variation for evolution

What is a microbial species?

specere, “to see”something as an individual entity

15 Mayr, E. in *The Species Problem* (ed. Mayr, E.) 1–22 (American Association for the Advancement of Science, Washington DC, 1957)

A species as a group of interbreeding individuals that is isolated from other such groups **by barriers to recombination**. If genetic exchange within a species is sufficiently extensive, and that between species is sufficiently low, species will be relatively homogeneous in themselves and ecologically distinct from other species

Cohan, F. M. What are bacterial species? *Annu. Rev. Microbiol.* 56, 457–487 (2002)

The ecological species concept, defines a species as a set of individuals that can be considered to be identical in all relevant ecological properties.

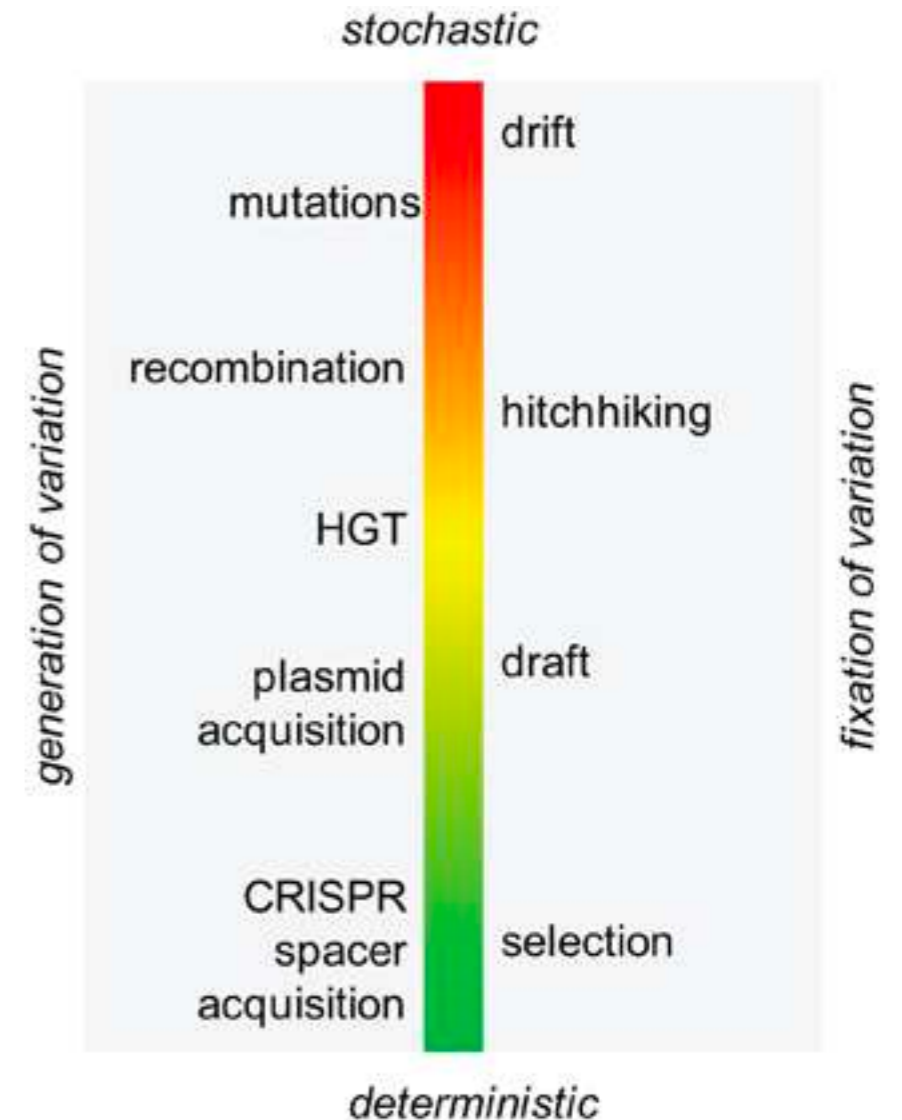
Bacteria-Archaea have ecological species ('ecotypes') and occupy discrete niches and that periodic selection will purge genetic variation within each niche without preventing divergence between the inhabitants of different niches.

..using genomic DNA

Evolution

Evolutionary outcomes are determined by core factors that shape the diversity of life: **adaptation, chance and history.**

Adaptation reflects the power of natural selection to drive populations along evolutionary paths to phenotypes of high fitness. If few paths are available, replicate populations will follow repeatable, perhaps even predictable, outcomes.



Smith Chelsea E., Smith Adam N. H., Cooper Tim F. and Moore Francisco B.-G. 2022

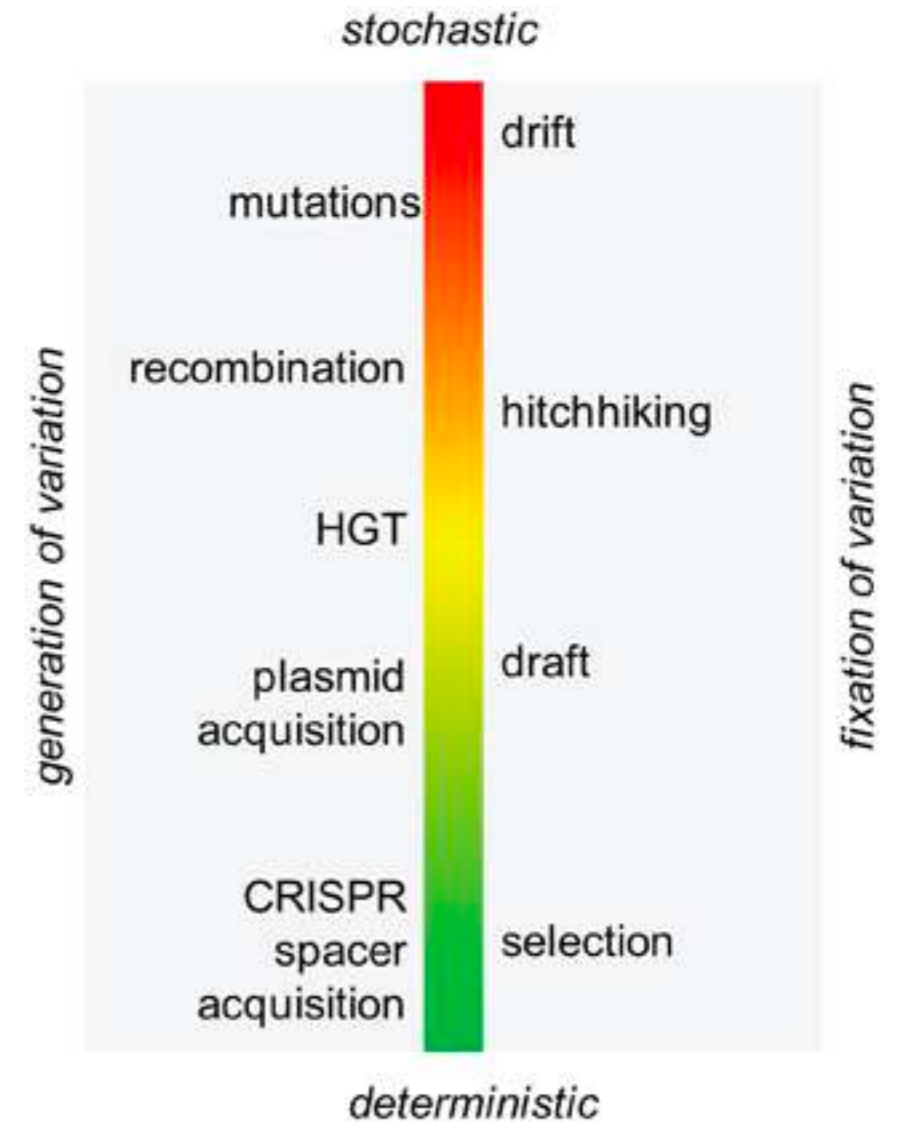
Eugene V. Koonin* and Yuri I. Wolf, 2015

Evolution

By contrast, chance and history promote evolutionary divergence.

Chance causes divergence between populations through stochastic differences in the occurrence and success of newly arising mutations.

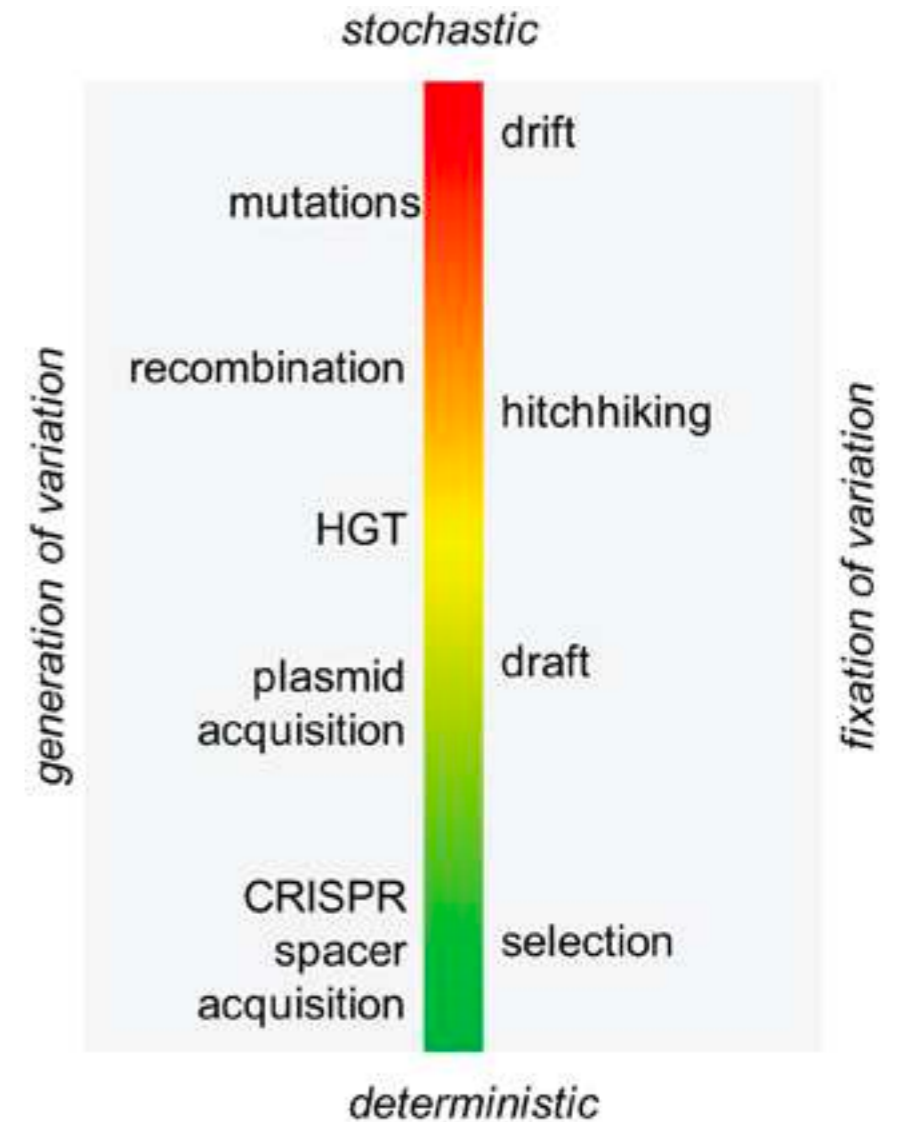
History, defined here as differences in the genetic starting points of selected populations, promotes divergence if evolutionary opportunities or constraints are contingent on specific genotypes.



Evolution

Determining the relative contribution of these forces, and how this might depend on the selective environment, is crucial to the goal of predicting evolutionary outcomes.

Evolution can be more adequately depicted as a **continuum of processes** from completely random ones, under the Wrightian modality defined by **random variation and random fixation of changes via genetic drift**; to the Darwinian modality with **random changes fixed by the deterministic process of selection**; to the Lamarckian mode in which both **variation and fixation are deterministic**.



Smith Chelsea E., Smith Adam N. H., Cooper Tim F. and Moore Francisco B.-G. 2022

Eugene V. Koonin* and Yuri I. Wolf, 2015

Evolution of microbial genomes: disentangling the effects of selection and loss bias on gene dynamics

Iranzo et al., 2017

The **evolution of microbial genomes** is generally interpreted in terms of the interplay between three factors:

★ (i) **gene gain**, via horizontal gene transfer (HGT) and gene duplication;

★ (ii) **gene loss**, via deletion;

★ (iii) **natural selection** that affects gene fixation and maintenance

The intrinsic bias toward DNA deletion (and hence gene loss) that characterizes mutational processes in prokaryotes results in nonadaptive genome reduction, whereas selection contributes to maintaining slightly beneficial genes

Mutations, I

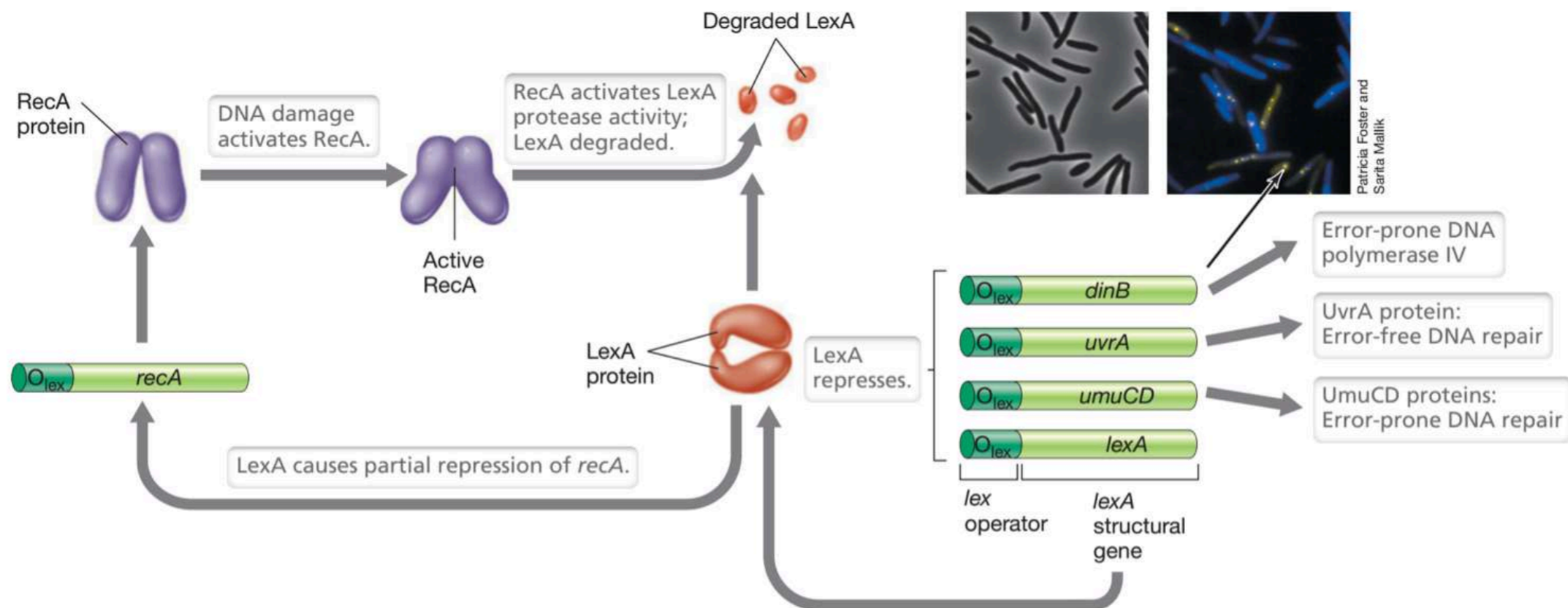
- Mutation is **heritable change** in genome **base sequence** (mother → cell progeny)
- Mutations → changes cell properties
- Mutations are beneficial, some are detrimental, but most are **neutral w. no effect**
- **Spontaneous mutations** occur without external intervention (occasional errors in pairing of bases by DNA polymerase during replication)
- **Induced mutations**, caused by agents in environment and by humans
- Exposure to natural radiation that **alters structure of bases** in DNA, or from a variety of chemicals that **chemically modify DNA**

TABLE 11.2 Chemical and physical mutagens and their modes of action

<i>Agent</i>	<i>Action</i>	<i>Result</i>
Base analogs		
5-Bromouracil	Incorporated like T; occasional faulty pairing with G	AT → GC and occasionally GC → AT
2-Aminopurine	Incorporated like A; faulty pairing with C	AT → GC and occasionally GC → AT
Chemicals reacting with DNA		
Nitrous acid (HNO ₂)	Deaminates A and C	AT → GC and GC → AT
Hydroxylamine (NH ₂ OH)	Reacts with C	GC → AT
Alkylating agents		
Monofunctional (for example, ethyl methanesulfonate)	Puts methyl on G; faulty pairing with T	GC → AT
Bifunctional (for example, mitomycin, nitrogen mustards, nitrosoguanidine)	Cross-links DNA strands; faulty region excised by DNase	Both point mutations and deletions
Intercalating agents		
Acridines, ethidium bromide	Inserts between two base pairs	Microinsertions and microdeletions
Radiation		
Ultraviolet (UV)	Pyrimidine dimer formation	Repair may lead to error or deletion
Ionizing radiation (for example, X-rays)	Free-radical attack on DNA, breaking chain	Repair may lead to error or deletion

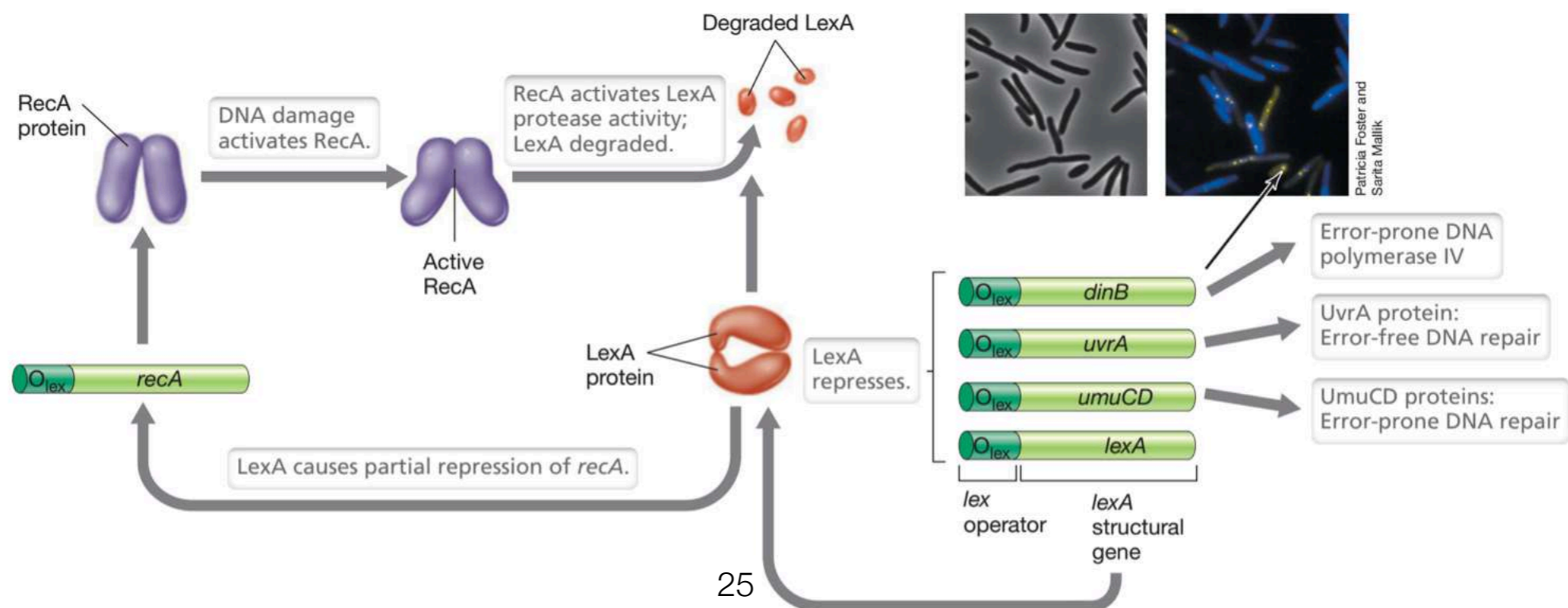
DNA Repair & SOS System, I

- DNA damage (e.g. large-scale damage from highly mutagenic chemicals or large doses of radiation), may cause lesions that **interfere with replication**
- **DNA replication will stall and lethal breaks in the chromosome** → activate the SOS repair system
- **SOS system DNA is repaired without a template** → with **random incorporation of dNTPs (TRANSLESION)** → can cause mutations
- Mutations may be less detrimental to cell survival than chromosome breaks
- In *E. coli* the **SOS repair** system forms a regulon, controls the transcription of approximately 40 genes → **for DNA damage tolerance and DNA repair**



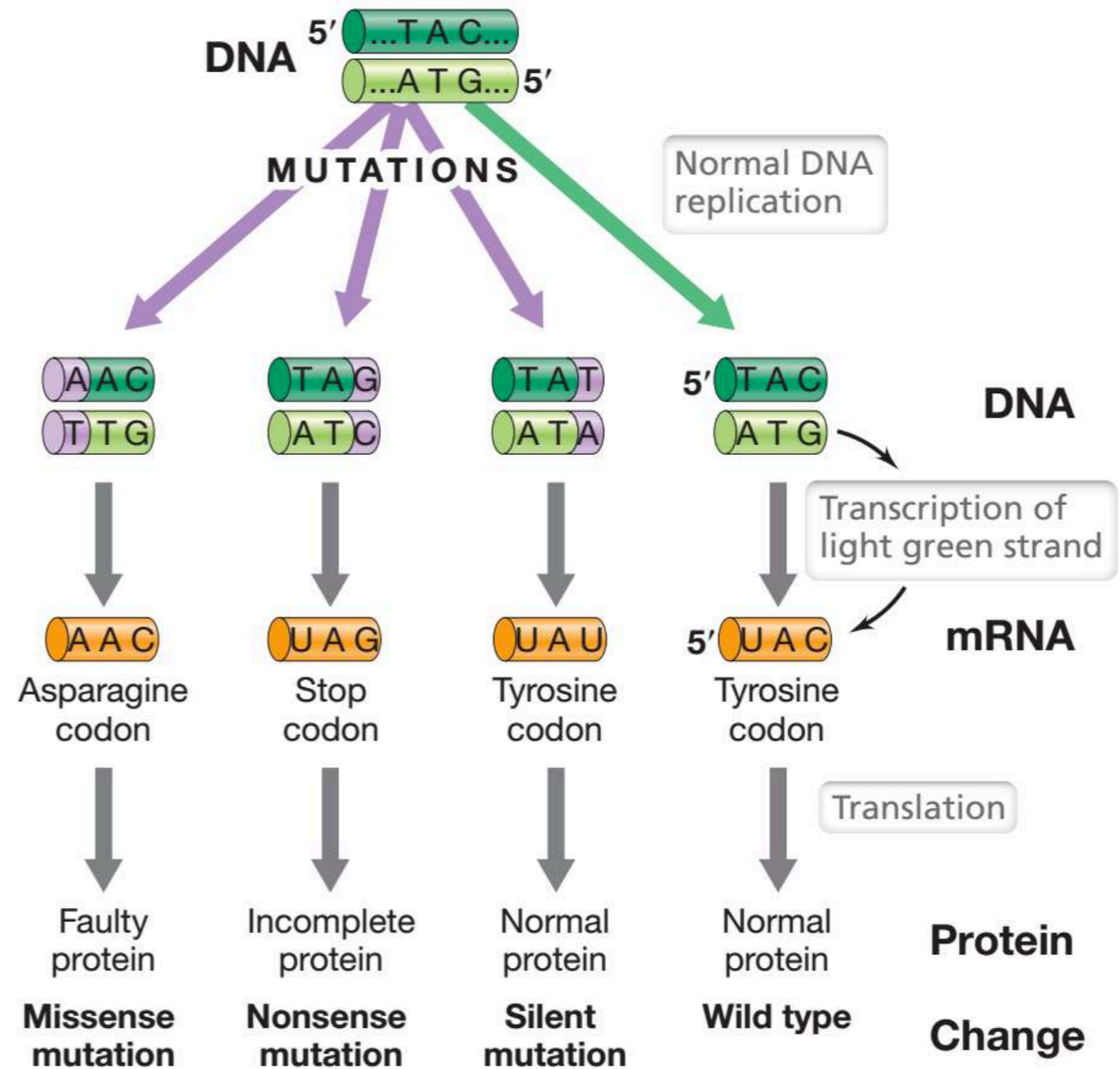
DNA Repair & SOS System, II

- In DNA damage tolerance, DNA lesions remain in the DNA, are bypassed by specialized DNA polymerases that can move past DNA damage → translesion synthesis
- In *E. coli*, **2 error-prone repair polymerases are DNA polymerase V** (encoded by *umuCD* genes), **DNA polymerase IV** (by *dinB* gene) → many mutations
- **LexA is a repressor** that normally prevents SOS expression
- **RecA protein**, which normally functions in **genetic recombination is activated by DNA damage (ssDNA when replication stalls)**
- Activated **RecA stimulates LexA to inactivate itself by self-cleavage** → coordinated expression of proteins that participate in DNA repair
- Once original DNA damage has been repaired, the SOS regulon is repressed



Mutations, II

- One base pair mutations are **point mutations** and occur when a **single base-pair substitution** takes place in DNA
- Results from a point mutation depends on exactly **where in genome** the mutation occurs and **the nature of the nucleotide change**



Mutations, III

- **Spontaneous mutation rate** is low, speed at which many prokaryotic cells divide and their characteristic exponential growth → **mutations accumulate in a population surprisingly fast**
- Single mutation brings about only a small change in cell
- **Genetic exchange often generates much larger change**
- ***Mutation + genetic exchange fuel the evolutionary process***
- If damaged DNA can be corrected before cell division, no mutation will occur

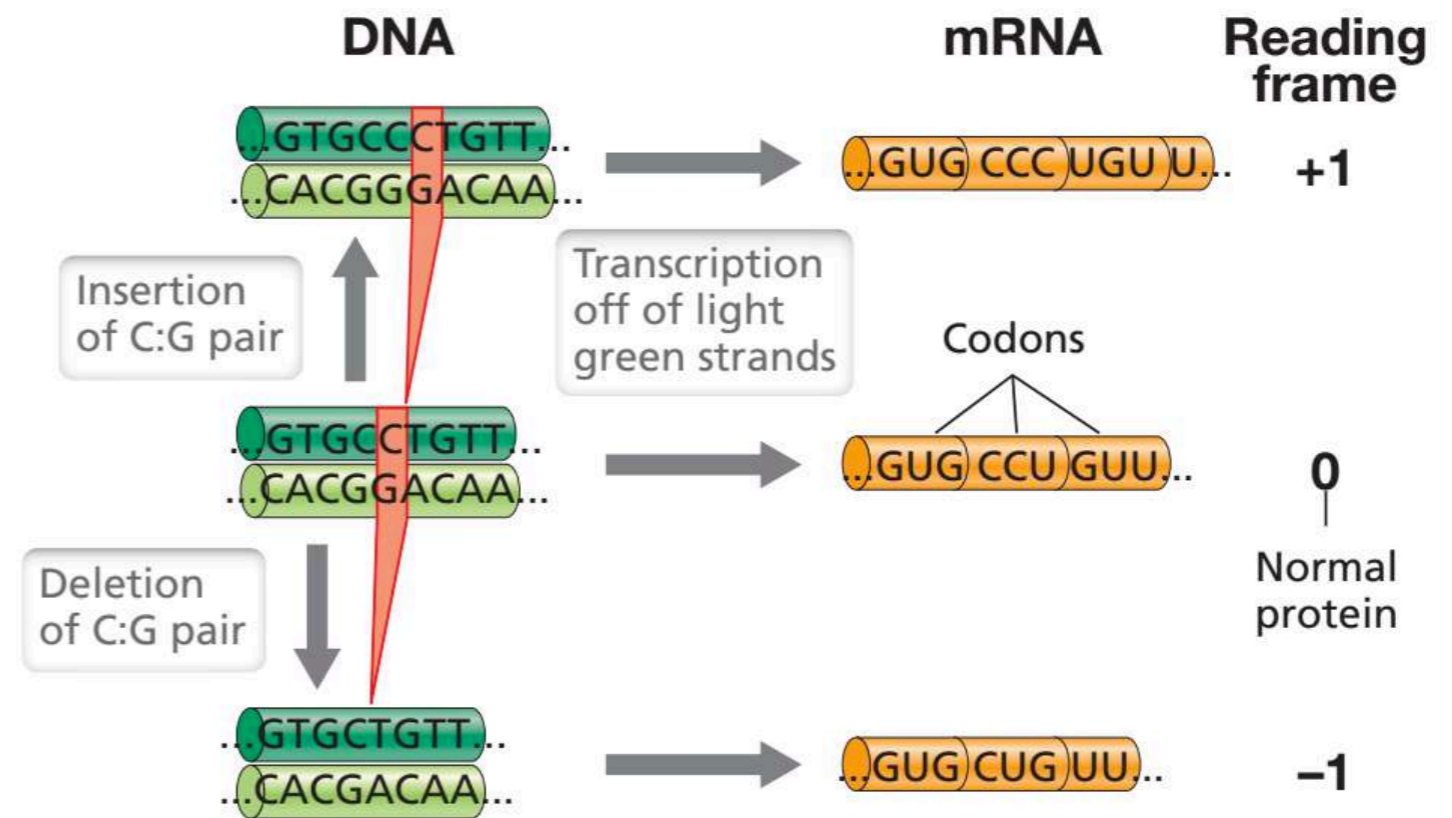


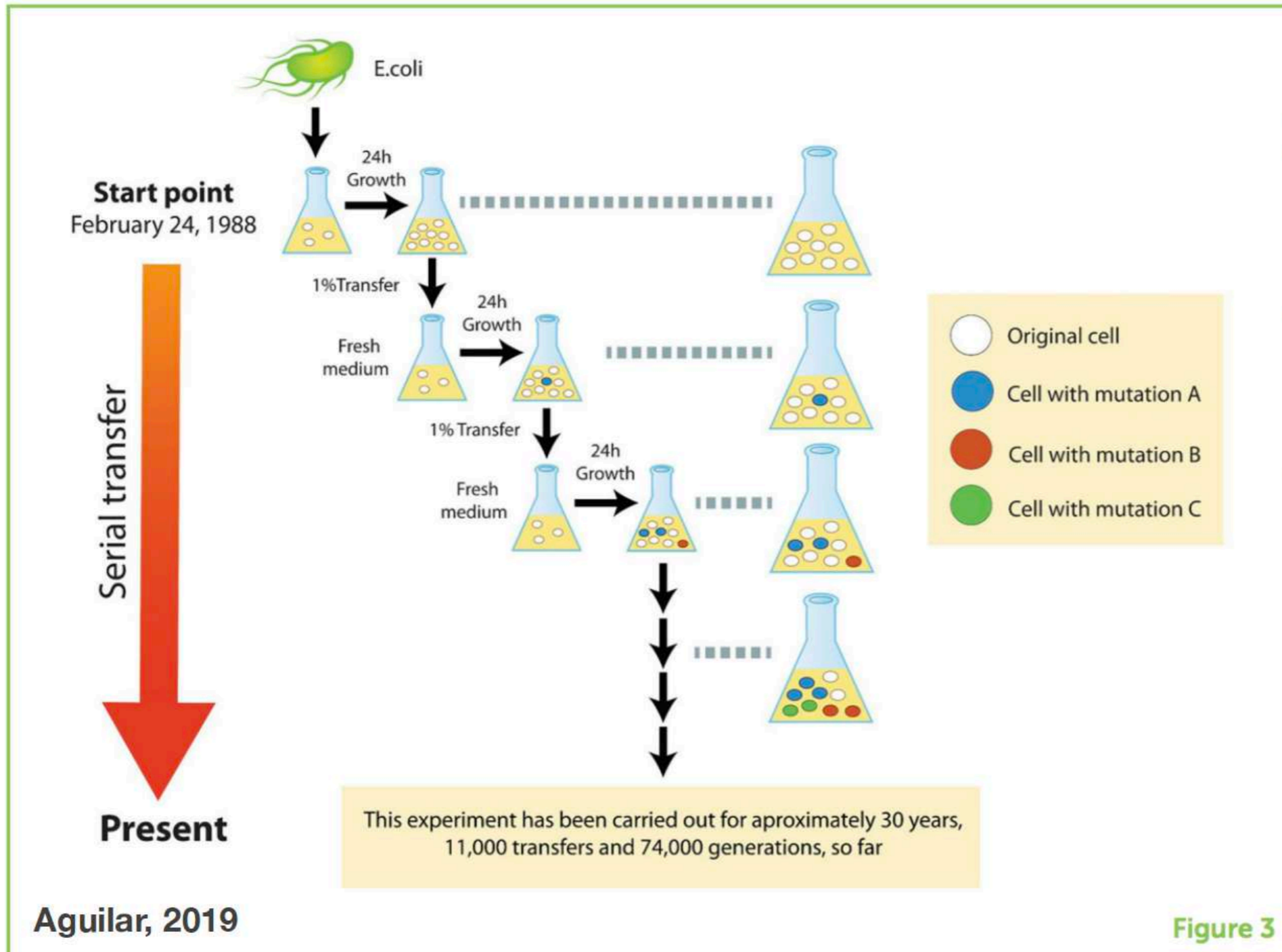
Figure 11.5 Shifts in the reading frame of mRNA caused by insertions or deletions. The reading frame in mRNA is established by the ribosome, which begins at the 5' end (toward the left in the figure) and proceeds by units of three bases (codons). The normal reading frame is referred to as the 0 frame, that missing a base the -1 frame, and that with an extra base the +1 frame.

Microbial species & Mutations

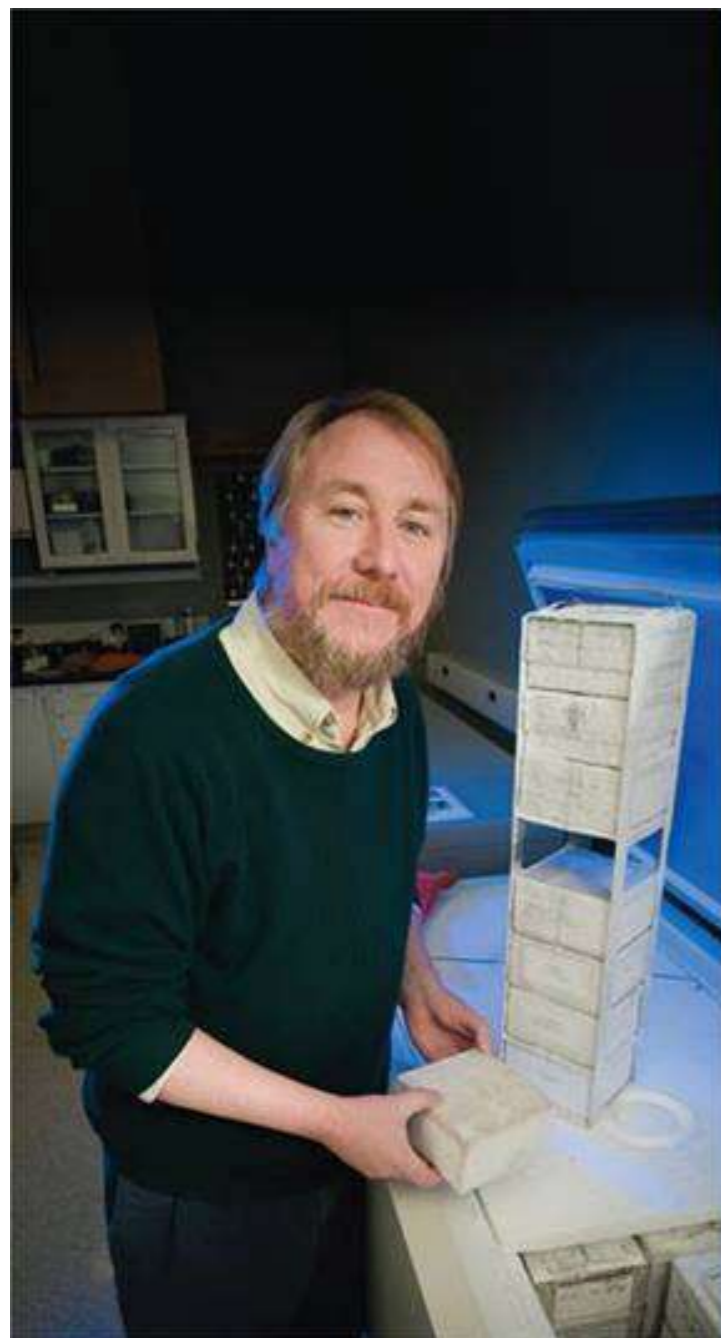
- The **rate of accumulation of mutations** within a lineage of bacteria depends on the **mutation rate** as well as on **natural selection and genetic drift**, which act upon the mutations
- **Non-lethal rates** of mutation from 10^{-9} to 10^{-3} mutations per genome per generation (in *Vibrio* species)
- **Not all portions** of bacterial **genome** are equally subject to mutations
- Mutation accumulation rates are **higher in accessory genes** than in core genes, unless a core gene is located near accessory genes or mobile genetic elements, and higher in secondary chromosomes than in primary chromosomes
- **Deletions are more frequent than insertions**, and non-functional sequences are readily lost from bacterial genomes
- Mutations that arise in one genome can be **passed vertically to descendants or horizontally to neighbouring cells**

Long-Term-Evolutionary Experiment (LTEE), Richard Lenski

12 populations of *Escherichia coli* in a simple laboratory environment (medium) for >30 years and 75000 generations from February 1988



- 12 replicate populations have been propagated in a glucose-limited medium
- Daily 100-fold dilutions and regrowth allow ~6.6 generations per day
- Every 500 generations (75 days), after the transfers into fresh medium, glycerol was added as a cryoprotectant to the remaining cultures, which were then stored for later research at -80°



Lenski's LONG-TERM Evolution Experiment

Twelve batches of bacteria, replicating and evolving for 25 years, yield some pretty big numbers.

58,000* GENERATIONS
(as of June 2013)

GENERATIONS PER DAY **6.6**



Lenski's experiment has been running for more than

25 years

at an ESTIMATED COST of **\$4** MILLION

10^{14} ROUGH NUMBER OF BACTERIAL CELLS

REPLICATE POPULATIONS **12**

All started with identical *E. coli*, but are now all different

The number of FROZEN VIALS **>4000** that hold ancestral and evolved bacteria

LIQUID MEDIA **>10,000** LITERS



FREEZERS **6**



Workforce involvement equals about

75 PERSON YEARS

30 PARTICIPATING GRADUATE STUDENTS AND POSTDOCS

OUTSIDE COLLABORATORS

40

>50 PUBLICATIONS

<https://the-ltee.org/about/>

Much of our understanding of microbial evolution and adaptation has come from experimental evolution [44], and reviews of the topic can be found elsewhere [45]. One example of the power of evolutionary experiments is the Long-Term Evolutionary Experiment (LTEE), started by Richard Lenski 30 years ago [46], which documented adaptive bacterial evolution in constant laboratory conditions and showed that different mutation rates can emerge in previously identical populations. This LTEE has also demonstrated the evolution of new metabolic capabilities [47] and the emergence of ecological interactions between two interdependent subpopulations harbouring different mutations [48,49]. Experimental evolution has

The first set of questions concerns the **dynamics of evolution**.

- Is evolution invariably slow and gradual?
- Or are there periods of rapid change and stasis, even in a constant environment?
- How long can fitness continue to improve, and by how much, before some limit is reached?

The second set concerns the **repeatability of evolution, especially those changes that are adaptive**.

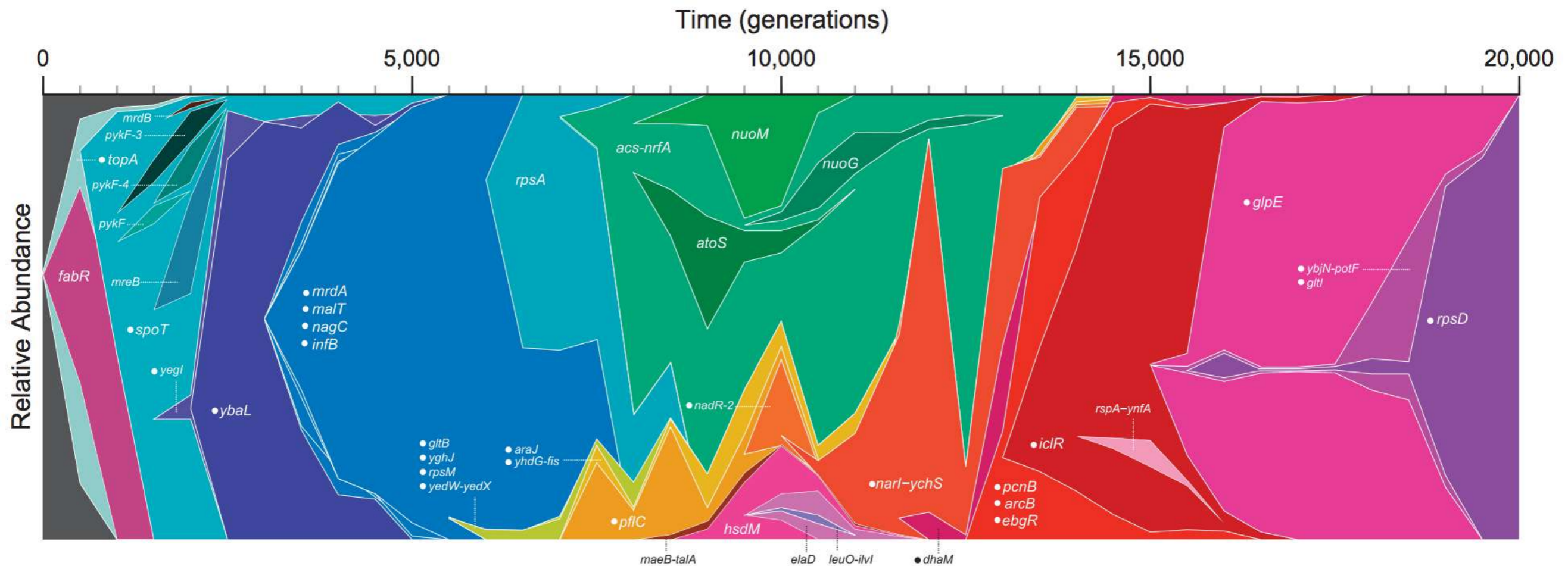
- How repeatable is evolution?
- Will the 12 populations evolve along similar paths?
- Or will they find different phenotypic solutions to their identical environments?
- How does their similarity or divergence depend on which traits are measured?

The third set of questions concerns the **coupling of phenotypic and genetic changes**.

- Are the rates of phenotypic and genetic evolution tightly coupled over time?
- Or does genetic change continue apace, even after adaptation has slowed or stopped?
- What specific mutations are responsible for the bacteria's adaptation?
- What are the molecular and physiological changes that make the later generations better adapted to the LTEE environment?
- If and when phenotypes evolve similarly in the replicate populations, does that imply parallel changes at the level of nucleotides, genes, or pathways?

12 populations of *Escherichia coli* in a simple laboratory environment (medium) for >25 years and 60 000 generations from February 1988

Richard Lenski



In population Ara-1, two lineages coexisted from ~ 7000 to ~ 14 000 generations, before one drove the other extinct. Muller plot showing the relative abundances of 42 mutations found in population Ara-1 during its first 20 000 generations

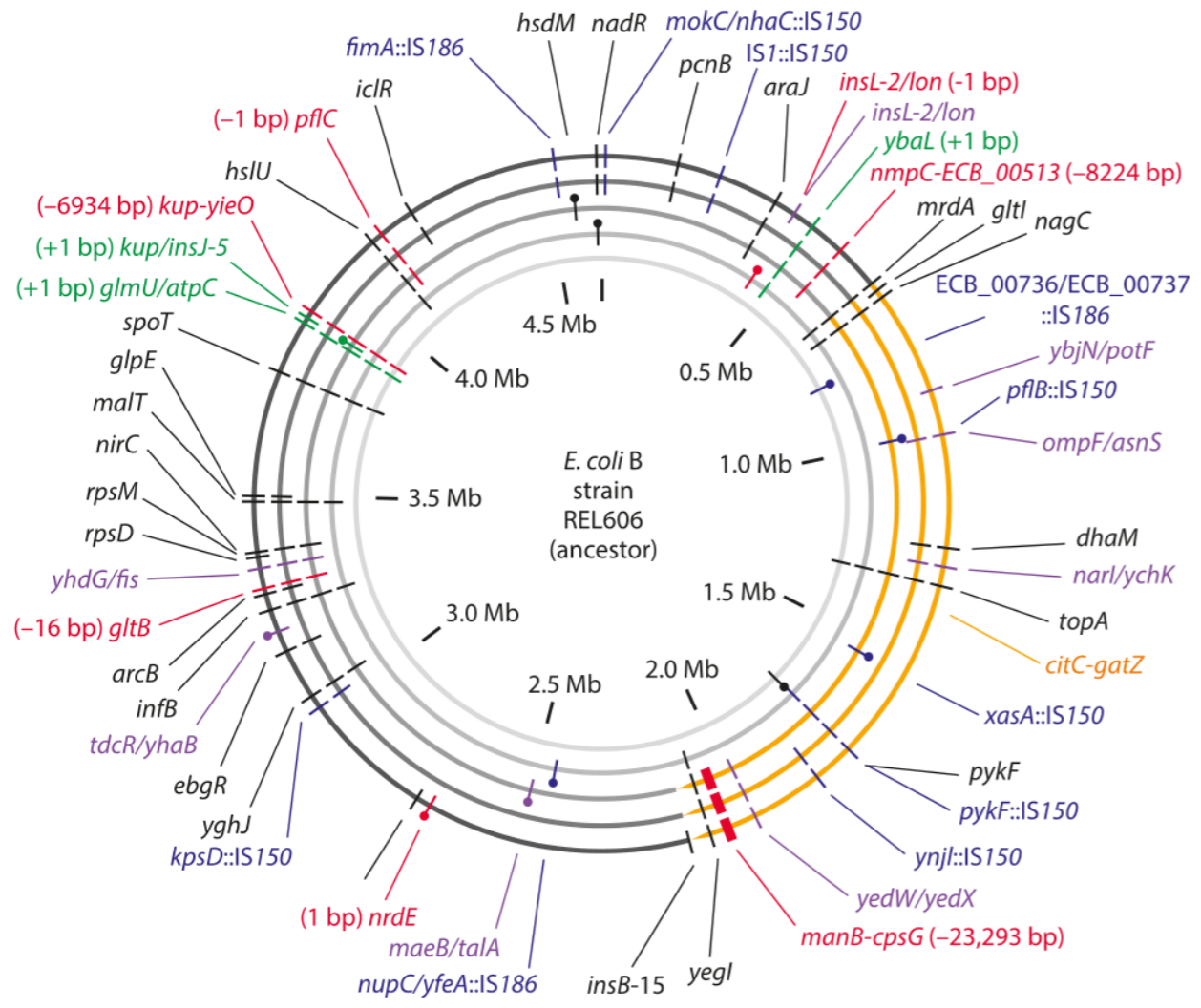
Sequencing measurements of fixed mutations over 20,000 generations in *E. coli*

Long-term experiment: compare full genome sequence at different times to reference sequence for the genome at the time the experiment started

Labels in outer ring show the specific mutations that were present after 20,000 generations

Sequencing of 19 whole genomes detected **25 synonymous mutation** (indicating neutral rather than selective changes) that got fixed in the 40,000 generations of experiment

Inference mutation rate is about 10^{-10} mutations per bp per replication in measured conditions



— clone sequence from generation:
 — 2 K — 5 K — 10 K — 15 K — 20 K
 ↗ off line of descent to 40 K clone

evolved mutations:
 — inversion — insertion — protein coding
 — deletion — IS insertion — intergenic
 — SNP

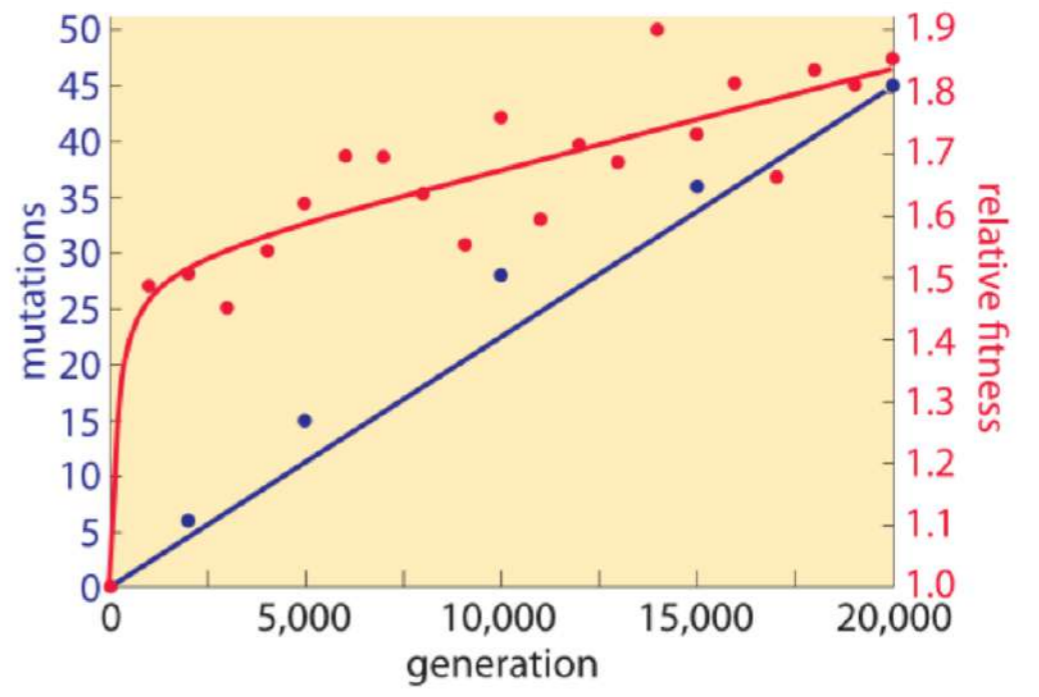
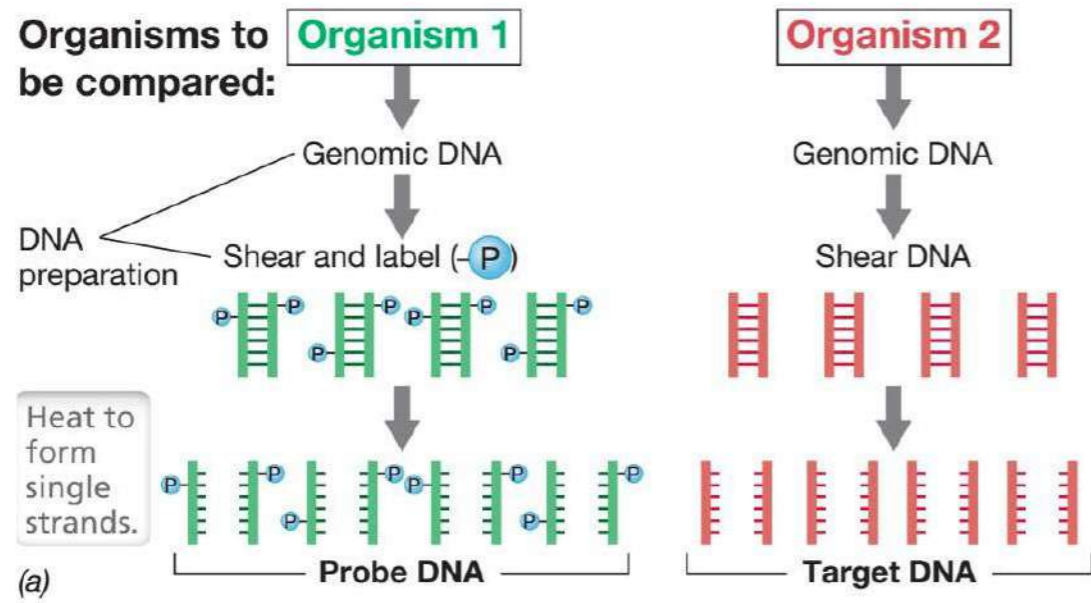


Figure 2: Mutation accumulation and fitness over time. Sequencing measurements make it possible to examine the rate of mutation accumulation and the corresponding fitness over time. Adapted from J. E. Barrick et al. Nature, 461:1243, 2009.

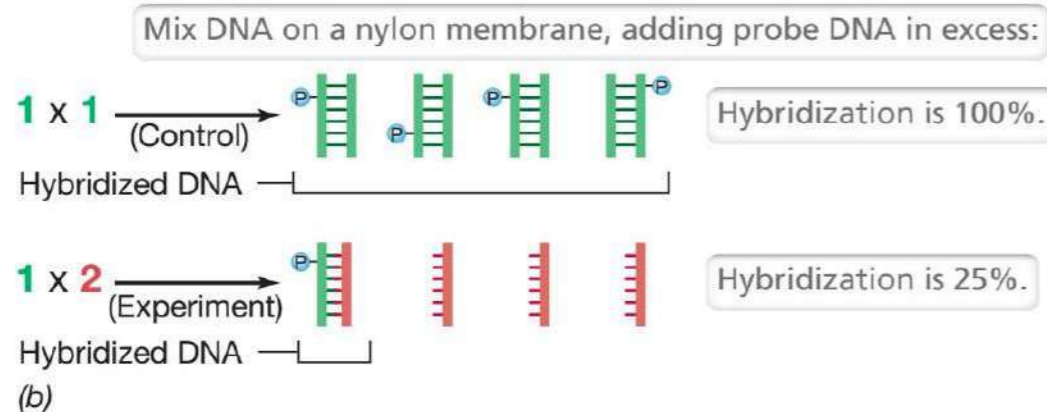
Long-Term Evolution Experiment (LTEE) results ...so far

- **Adaptation by Natural Selection:** The LTEE provides a simple, compelling demonstration of the process of adaptation by natural selection.
- **Endless Adaptations:** The bacteria continue to become better and better adapted to the LTEE environment over time, and it appears their fitness may continue to increase indefinitely, albeit at a slower pace.
- **Repeatability of Evolution:** The LTEE has produced many striking examples of both parallel (repeatable) and divergent changes across the replicate populations.
- **Evolution of Novelty:** The LTEE provides fascinating cases of the origin and evolution of a new function and complex ecological interactions.
- **Changing Mutation Rates:** Several LTEE lines have evolved large changes in their spontaneous mutation rates, reflecting a tradeoff between short-term fitness and long-term evolvability.

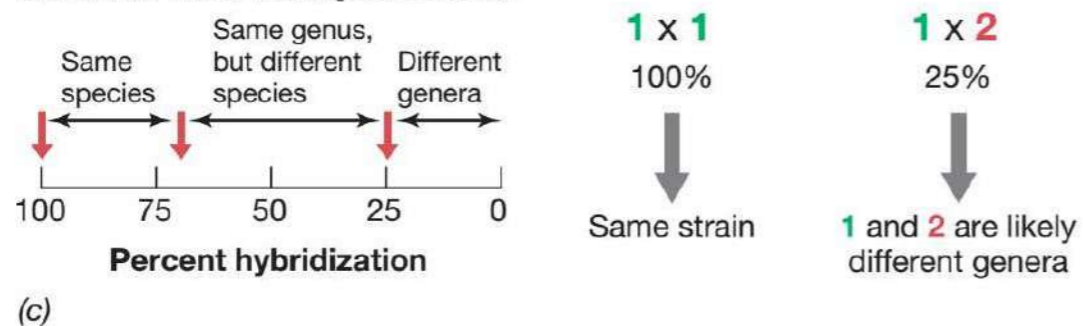
Microbial Species I



Hybridization experiment:

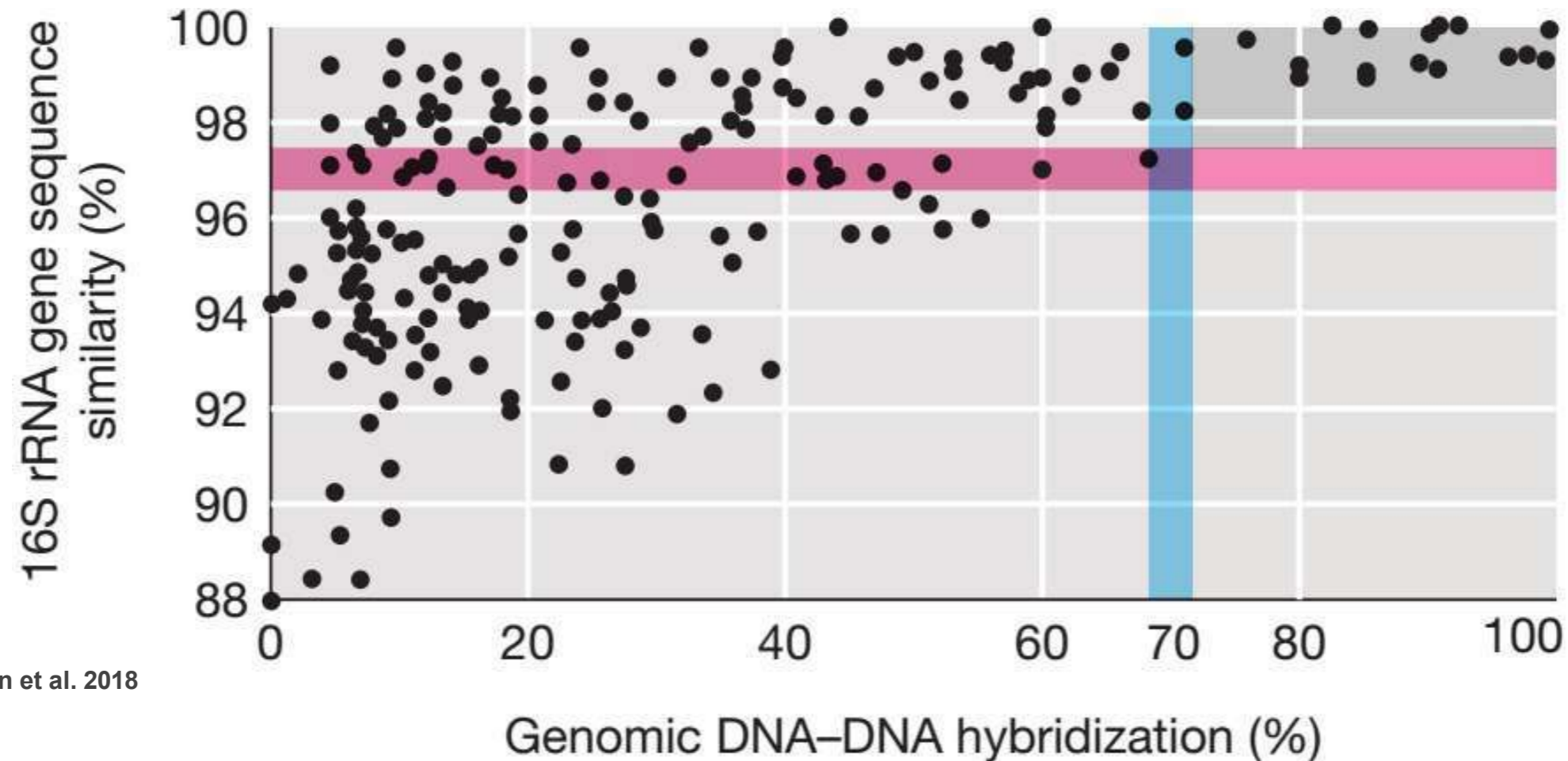


Results and interpretation:



- Microbes are currently assigned to a **common species** if their **reciprocal, pairwise DNA re-association values are $\geq 70\%$ in DNA–DNA hybridization** experiments under standardized conditions and their ΔT_m (melting temperature) is $\leq 5^\circ\text{C}$
- All strains within a species must possess a **certain degree of phenotypic consistency**, and species descriptions should be based on **more than one type strain**
- A species name is only assigned if its members can be distinguished from **other species** by at least one diagnostic phenotypic trait

Microbial Species II



Madigan et al. 2018

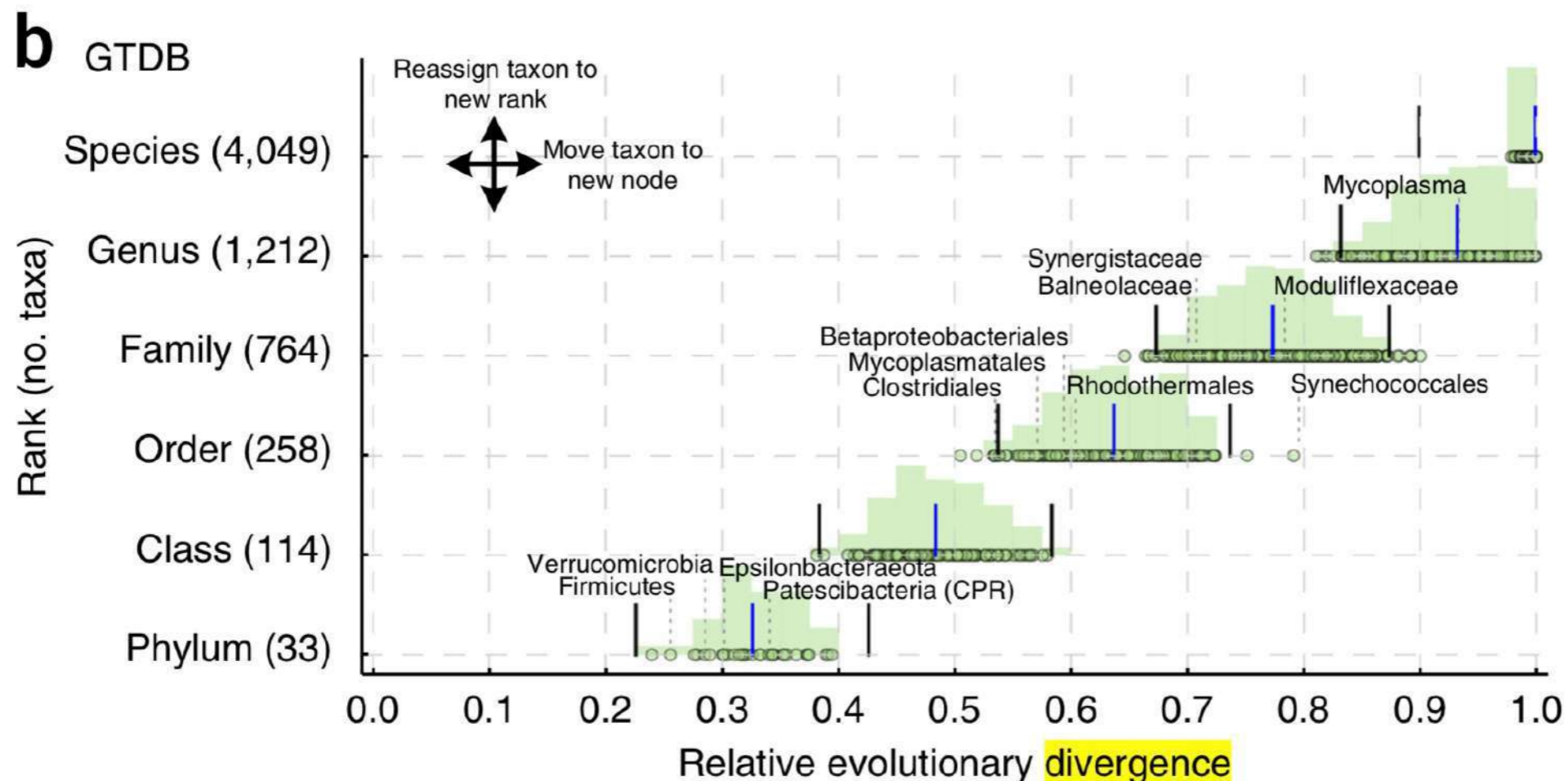
- Microbes with **16S ribosomal RNAs (rRNAs)** that are **$\leq 98.7\%$ identical** are always members of **different species**, because such strong differences in rRNA correlate with **$< 70\%$ DNA-DNA similarity**
- Opposite is not necessarily true, and distinct species have been occasionally described with 16S rRNAs that are **$> 98.7\%$ identical**

Microbial Species III

- **Most uncultured microbes** cannot be assigned to a classical species because we **do not know their phenotype**
- In some cases, uncultured microbes can be assigned a provisional '***Candidatus***' designation if their **16S rRNA sequences are sufficiently different from those of recognized species**, if experimental in situ hybridization can be used to specifically detect them and if a basic description of their morphology and biology has been provided
- **OTU, operational taxonomic unit**, is a definition to classify groups of closely related individuals. It is based on an **empirical observation that 98% similarity threshold on the 16S ribosomal RNA gene** (database reference dependency, loss resolution)
- **ASV, amplicon sequence variance, unique, DNA sequences without clustering, highest degree of resolution** (independent from reference database)
- **Basis of the average nucleotide identity (ANI) of all orthologous genes in complete genome sequences of pairs of strains** → whole genome comparison (**94-96% protein-genes**)

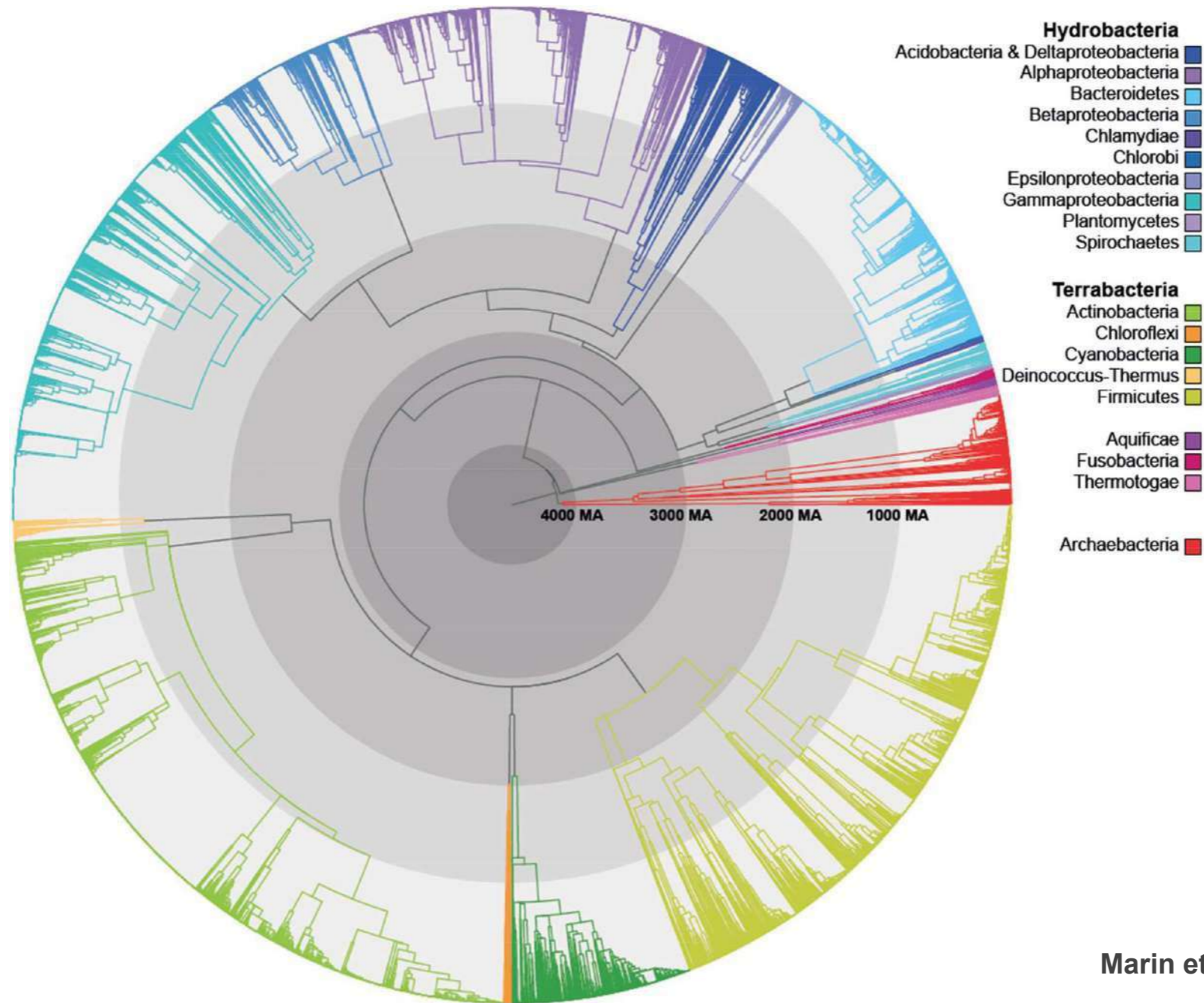
Relative evolutionary divergence

RED values provide an **operational approximation of relative time** with extant taxa existing in the present (RED=1), the last common ancestor occurring at a fixed time in the past (RED=0), and internal nodes being linearly interpolated between these values according to lineage-specific rates of evolution



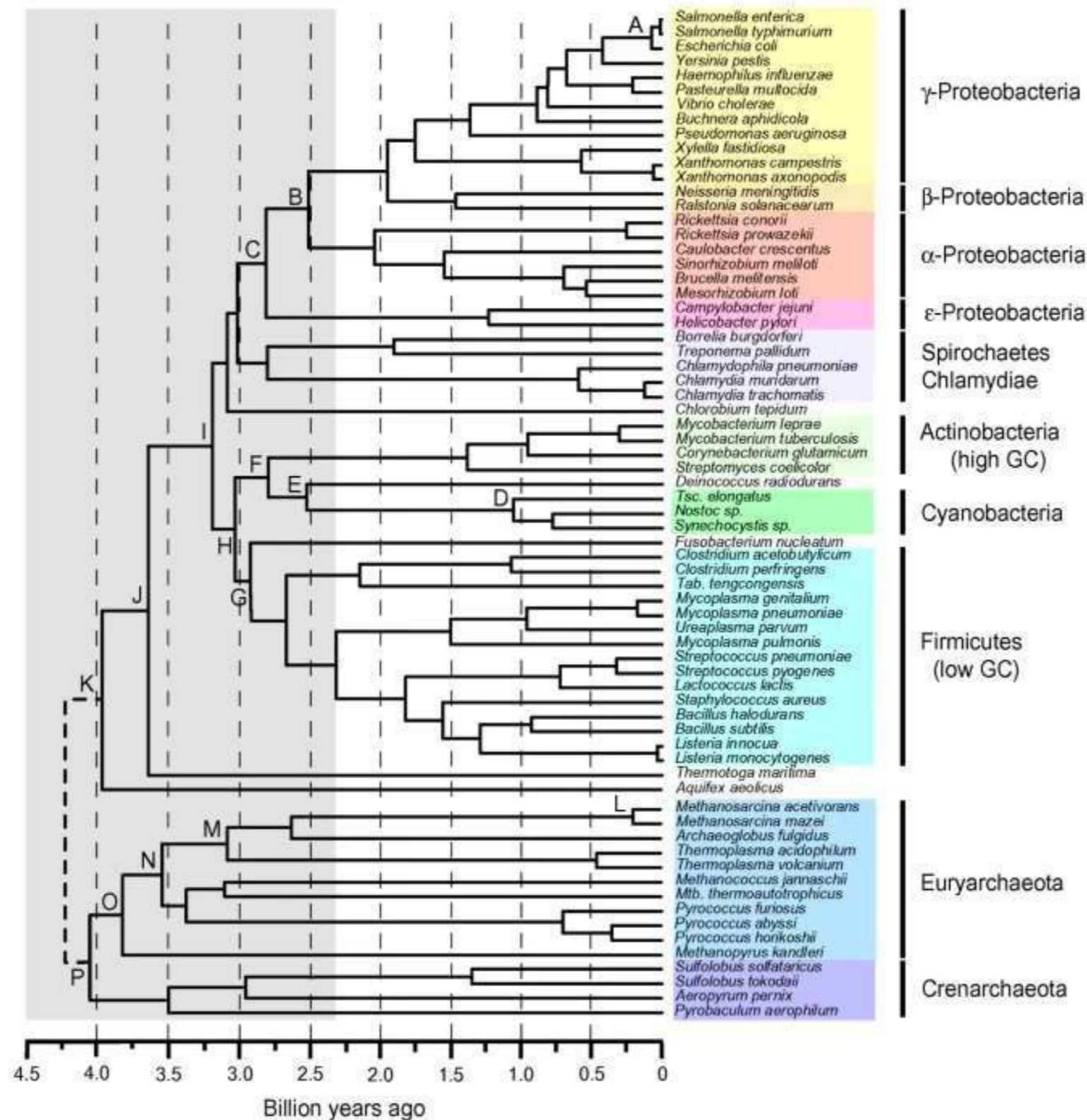
Prokaryote timetree (PTT)

PTT (topology A; 11,784 species) based on the SSU rRNA genes
Divergence times



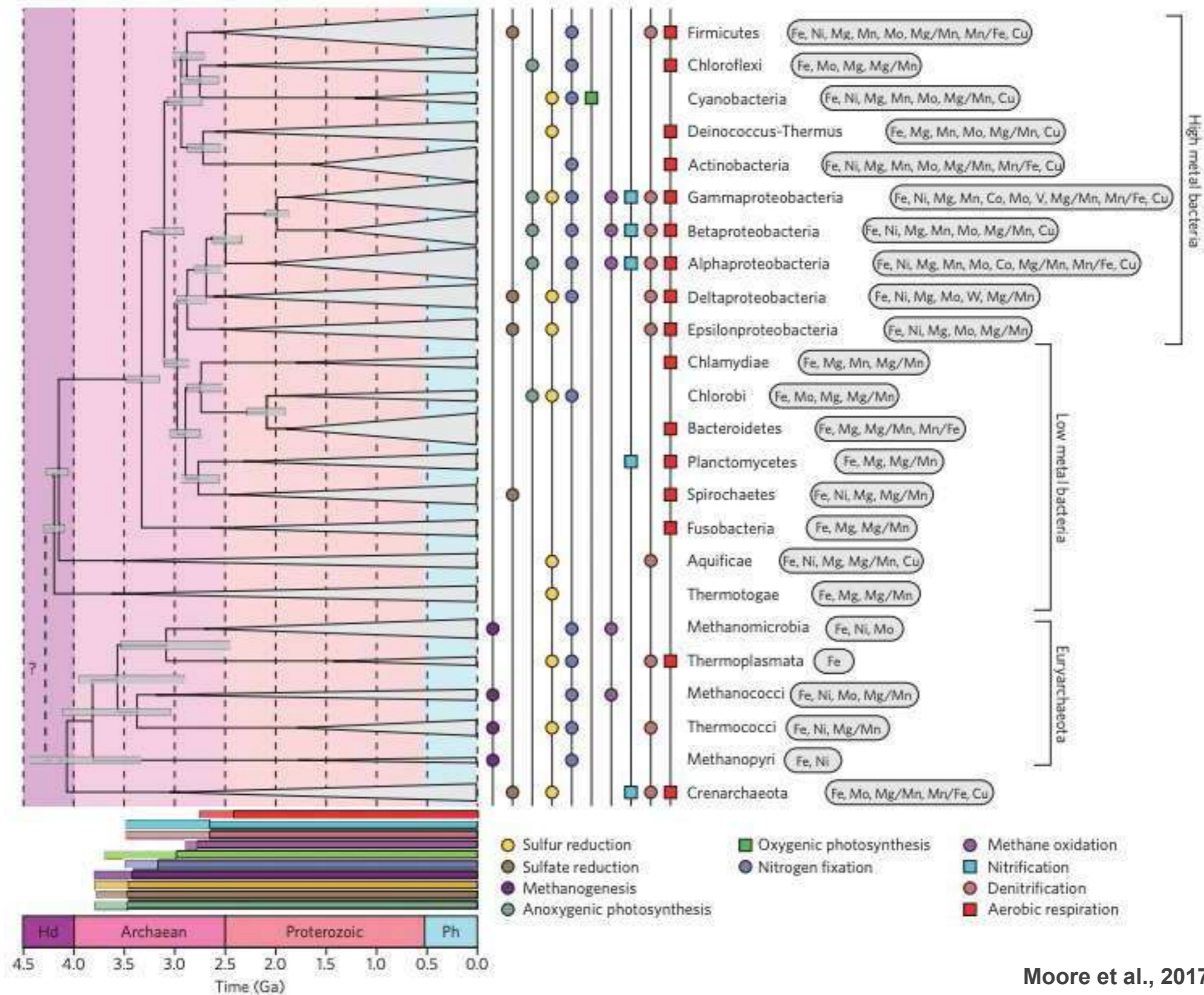
Marin et al., 2016

A genomic timescale of prokaryote evolution



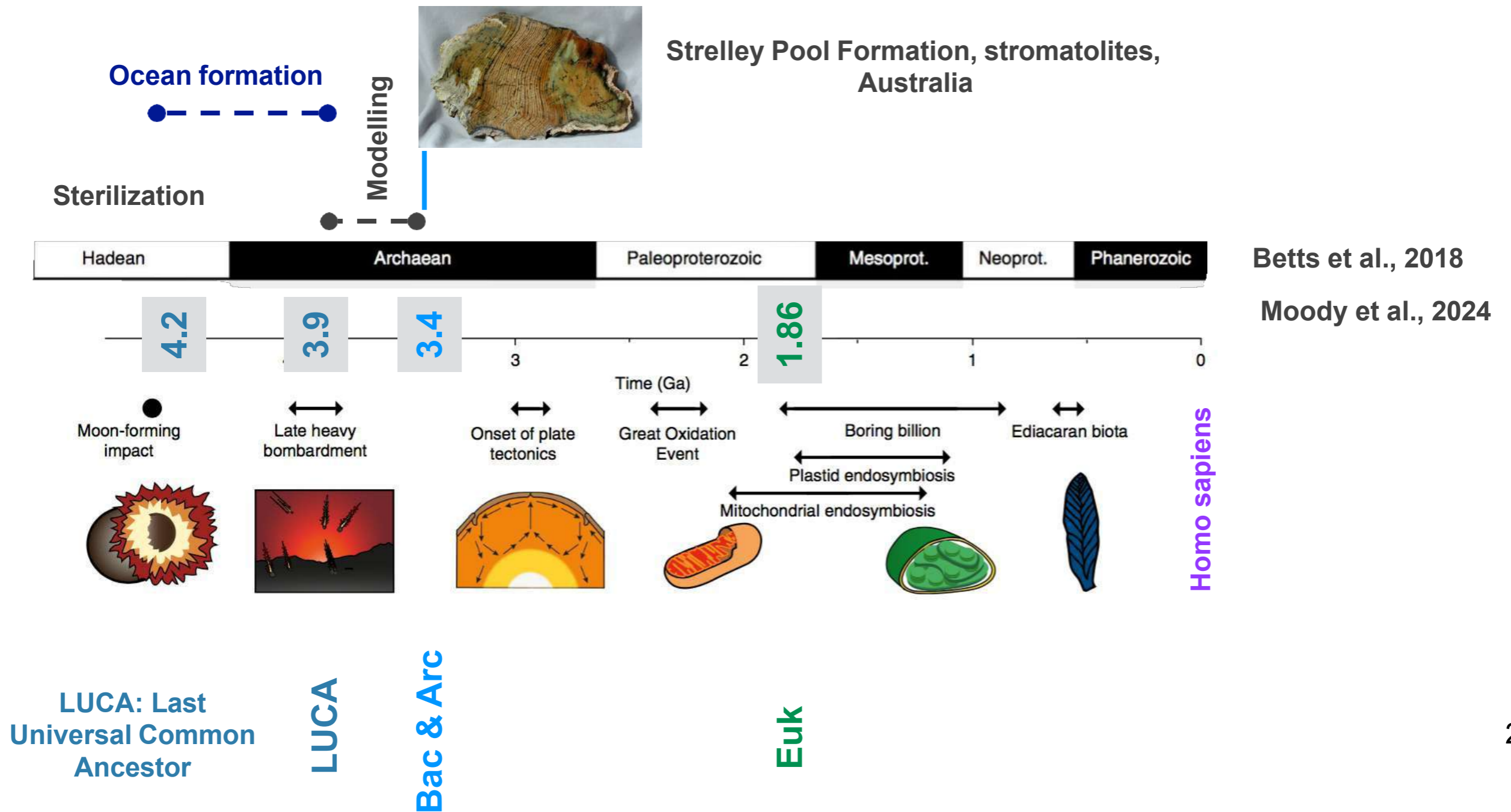
Battistuzzi et al., 2004

Phylogenetic tree of the main lineages of Bacteria and Archaea and their putative divergence times



Moore et al., 2017

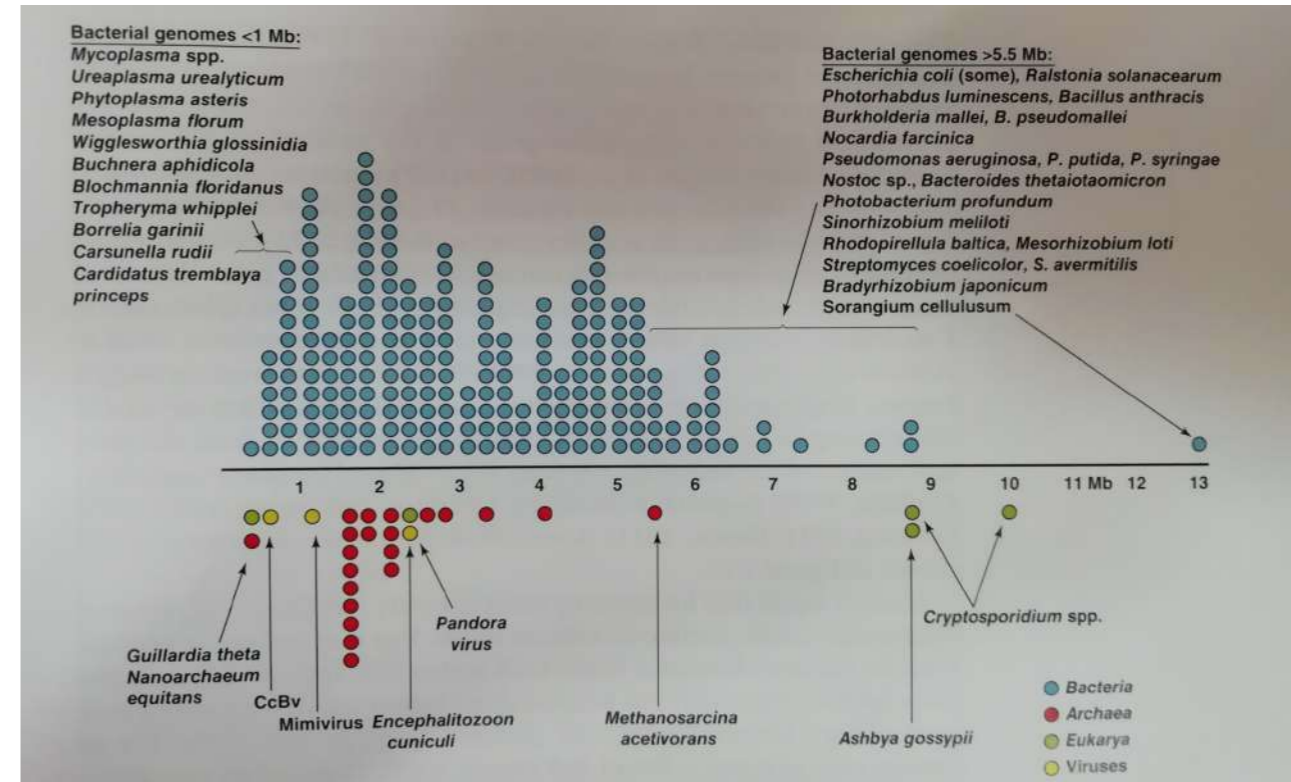
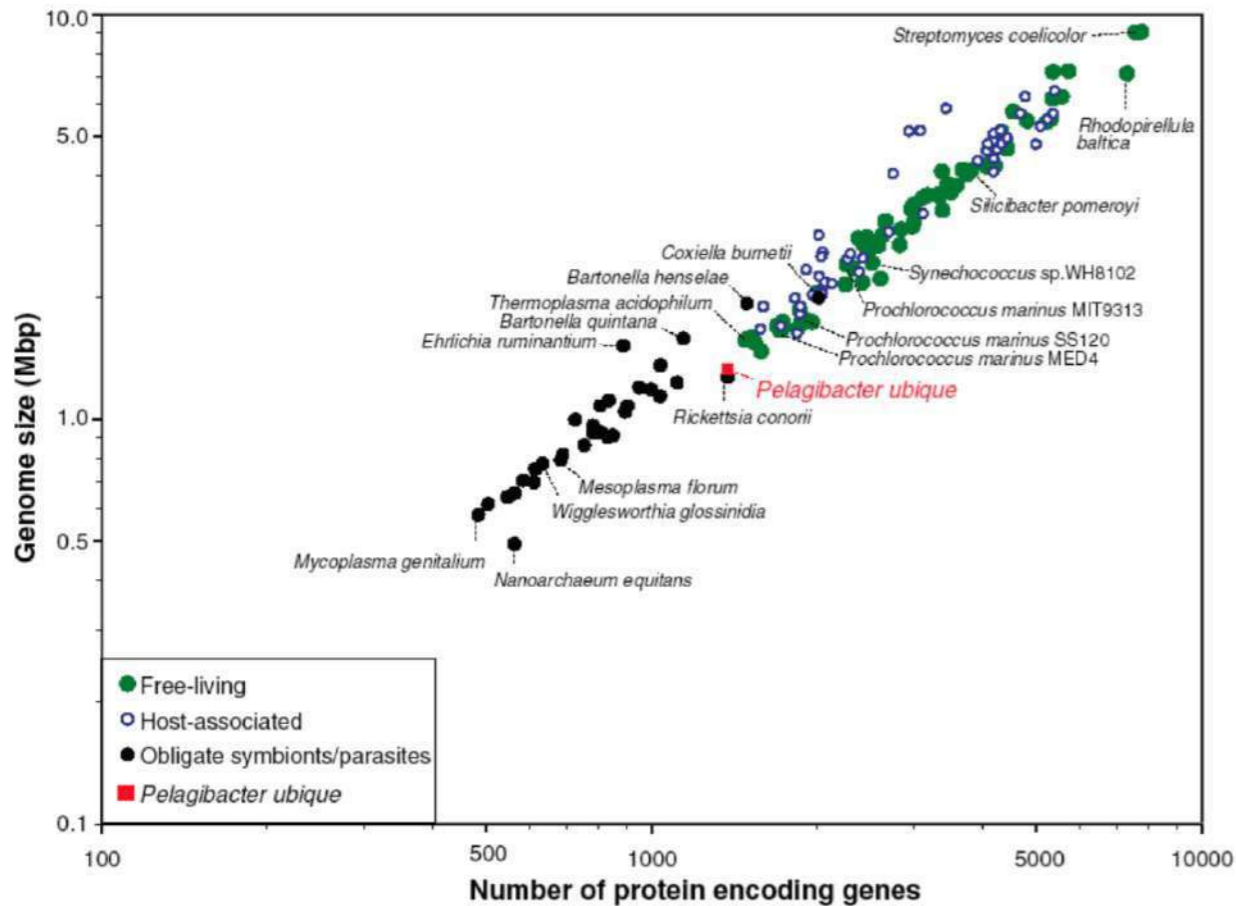
Reconstruction the microbial “coral” of life



- About 1.4–1.9million extant bacterial lineages when lineages are defined by 99% similarity in the 16S ribosomal RNA gene, and that bacterial diversity has been continuously increasing over the past 1billion years (Gyr)
- Recent bacterial extinction rates are estimated at 0.03–0.05per lineage per million years (lineage–1Myr–1), and are only slightly below estimated recent bacterial speciation rates
- Most bacterial lineages ever to have inhabited this planet are estimated to be extinct

Louca et al., 2018

Wide range of microbial genomes



Madsen, 2016

Giovannoni et al., 2005

- Genomes are constantly changes
- Genome size and genes related to life style

Common multiples are:

- 1 kb = 10^3 bp
- 1 Mb = 10^6 bp
- 1 Gb = 10^9 bp

Bacterial genomes are typically expressed in Mb

Cultivability and Phenotypic Analysis

- Phenotype: the physical and chemical characteristics of an organism that can be observed or measured

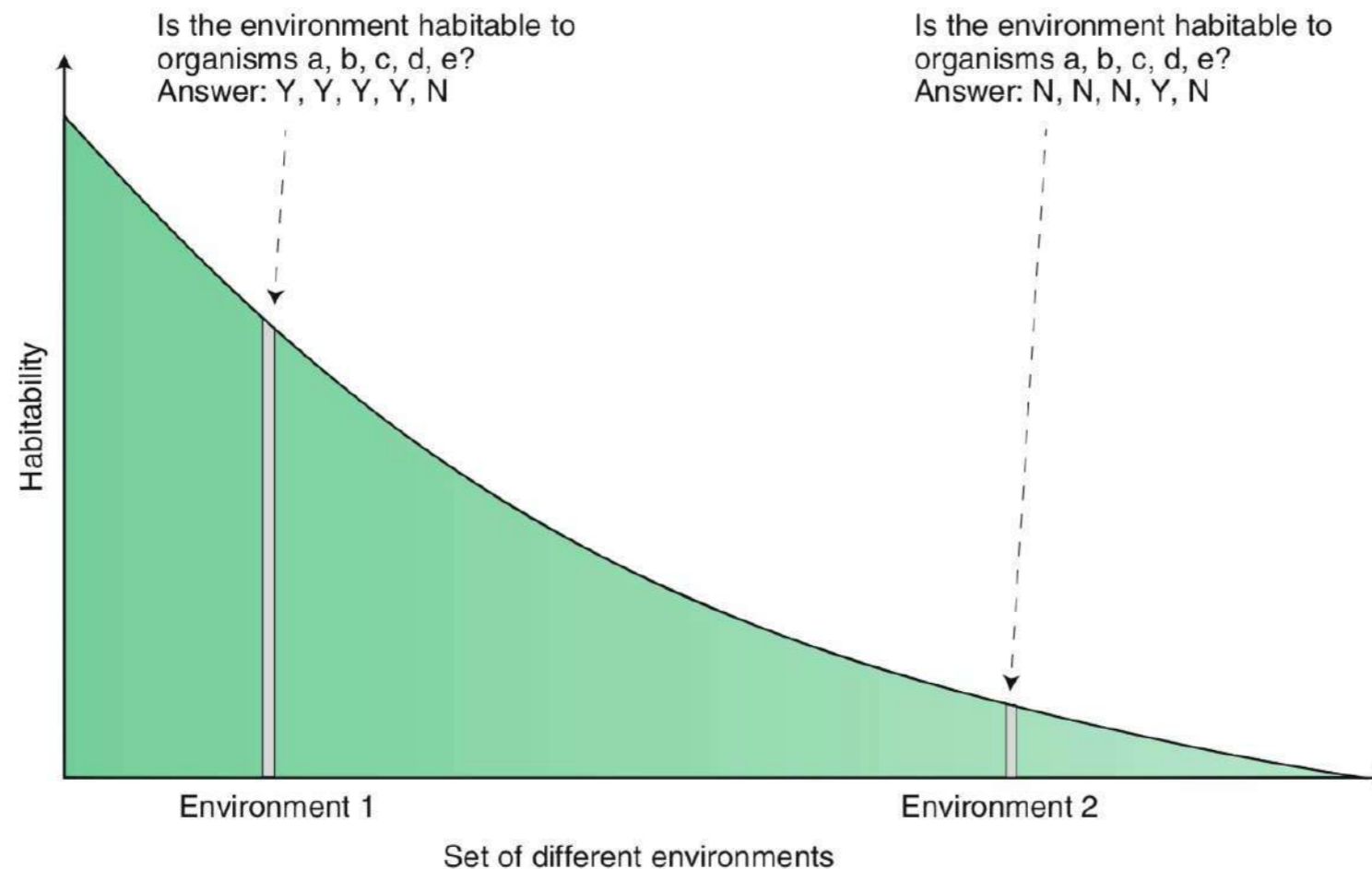
TABLE 13.1 Some phenotypic characteristics of taxonomic value

Category	Characteristics
Morphology	Colony morphology; Gram reaction; cell size and shape; pattern of flagellation; presence of spores, inclusion bodies (e.g., PHB, ^a glycogen, or polyphosphate granules, gas vesicles, magnetosomes); capsules, S-layers, or slime layers; stalks or appendages; fruiting body formation
Motility	Nonmotile; gliding motility; swimming (flagellar) motility; swarming; motile by gas vesicles
Metabolism	Mechanism of energy conservation (phototroph, chemoorganotroph, chemolithotroph); utilization of individual carbon, nitrogen, or sulfur compounds; fermentation of sugars; nitrogen fixation; growth factor requirements
Physiology	Temperature, pH, and salt ranges for growth; response to oxygen (aerobic, facultative, anaerobic); presence of catalase or oxidase; production of extracellular enzymes
Cell lipid chemistry	Fatty acids; ^b polar lipids; respiratory quinones
Cell wall chemistry	Presence or absence of peptidoglycan; amino acid composition of cross-links; presence or absence of cross-link interbridge
Other traits	Pigments; luminescence; antibiotic sensitivity; serotype; production of unique compounds, for example, antibiotics

Niche

Habitability

- **Habitability is a binary concept** at a fundamental level
- Consider an environment with **respect to one microorganism then integrate** the answers for all microbes –> derive of a continuum
- Assessment of habitability is circumscribed by the state of biological knowledge and it is always open to improvement

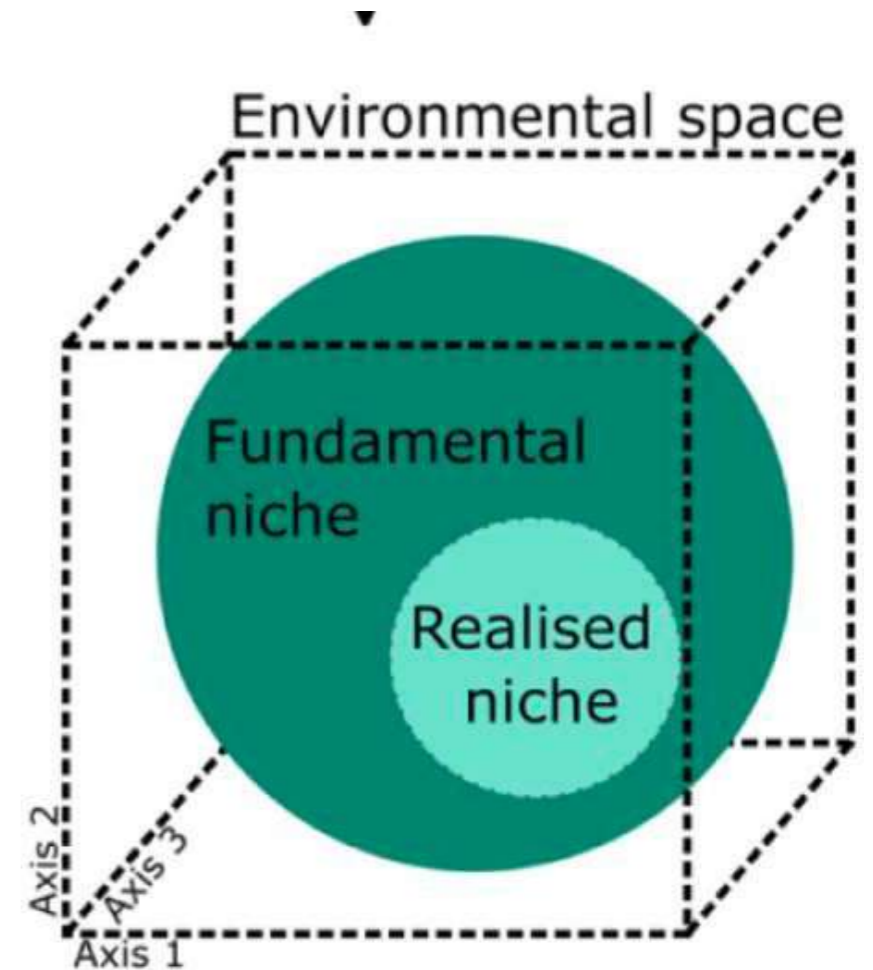


Cockell et al. 2019

Hutchinson's definitions:

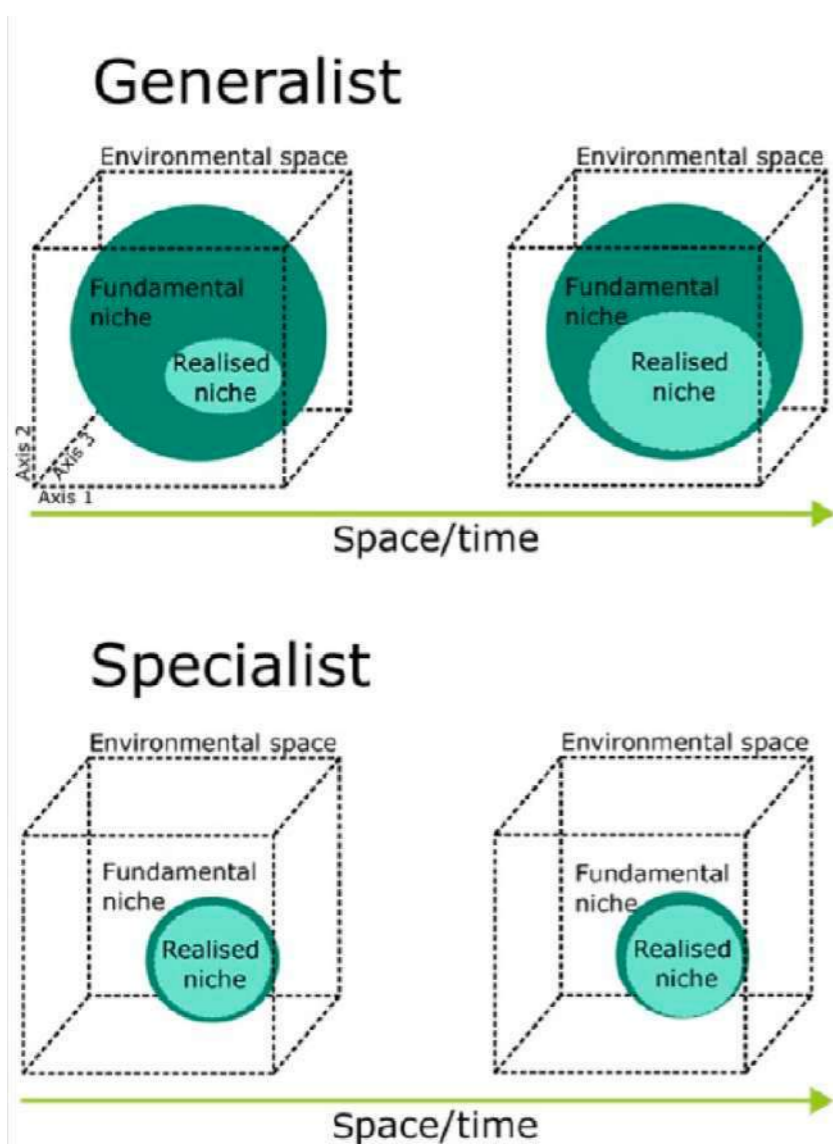
1. **Fundamental environmental niche:** the set of environmental conditions in which a species can theoretically (i.e., physiologically) live and reproduce in (e.g., as defined experimentally)
2. **Realised environmental niche:** the restricted set of conditions a species actually occupies in situ when accounting for biological interactions (e.g., competition, predation), thus a subset of the fundamental niche

Niches as '**n-dimensional hypervolumes**', where the dimensions are the set of abiotic conditions that define the requirements of an individual or a species for its population to persist, constrained or not by biotic factors



Malard & Guisan 2023

Sales, L.P. et al. (2021) What do you mean by 'niche'? Modern ecological theories are not coherent on rhetoric about the niche concept. Acta Oecol. 110, 103701



Malard & Guisan 2023

- **Generalist species can thrive in a variety of habitats or situations**
- **Specialists are restricted to a smaller set of conditions**

GENES

Metabolic plasticity is the capacity to alter a physiological response to environmental conditions

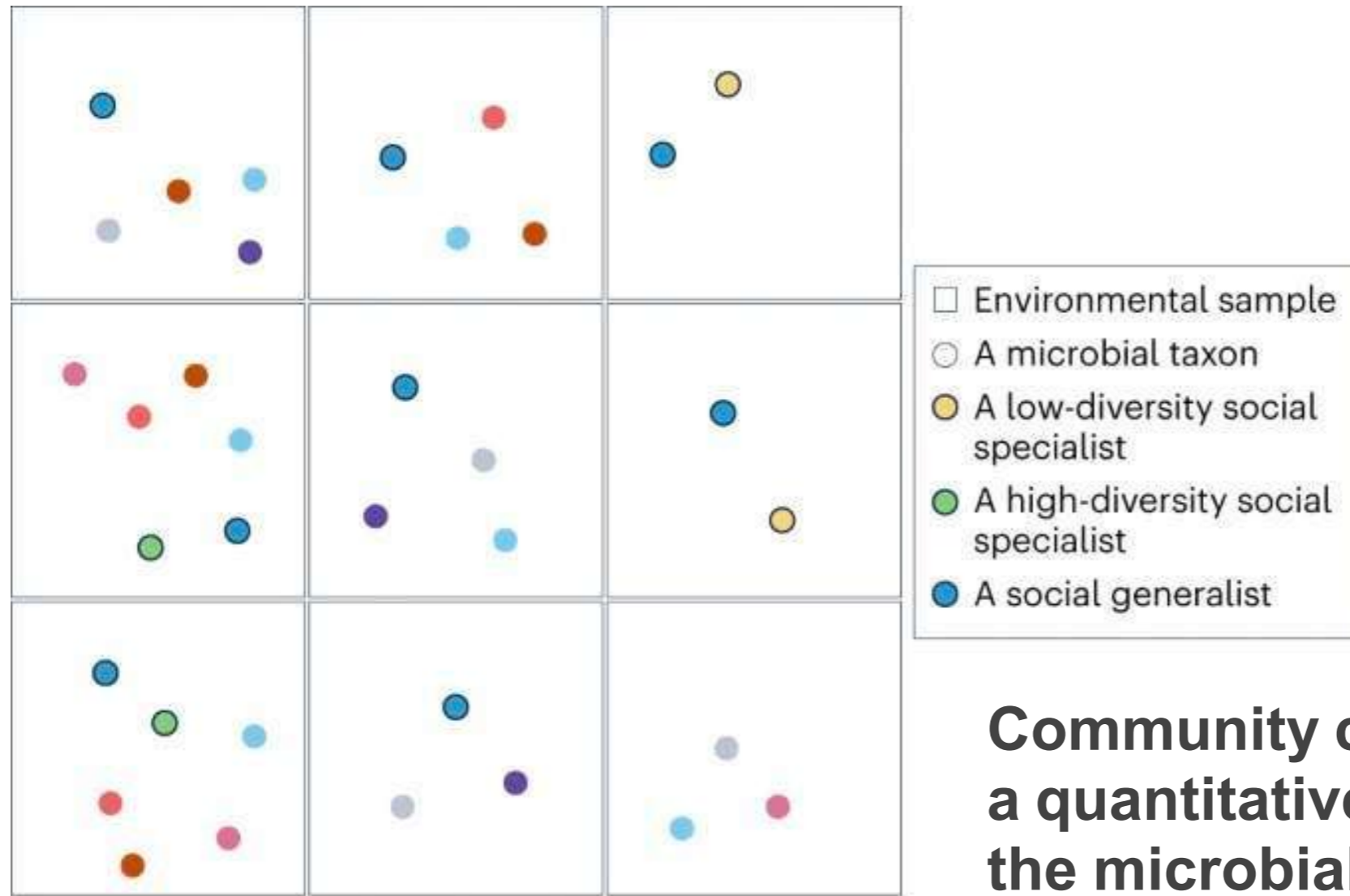
Generalist – > a large fundamental metabolic niche with high metabolic plasticity, occupying different fractions of the fundamental niche as a function of the environmental conditions and potentially changing in time and/or space

Specialist with a restricted distribution likely has a small fundamental metabolic niche because it may **lack many of the genes required to adapt to other environmental conditions** – > the fundamental metabolic niche is likely small with limited metabolic plasticity and, as a result, a specialist will always occupy the same fraction of the fundamental niche, performing the limited number of functions encoded in its genome

The social niche

‘**Social niche**’, which reflects the degree of **constraint** in the community of **other microbes** with which the species is observed in environmental samples

Social niche gradient at the microscale



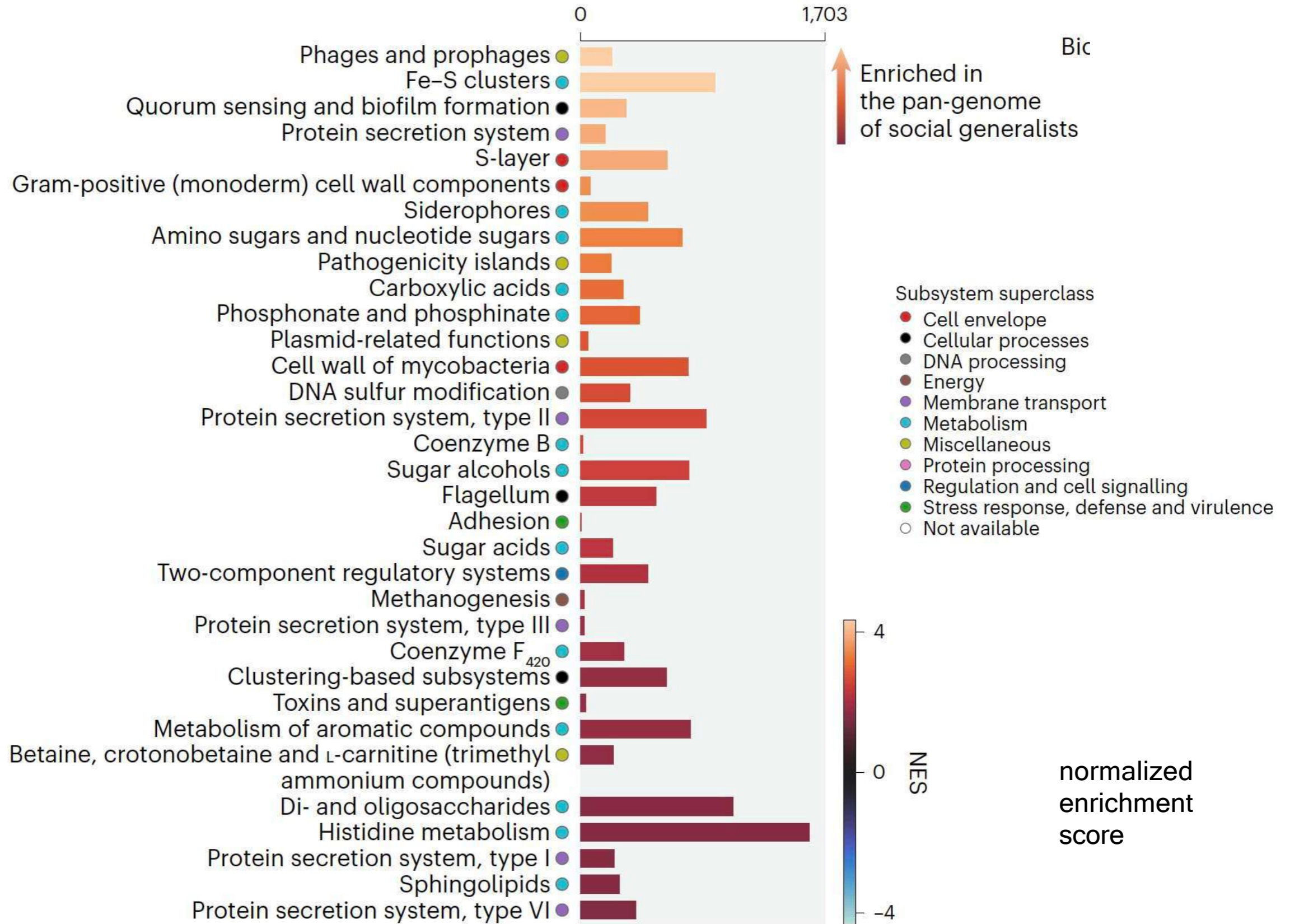
Community composition similarity as a quantitative ecological feature of the microbial social niche

Biodiversity

- The squares represent independent environmental samples comprising several microbial taxa, as coloured circles
- The dark blue microorganism occurs in communities that are compositionally very dissimilar across the different samples: social generalist
- The yellow microorganism always occurs with the same dark blue taxon: a social specialist
- **Social specialists can be found in either low-diversity samples (as with the yellow microorganism) or in high-diversity samples (as with the green microorganism, which is always found in samples with the same composition)**

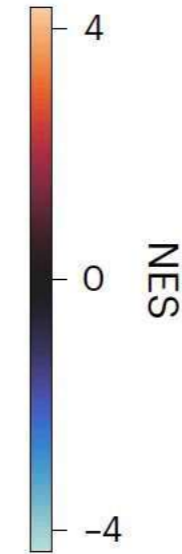
Social niche breadth: Social Generalists

von Meijenfeldt et al., 2023



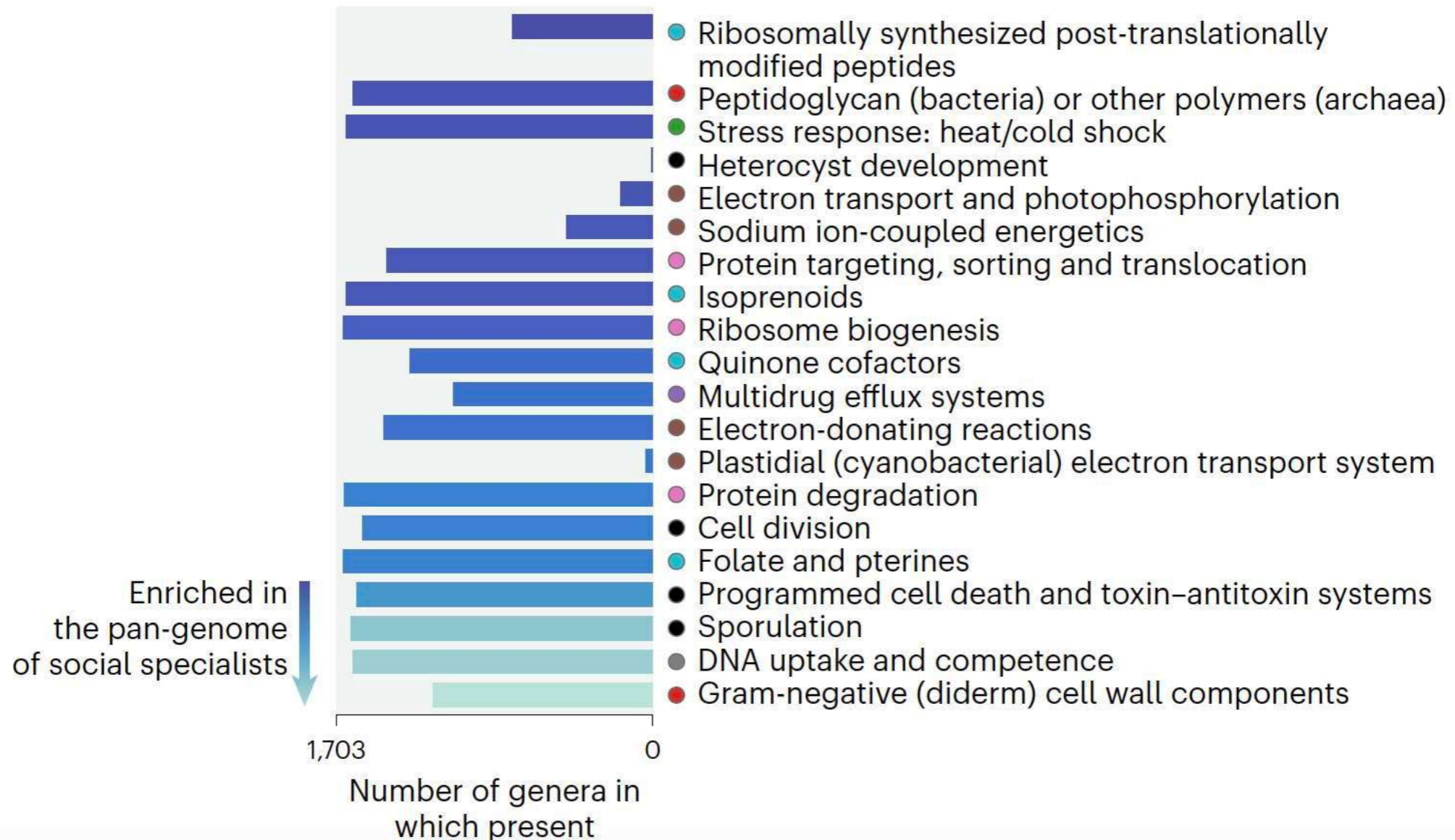
Social niche breadth: Social Specialists

- Subsystem superclass
- Cell envelope
 - Cellular processes
 - DNA processing
 - Energy
 - Membrane transport
 - Metabolism
 - Miscellaneous
 - Protein processing
 - Regulation and cell signalling
 - Stress response, defense and virulence
 - Not available



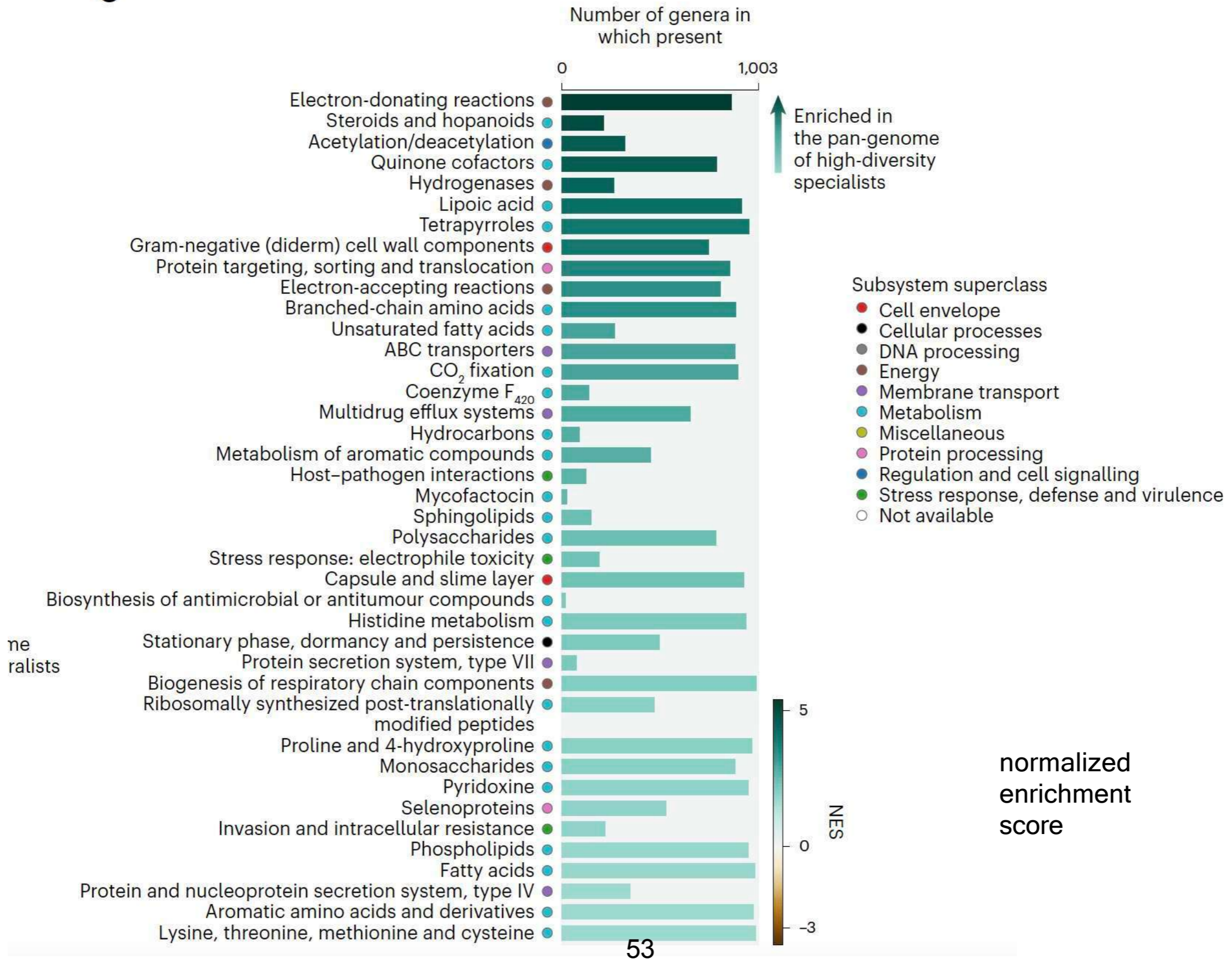
normalized enrichment score

von Meijenfeldt et al., 2023



Social niche breadth: High-diversity specialists

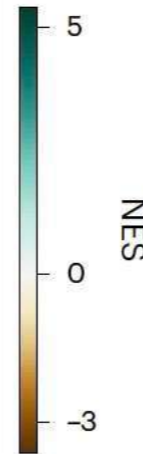
C



Social niche breadth: Low-diversity specialists

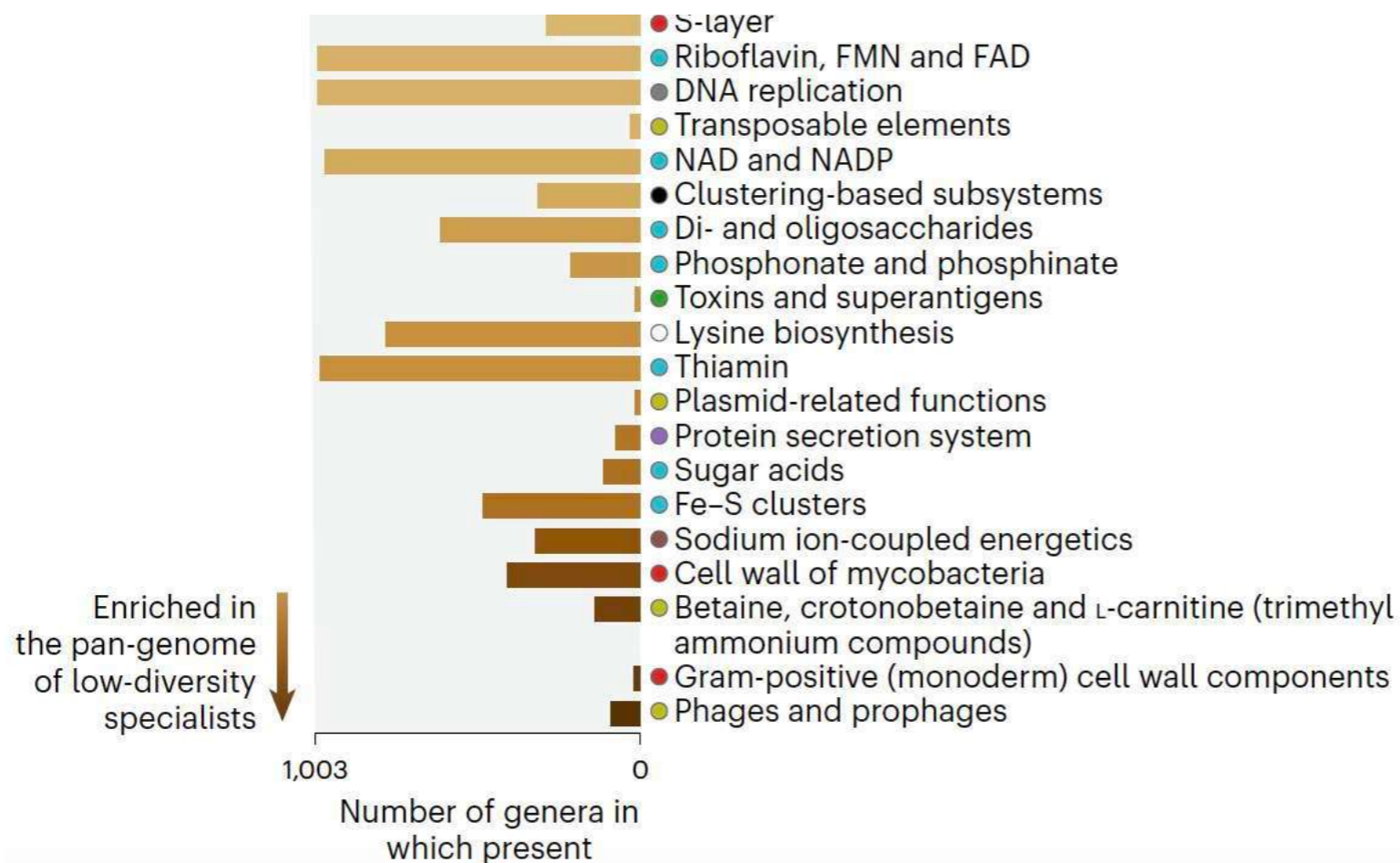
Subsystem superclass

- Cell envelope
- Cellular processes
- DNA processing
- Energy
- Membrane transport
- Metabolism
- Miscellaneous
- Protein processing
- Regulation and cell signalling
- Stress response, defense and virulence
- Not available



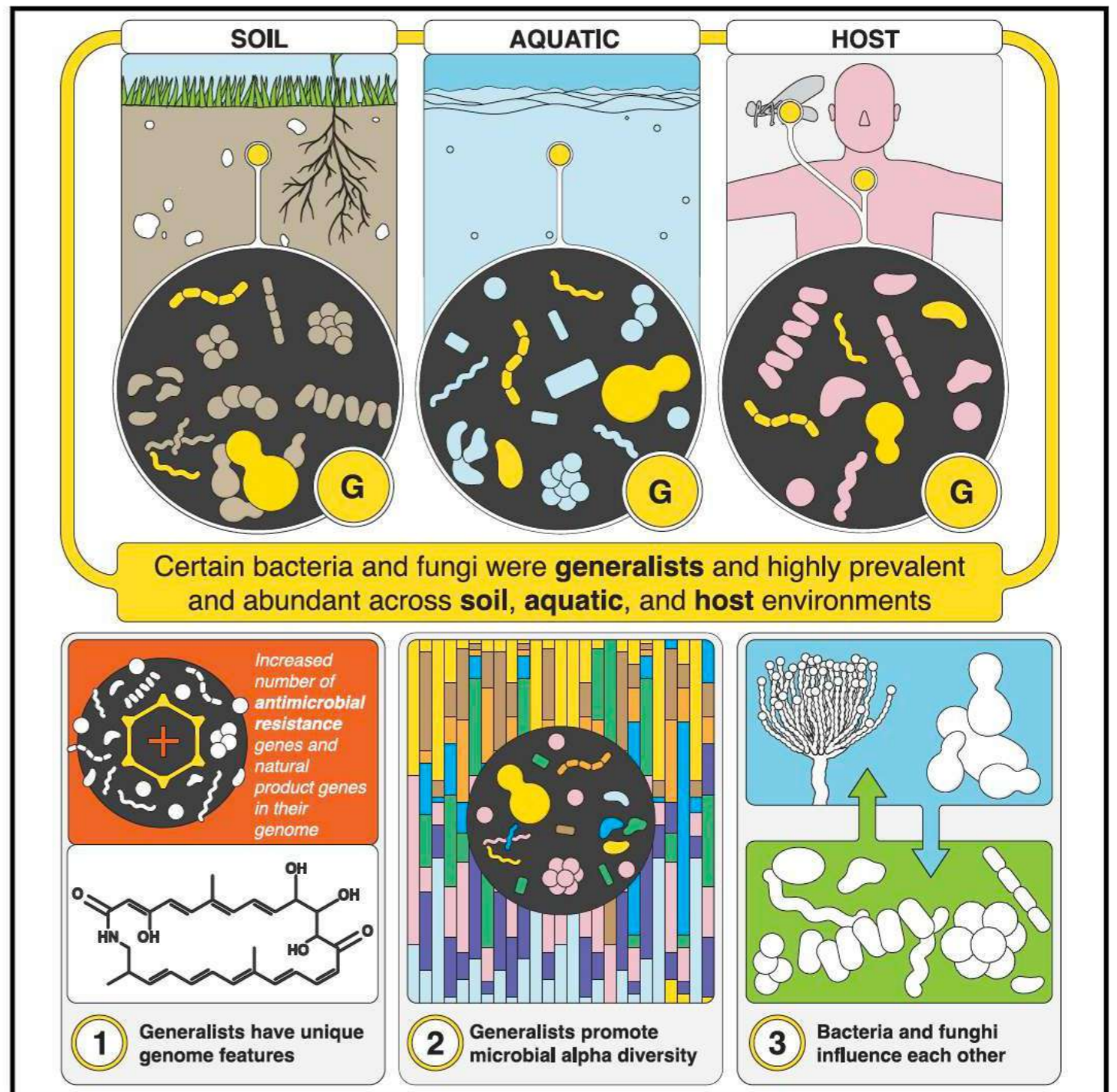
normalized
enrichment
score

von Meijenfeldt et al., 2023



Generalists vs. Specialists

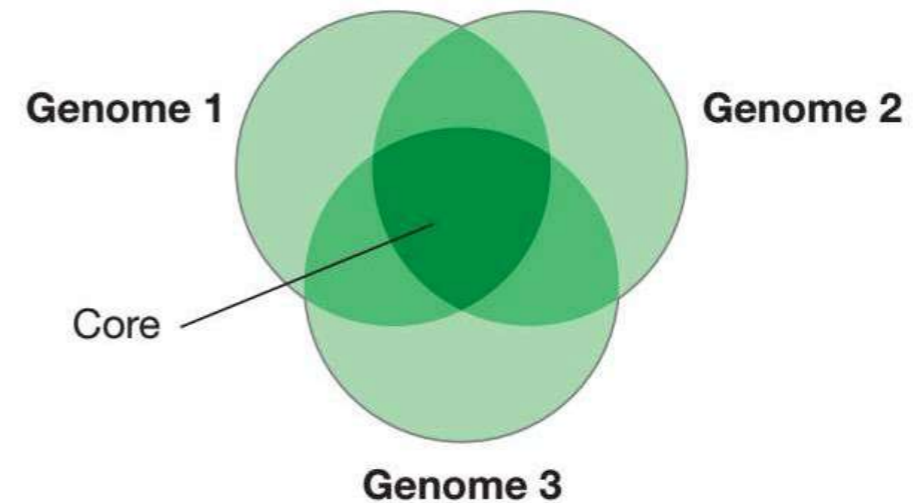
- Bacterial and fungal **generalists** are **widely distributed** in aquatic, host, and soil biomes
- Generalists have **larger genomes** with more **secondary metabolites** and **AMR genes**
- Samples containing generalists show **higher alpha diversity**
- Generalists **underpin cross-kingdom** community structure



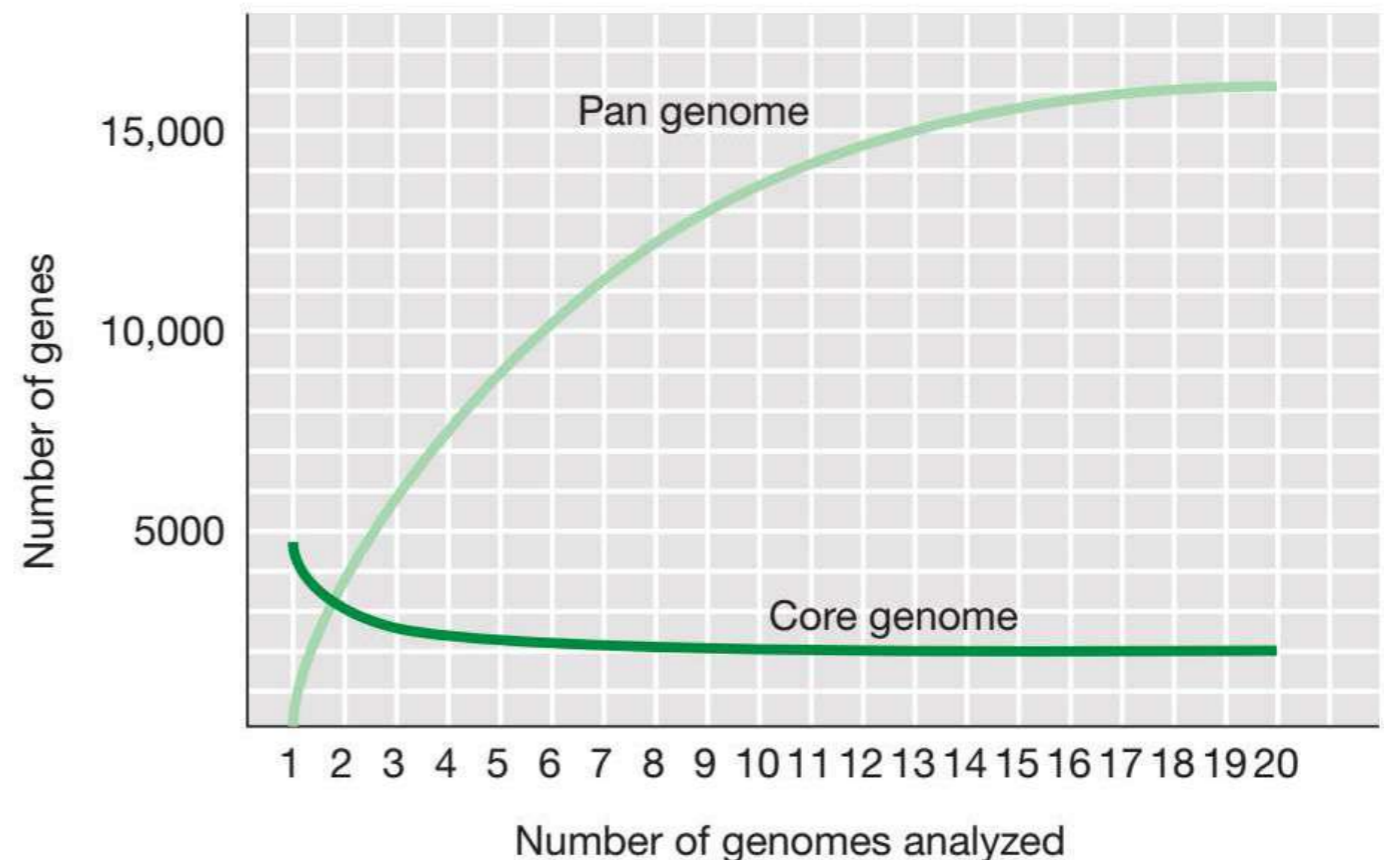
Ecological theory predicts that generalists, or organisms that are fit across a wider range of conditions, will be more resilient to changing environmental conditions

Microbial genome

- Microbial genomes are **dynamic**: genome size and gene content can vary considerably between strains of a species
- **Core genome** is defined as the **set of all genes shared** by a species
- **Pan genome** is defined as the core genome plus **genes whose presence varies among strains of a species**



(a)



(b)

Generalist vs Specialist genome structure

Genome structure reflects microbial lifestyle

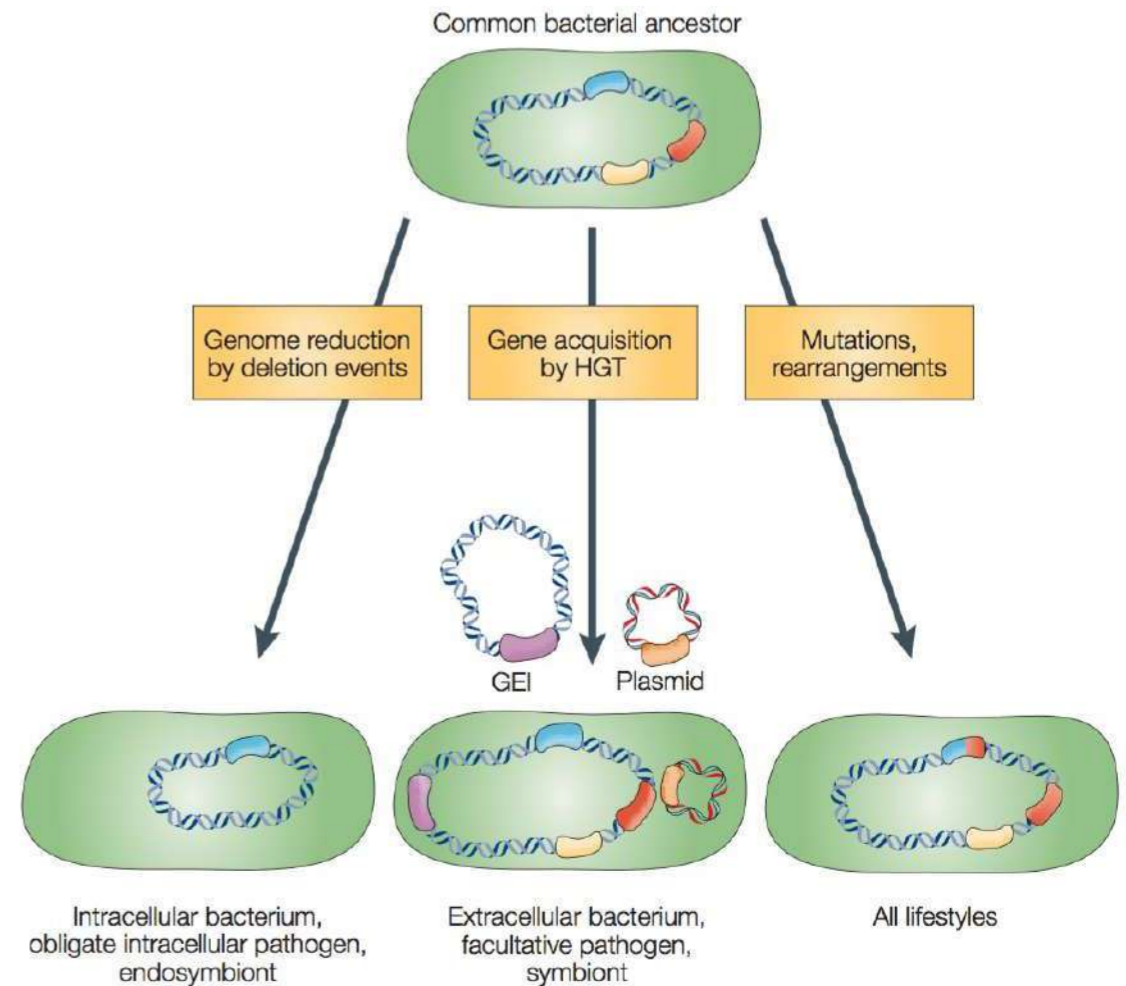
Genome reduction is common in **intracellular bacteria**

(obligate intracellular pathogens, endosymbionts)
contributes to the evolution of strictly host-dependent bacterial variants – as microbes rely on the host cell to compensate for the gene functions that are lost

Gene acquisition by horizontal transfer between different species is common in **extracellular bacteria** (facultative pathogens, symbionts), which involves **mobile genetic elements** (plasmids, genomic islands, GEIs, and bacteriophages), **increases the versatility and adaptability** of the recipient – allows microbes to **adapt** to a new or changing environment

Point mutations and genetic rearrangements constantly contribute to evolution of new gene variants in **all types** of bacteria

Generalist genera are older than specialist genera and have large and open pan-genomes with which they have adapted to different habitats



Keystone Species

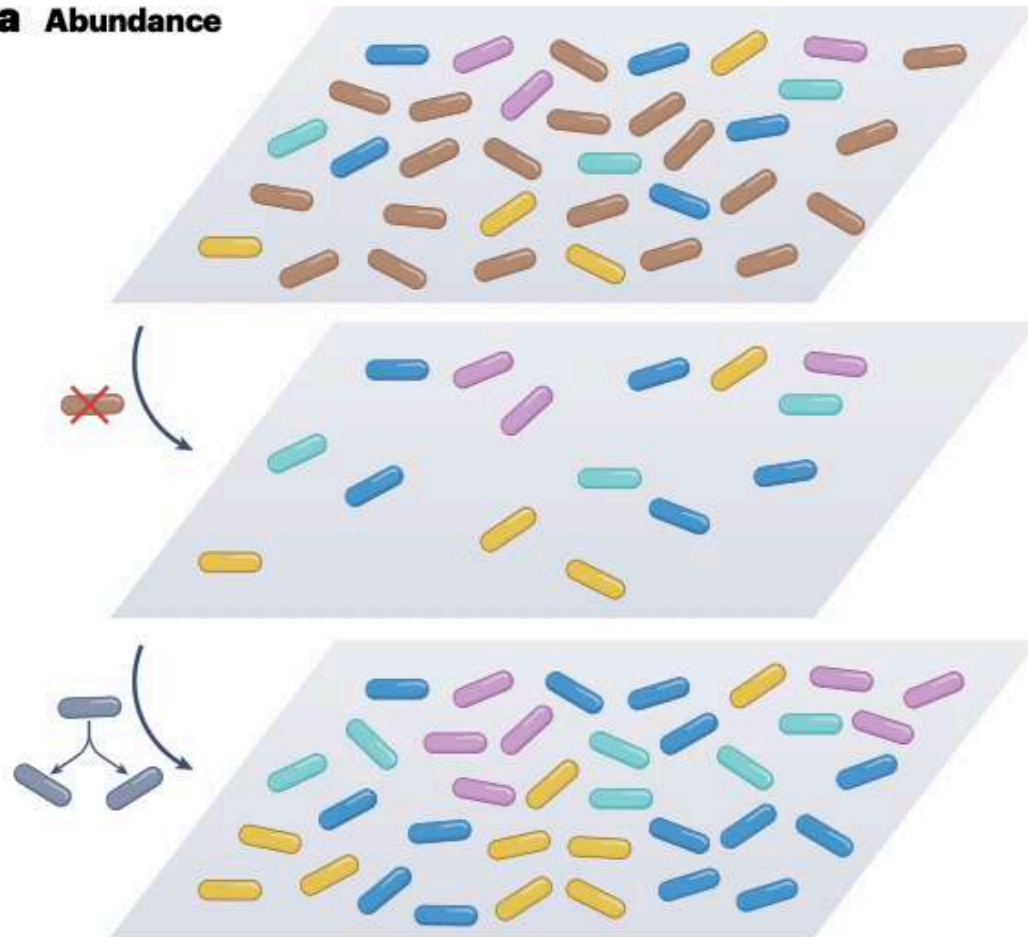
Microbial Guilds

Functional Hubs

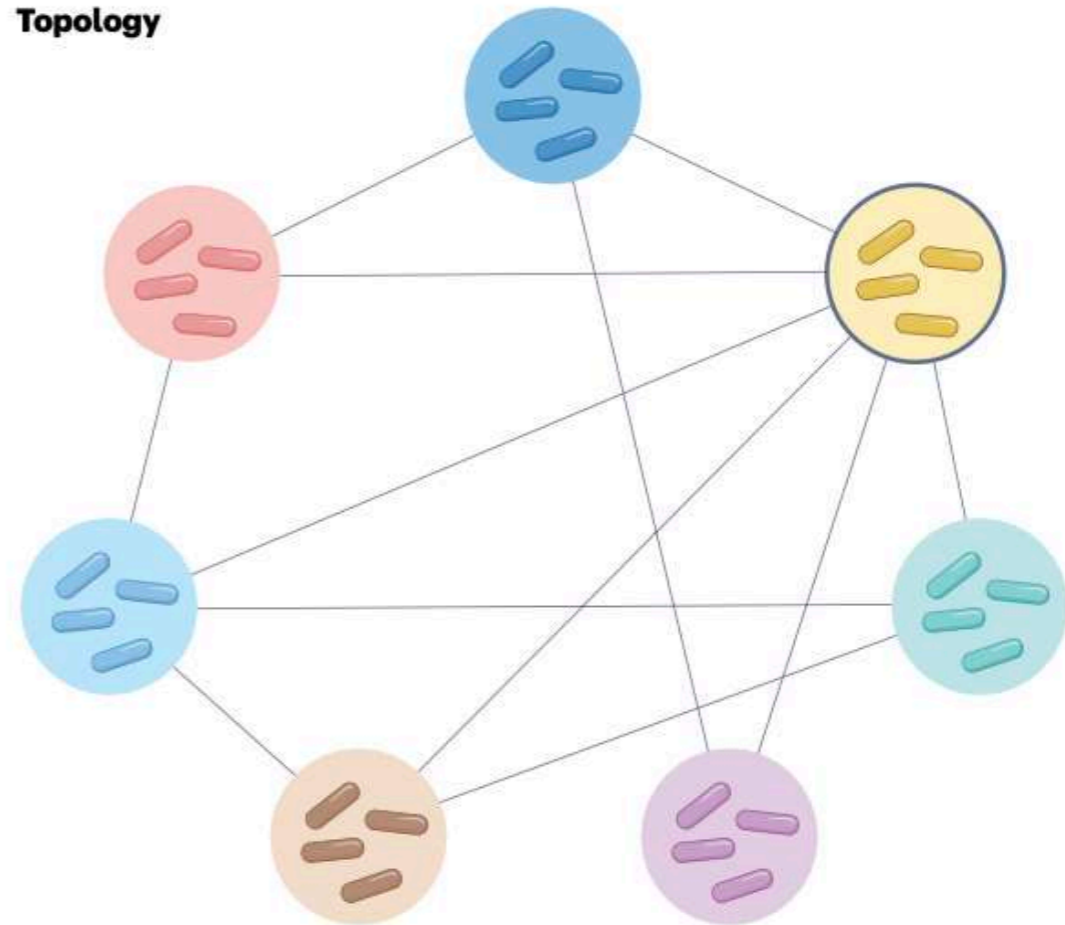
Feature	Keystone Species	Microbial Guild	Functional Hub
Defined by	Impact on community	Shared ecological function	Network connectivity
Abundance	Often low	Variable	Variable
Role	Critical for stability	Redundant contributors	Connector or coordinator
Identified by	Experimental removal, impact	Functional assays	Co-occurrence network analysis

Mechanisms of keystone-ness

a Abundance



b Topology



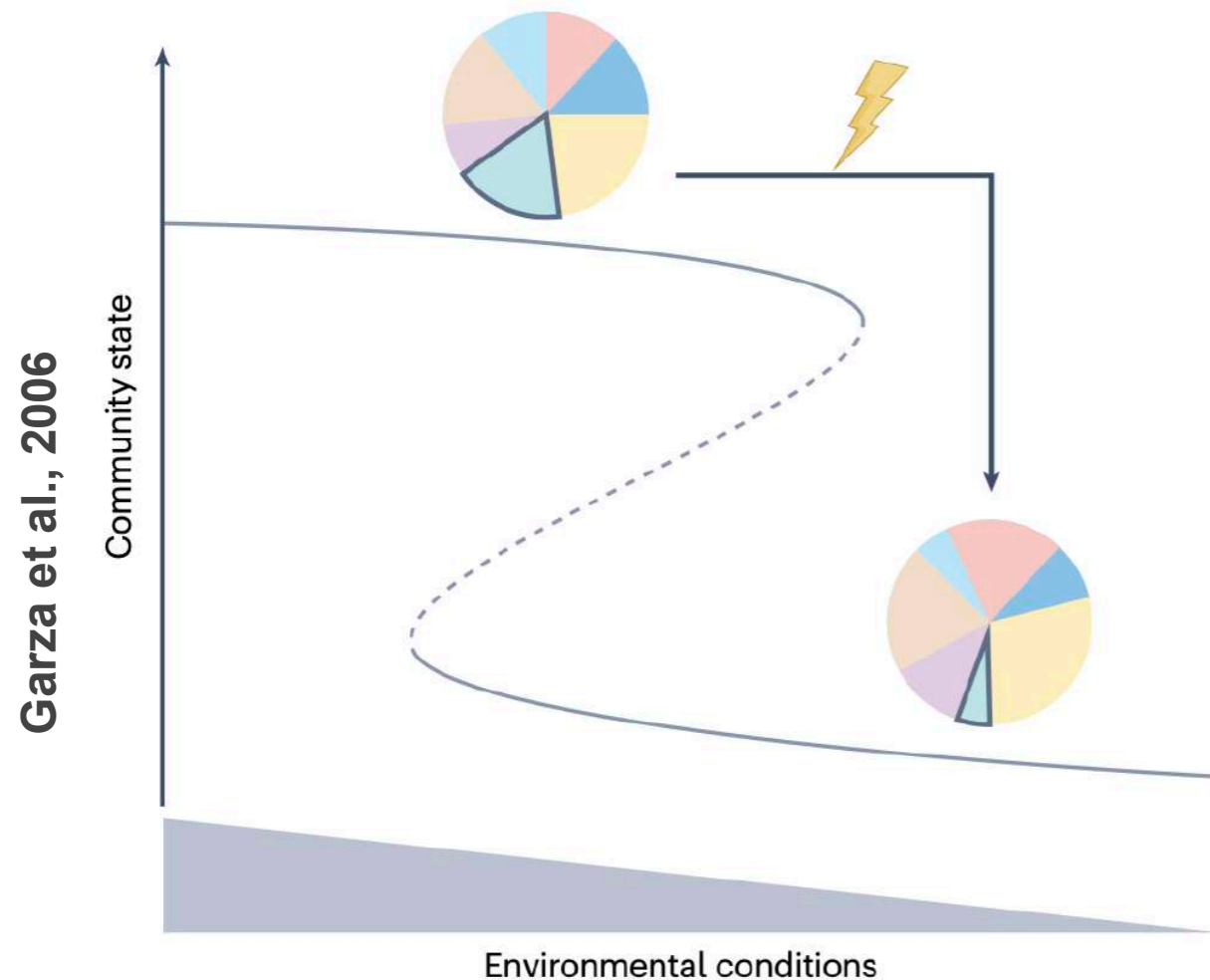
Garza et al., 2006

Abundance: the removal of an abundant taxon (top and middle panels) leaves more space and resources for other taxa to grow (bottom panel, indicated by cell division)

Topology: taxa or functions that are directly or indirectly connected to many other taxa or functions have a disproportionately high influence on community composition (yellow cells)

Mechanisms of keystoneeness

c Multistability



Multistability: the perturbation of taxa that are tipping elements (bold border in the pie charts) can induce a switch from one steady state to another.

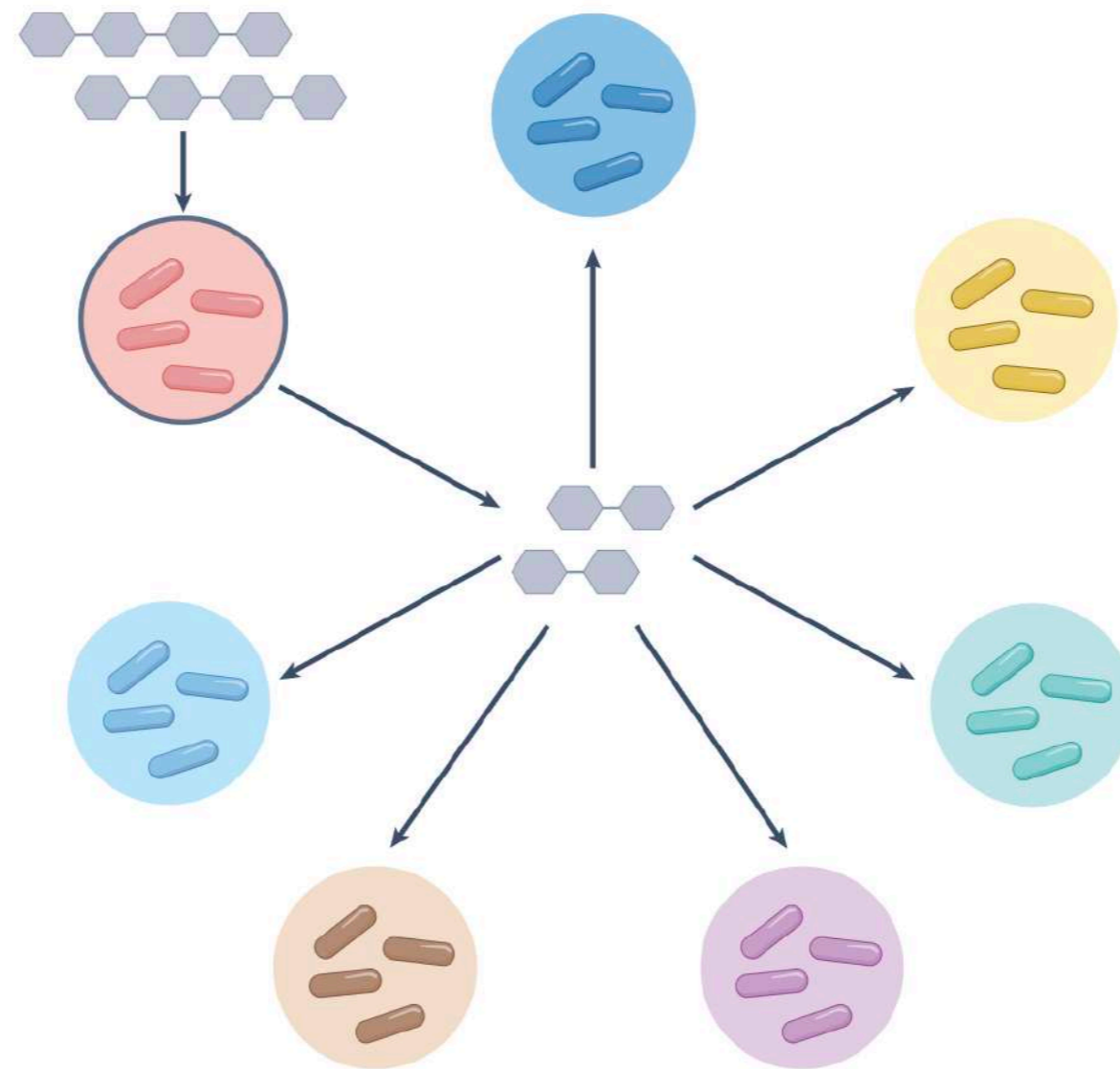
The x-axis represents changing environmental conditions, and the lightning bolt represents the perturbation that drives the community to a new state (indicated by the arrow).

The bold line represents stable and the dashed line represents unstable steady states of a microbial community in specific environmental conditions.

The mirrored S shape means that the microbial community can occur in more than one stable state in the same environmental conditions.

Mechanisms of keystoneeness

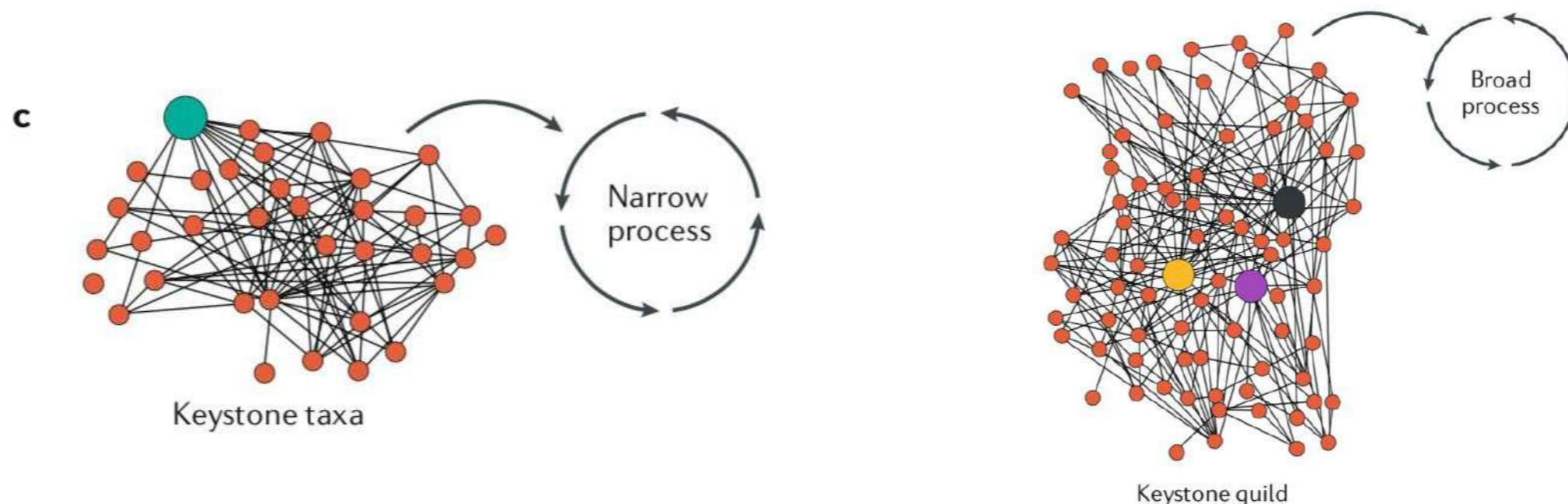
d Unique function



Unique function: taxa with unique functions that impact several other community members can be keystones. This is exemplified here by the red taxon, which degrades a polymer into simpler units that other taxa can then consume

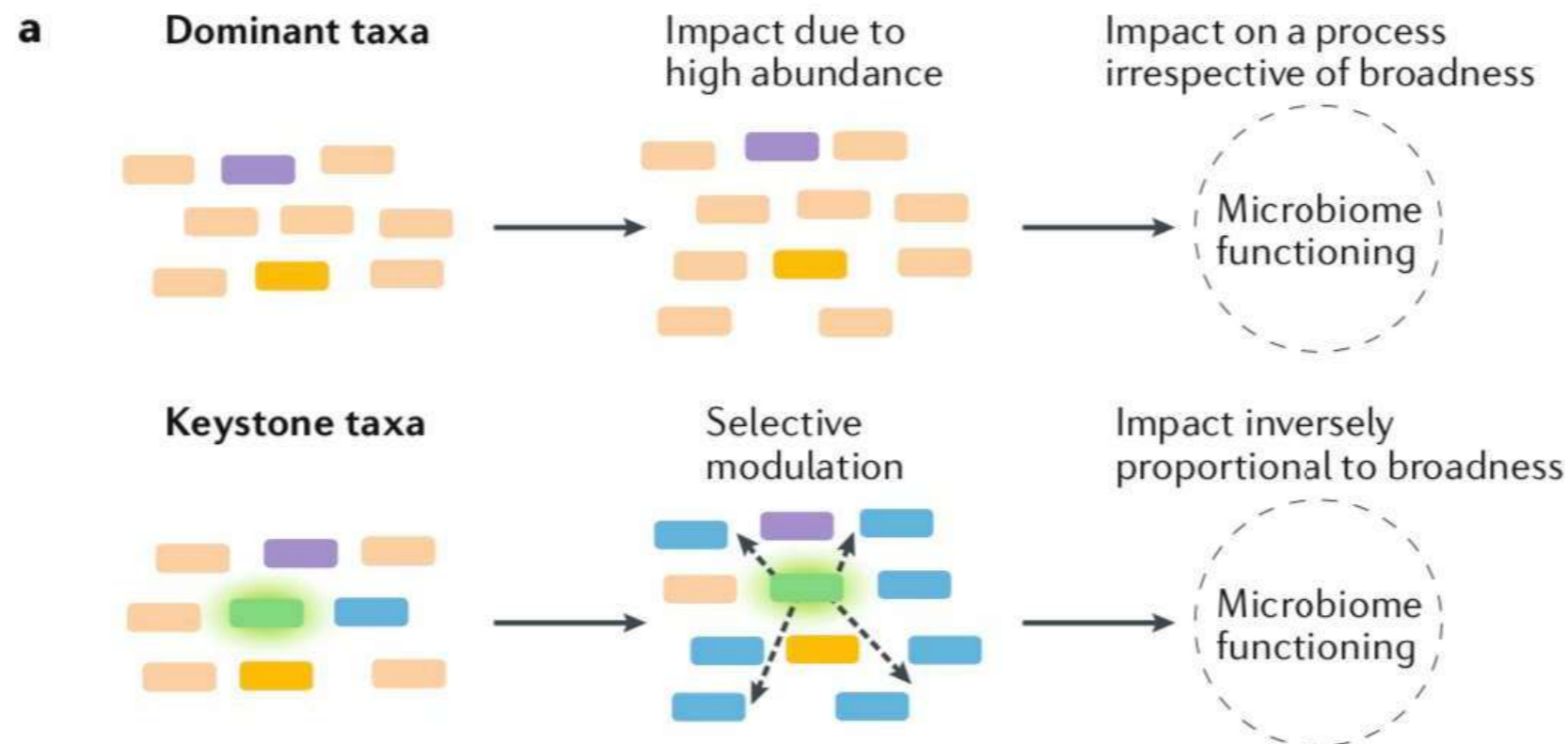
Keystone taxa, I

- **Microbial keystone taxa** are **highly connected** taxa that individually or in a guild (**groups of keystone taxa with similar functioning**) exert a **considerable influence** on microbiome structure and functioning irrespective of their abundance across space and time
- Microbial keystone taxa have a unique and crucial role in microbial communities, and their removal can cause a **dramatic shift** in microbiome structure and functioning
- **Keystone taxa are driver of microbiome structure and functioning**



Keystone taxa, II

- Keystone taxa (green) **exert their influence irrespective of their abundance**
- **Breadness implies** that a **particular process consists of many steps** and involves **diverse** microbial groups
- Keystone taxa exert their **influence by selectively modulating accessory microorganisms**, and thus, they might have a greater influence on **narrow processes (the processes that consist of a single step or a few steps and involve a select group of microorganisms)**
- Accessory microorganisms whose abundance is selectively promoted by keystone taxa are shown in blue, whereas other community members are shown in dark orange and purple



Computational vs Empirical

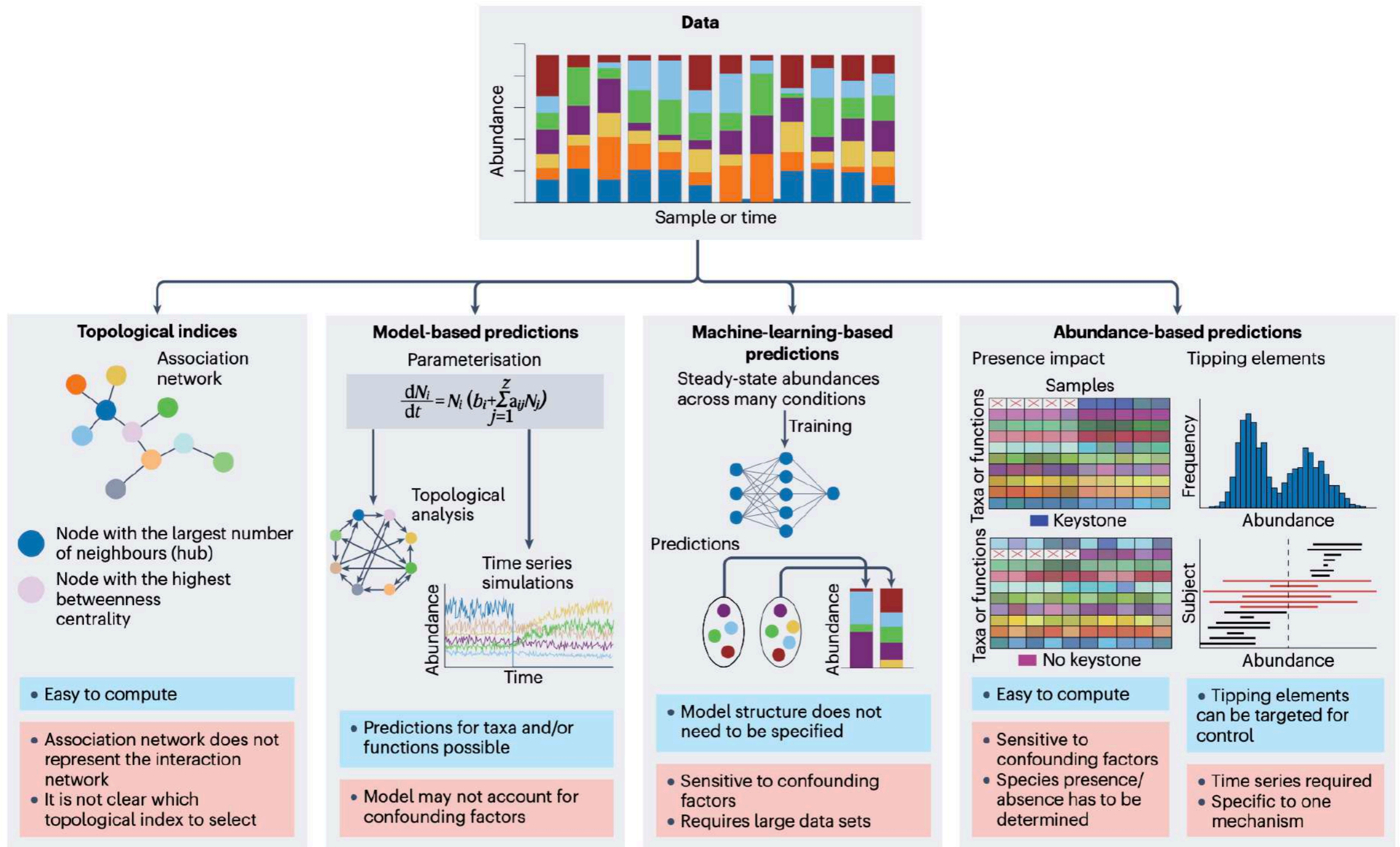
Ecosystem or habitat	Keystone taxa ^a	Refs
Computational inference		
Grasslands	<ul style="list-style-type: none"> Burkholderiales Sphingobacteriales Clostridiales Actinomycetales Acidobacteria GP4 	34–36
Forest or woodlands	<ul style="list-style-type: none"> Actinomycetales Acidobacteria GP4 Rhizobiales Burkholderiales Clostridiales Sphingobacteriales Rhodobacterales Verrucomicrobia 	8,35,37,38,61
Agricultural lands	<ul style="list-style-type: none"> <i>Gemmatimonas</i> Acidobacteria GP17 Xanthomonadales Rhizobiales Burkholderiales Solirubrobacterales Verrucomicrobia 	35,40,42,43
Arctic and Antarctic ecosystems	<ul style="list-style-type: none"> Rhizobiales Burkholderiales Actinobacteria Alphaproteobacteria 	25,26,44,46
Contaminated soil	<ul style="list-style-type: none"> Rhizobiales <i>Nitrospira</i> Pseudomonadales Actinobacteria 	47,48
Plant-associated microbiota	<ul style="list-style-type: none"> Acidobacteria GP1, GP3 and GP6 Rhizobiales Burkholderiales Pseudomonadales Bacteroidetes Frankiales 	40,49,50
Aquatic ecosystems	<ul style="list-style-type: none"> <i>Pelagibacter</i> Oceanospirillales Flavobacteriaceae <i>Nitrospira</i> Rhodobacteradaceae Alteromonadaceae <i>Chromatium</i> Rhizobiales Burkholderiales <i>Chlorobium</i> Verrucomicrobia <i>Chloracidobacterium</i> Chloroflexi <i>Candidatus OP3</i> 	24,51–55,72

Empirical evidence		
Agricultural lands ^b	<ul style="list-style-type: none"> <i>Gemmatimonas</i> Acidobacteria 	39,41
Phyllosphere	<ul style="list-style-type: none"> <i>Albugo</i> <i>Dioszegia</i> 	20
Human oral microbiome	<i>Porphyromonas gingivalis</i>	64,74
Human gut microbiome	<ul style="list-style-type: none"> <i>Helicobacter pylori</i> <i>Methanobrevibacter smithii</i> Actinobacteria <i>Bacteroides fragilis</i> <i>Bacteroides stercoris</i> <i>Bacteroides thetaiotaomicron</i> <i>Ruminococcus bromii</i> <i>Klebsiella pneumoniae</i> <i>Proteus mirabilis</i> 	22,23,56–60,76

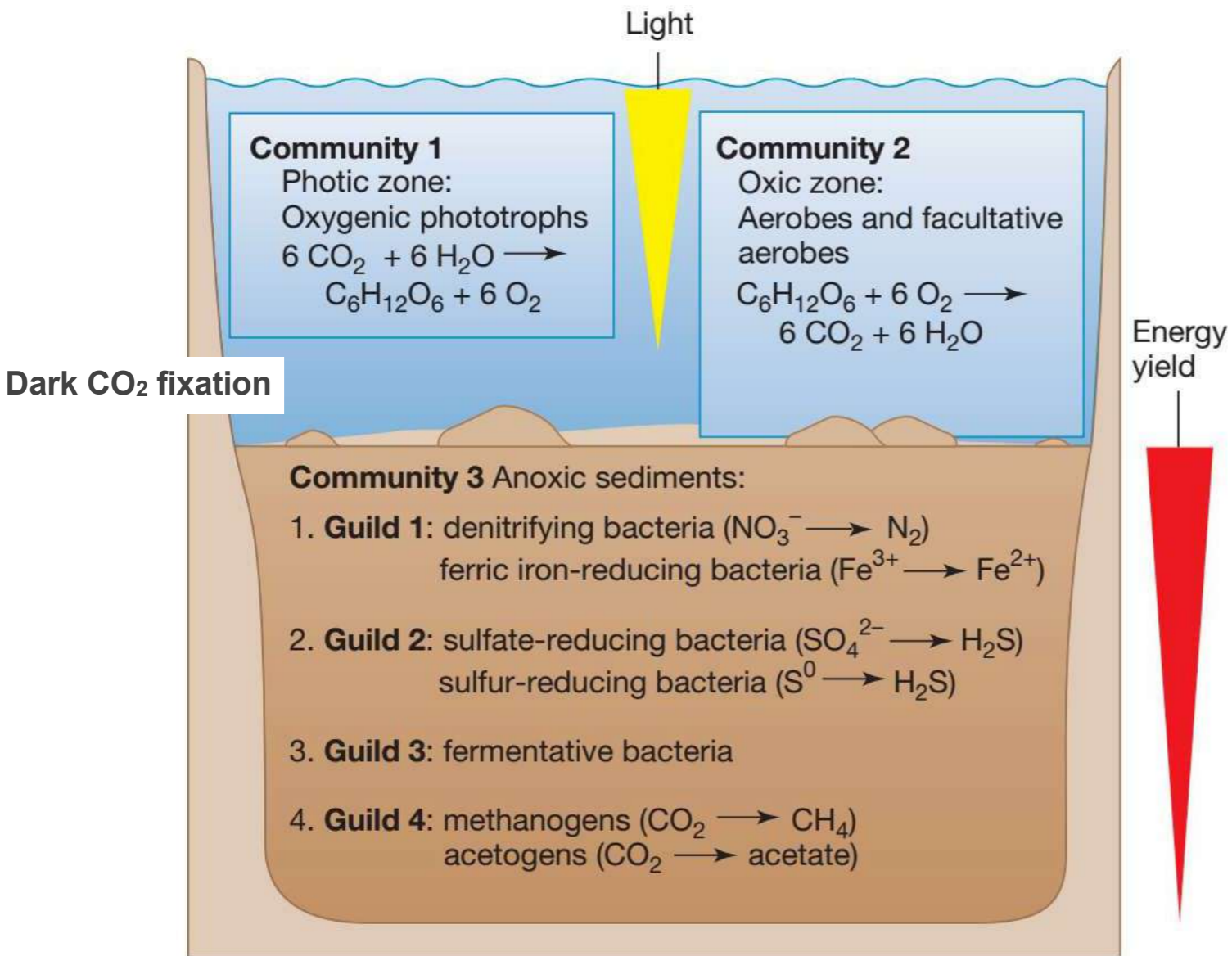
- **Keystone species** are microbes that, despite their low abundance, have a **disproportionately large impact** on the ecosystem (e.g., methanotrophs controlling methane emissions)
- Blended strategies to tap into diversity and functioning in ecosystems
- Understanding keystone taxa is essential in order to **predict microbial response to natural and anthropogenic-induced changes**

Keystone prediction methods

Garza et al., 2006



Microbial Guilds



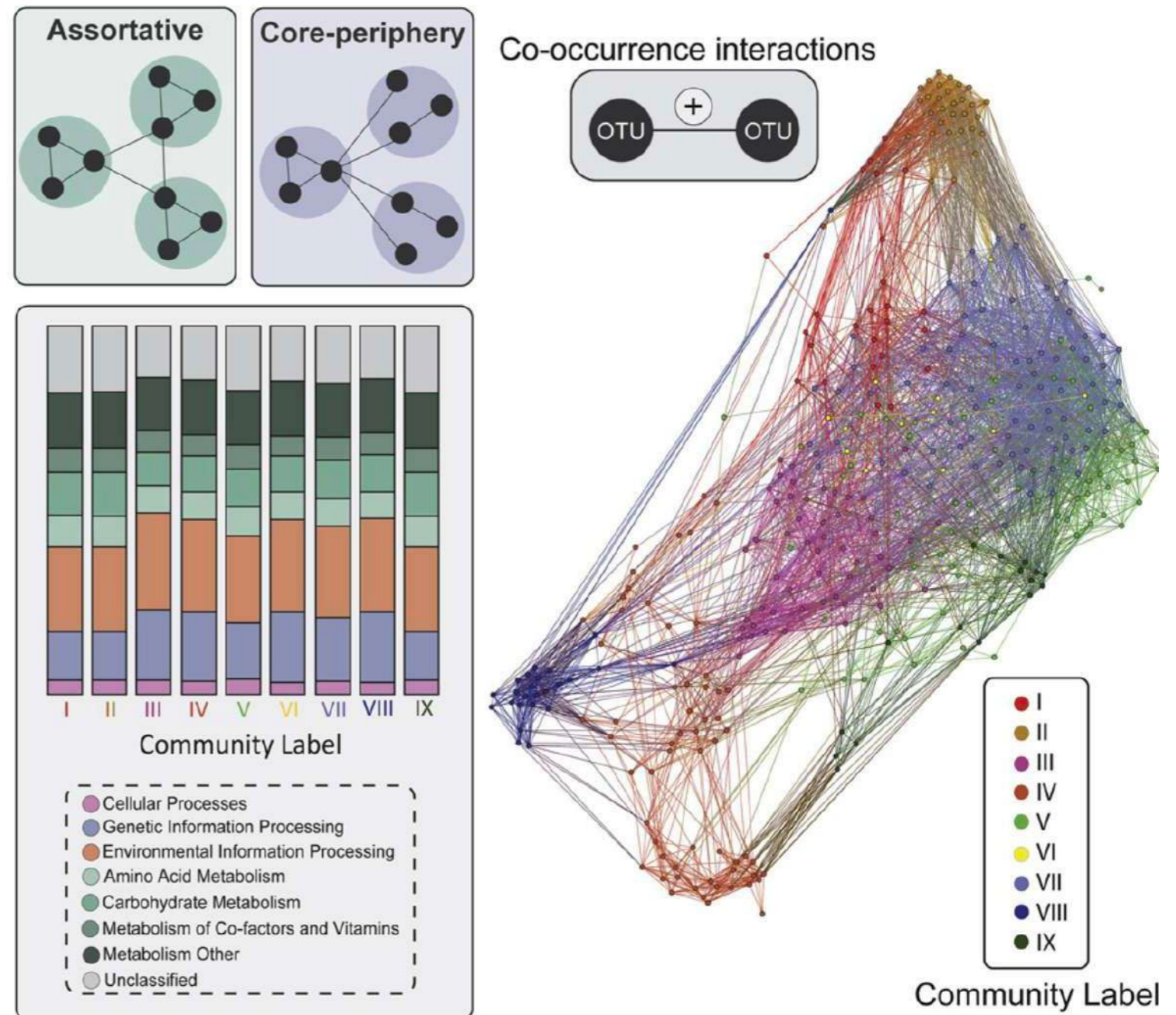
- **Microbial guilds** are groups of microbes that perform the same **functional role** in the ecosystem, regardless of their taxonomic identity
- **Keystone species** and **microbial guilds** concepts help us understand **function-based** relationships rather than just who is present

Figure 20.2 Populations, guilds, and communities. Microbial communities consist of populations of cells of different species. A freshwater lake ecosystem would likely have the communities shown here. The reduction of NO_3^- , Fe^{3+} , SO_4^{2-} , S^0 , and CO_2 are examples of anaerobic respirations. The region of greatest activity for each of the different respiratory processes would differ with depth in the sediment. As more energetically favorable electron acceptors are depleted by microbial activity near the surface, less favorable reactions occur deeper in the sediment.

Functional Hubs

- **Definition:** Species (or taxa) that are **highly connected** in microbial interaction networks – they interact with many others and **coordinate or stabilize** community function.
- **Key Traits:**
 - Identified via **network analysis**
 - May overlap with keystone species
 - Can be connectors, mediators, or “communication centers”

Gut microbiome: functionally redundant mixed mesoscale architecture



Distinct ecological roles

1. Keystone Species

- **Definition:** A species that has a **disproportionately large impact** on the structure or function of an ecosystem, **relative to its abundance**.
- **Key Traits:**
 - Not necessarily abundant
 - Removal causes a **cascade of changes** in community composition or function
- **Microbial Example:**
 - *Nitrosopumilus maritimus* (an ammonia-oxidizing archaeon) plays a critical role in marine nitrogen cycling, even though it may be rare.
- **Analogy:** Like a key stone in an arch – remove it, and the whole system collapses.

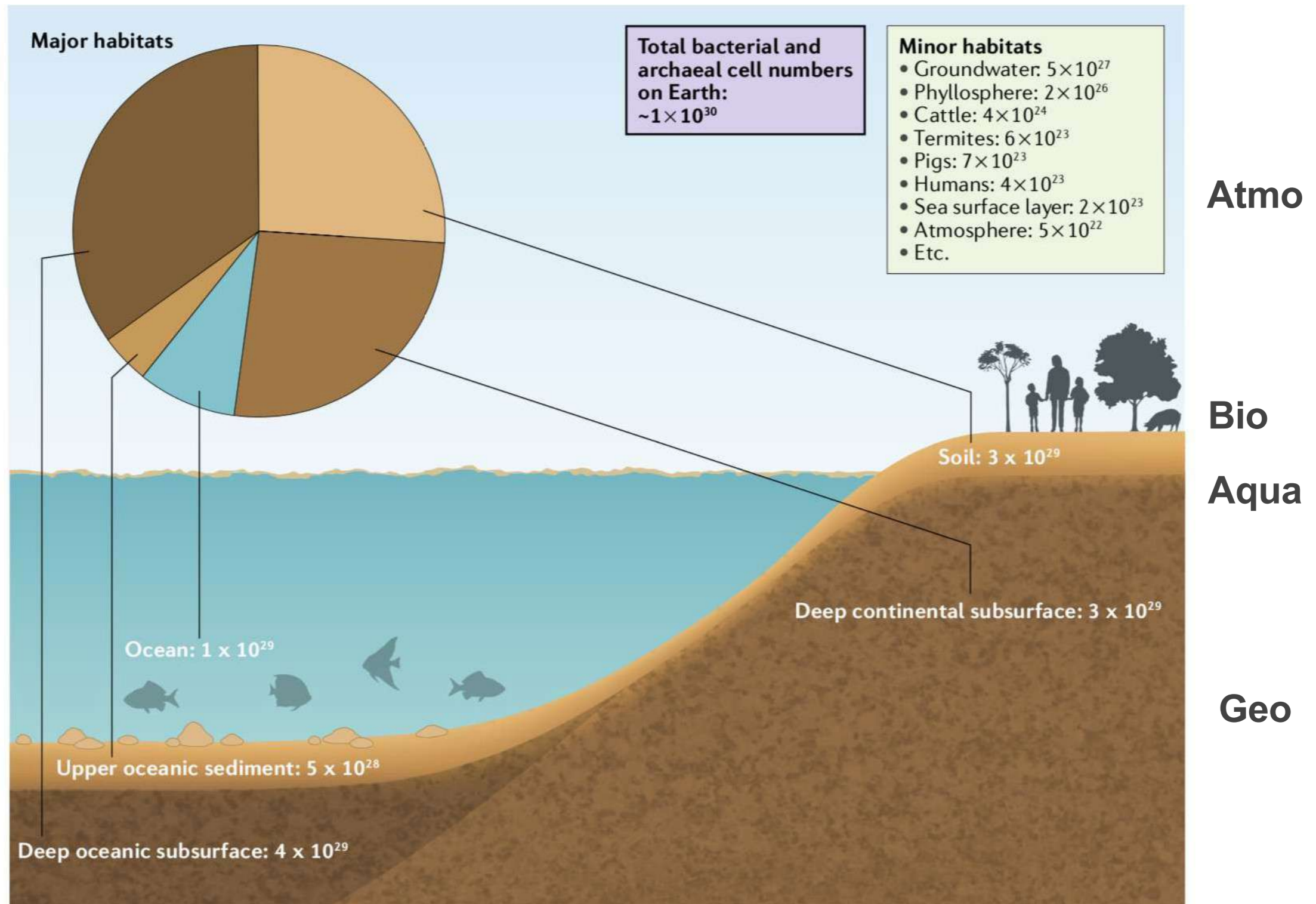
2. Microbial Guilds

- **Definition:** A group of **taxonomically different microbes** that perform the **same ecological function**.
- **Key Traits:**
 - Defined by **function**, not species identity
 - Often found across different environments
- **Microbial Example:**
 - **Denitrifiers** (e.g., *Pseudomonas*, *Paracoccus*, *Bacillus*) – all reduce nitrate to nitrogen gas
- **Analogy:** Like different brands of workers doing the same job – plumbers from different companies all fixing pipes.

3. Functional Hubs

- **Definition:** Species (or taxa) that are **highly connected** in microbial interaction networks – they interact with many others and **coordinate or stabilize** community function.
- **Key Traits:**
 - Identified via **network analysis**
 - May overlap with keystone species
 - Can be connectors, mediators, or “communication centers”
- **Microbial Example:**
 - A bacterium that maintains connections between nitrogen cyclers, carbon degraders, and methanogens in a soil network.
- **Analogy:** Like an airport hub – even if it’s not the biggest city, it connects many routes and keeps the system flowing.

Microbial abundance



Microbial Diversity

- > ***16S rRNA gene***
- > **Whole genome**
- > ***Metagenome***
- > **Metagenome Assembled Genome**

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
- **Earth Microbiome Project**



Earth Microbiome Project

The Earth Microbiome Project (EMP, <http://www.earthmicrobiome.org>) was founded in 2010 to sample the Earth's microbial communities at an unprecedented scale in order to advance our understanding of the organizing biogeographic principles that govern microbial community structure.

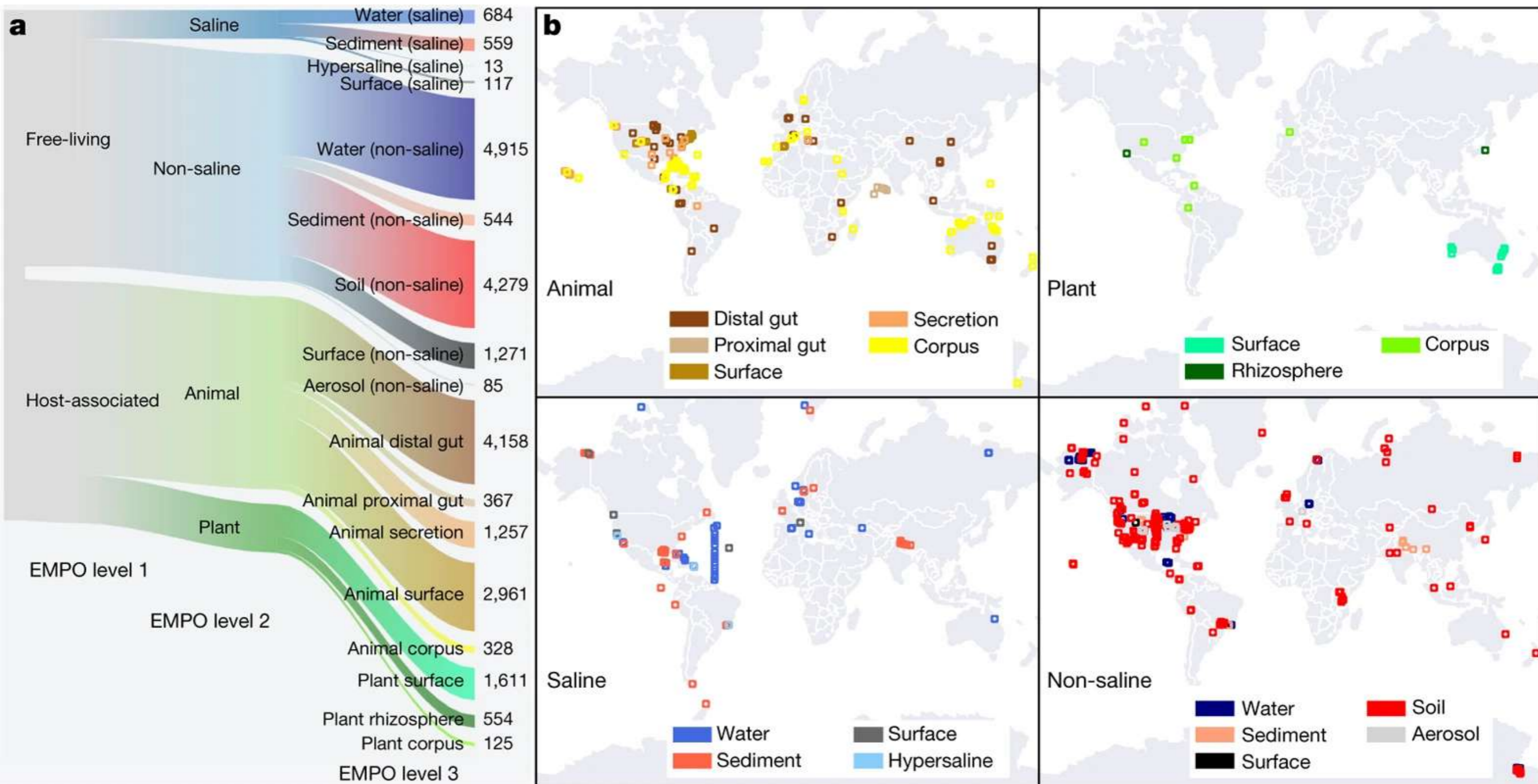
We recognized that open and collaborative science, including scientific crowdsourcing and standardized methods⁸, would help to reduce technical variation among individual studies, which can overwhelm biological variation and make general trends difficult to detect

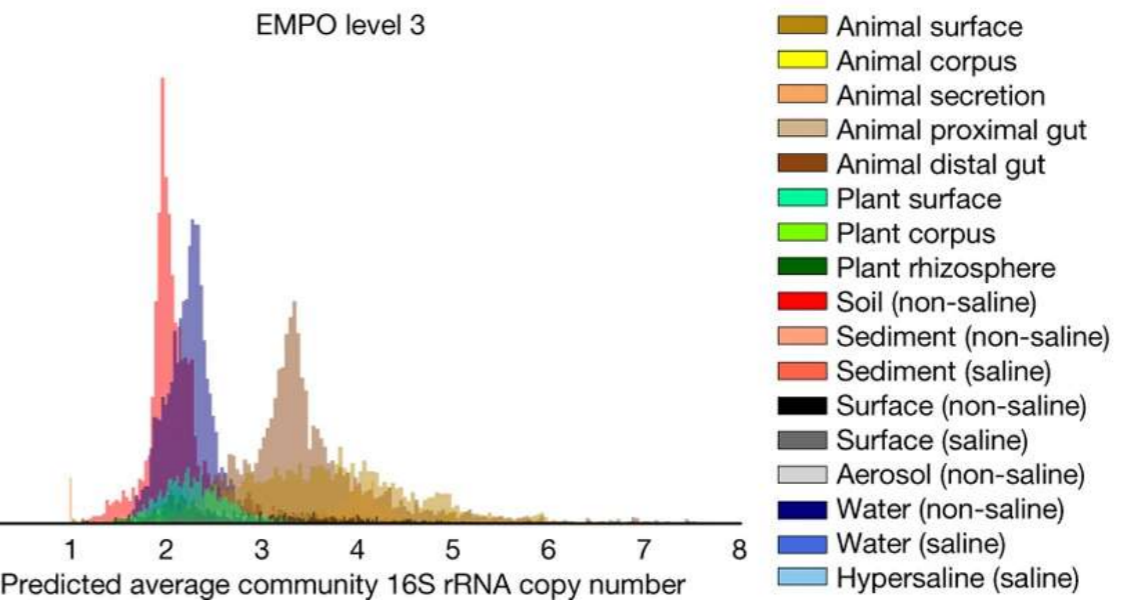
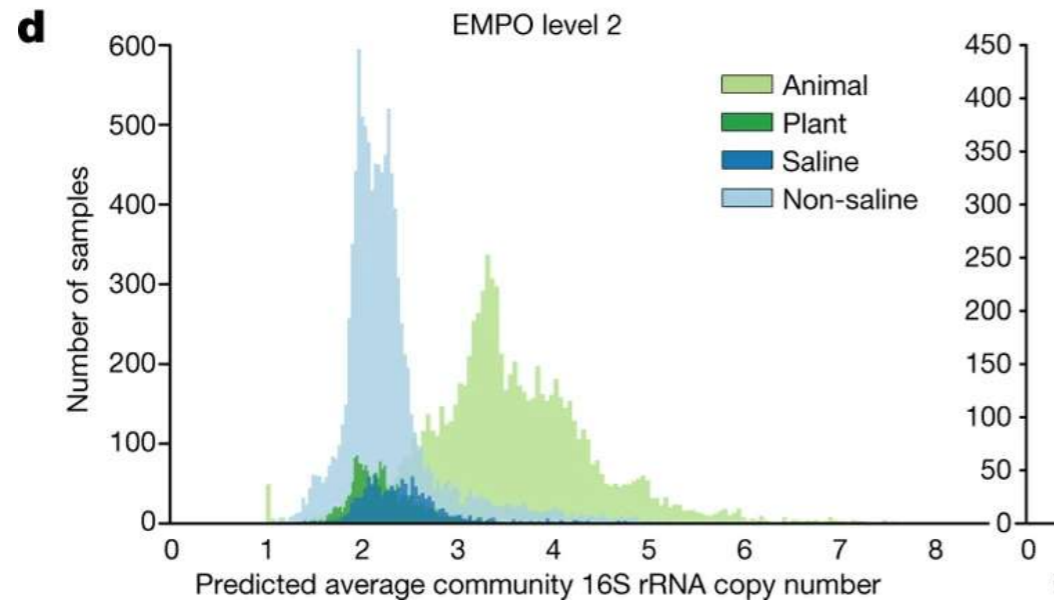
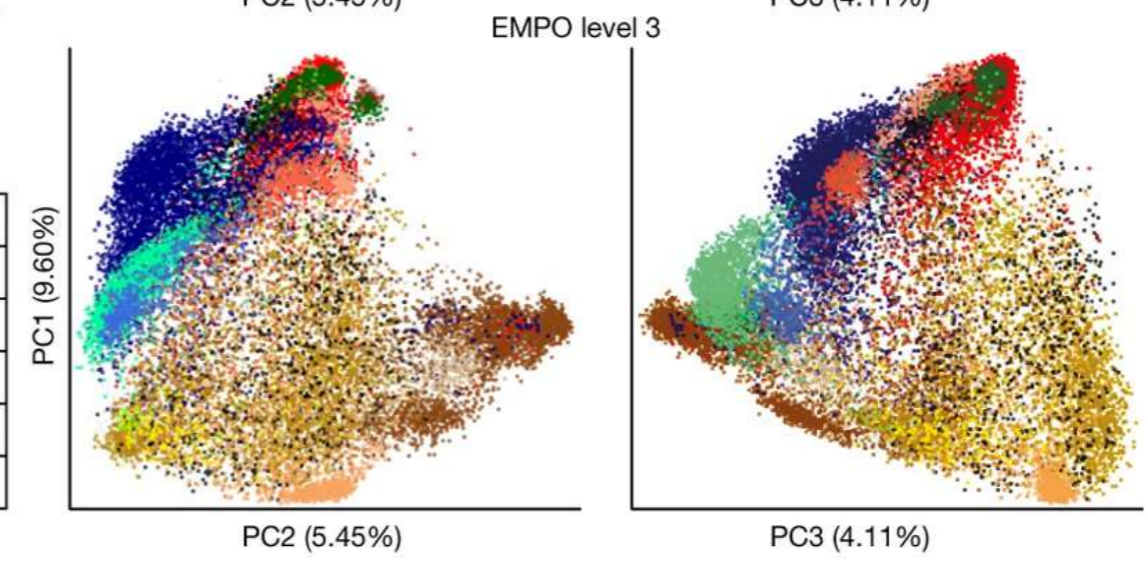
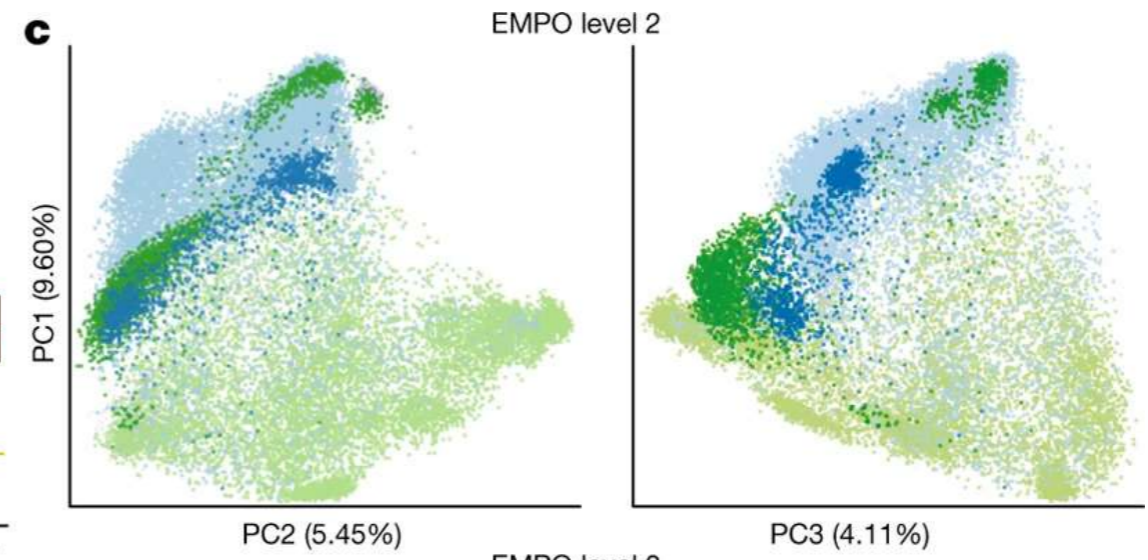
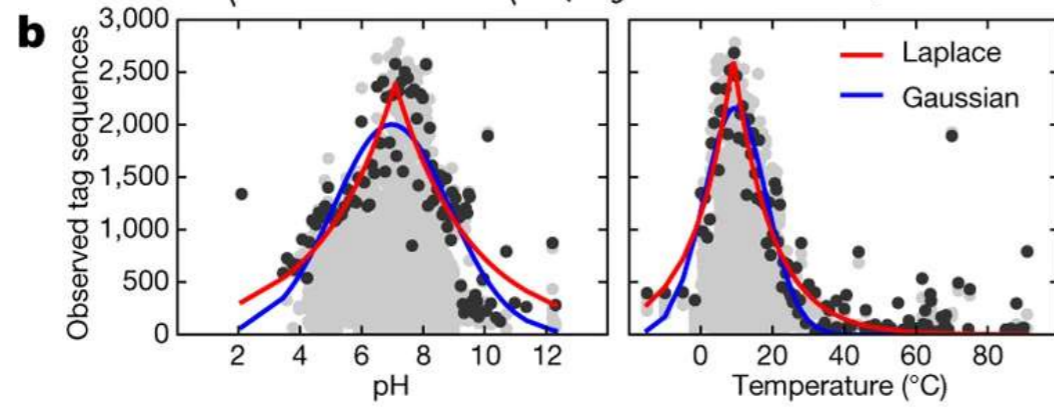
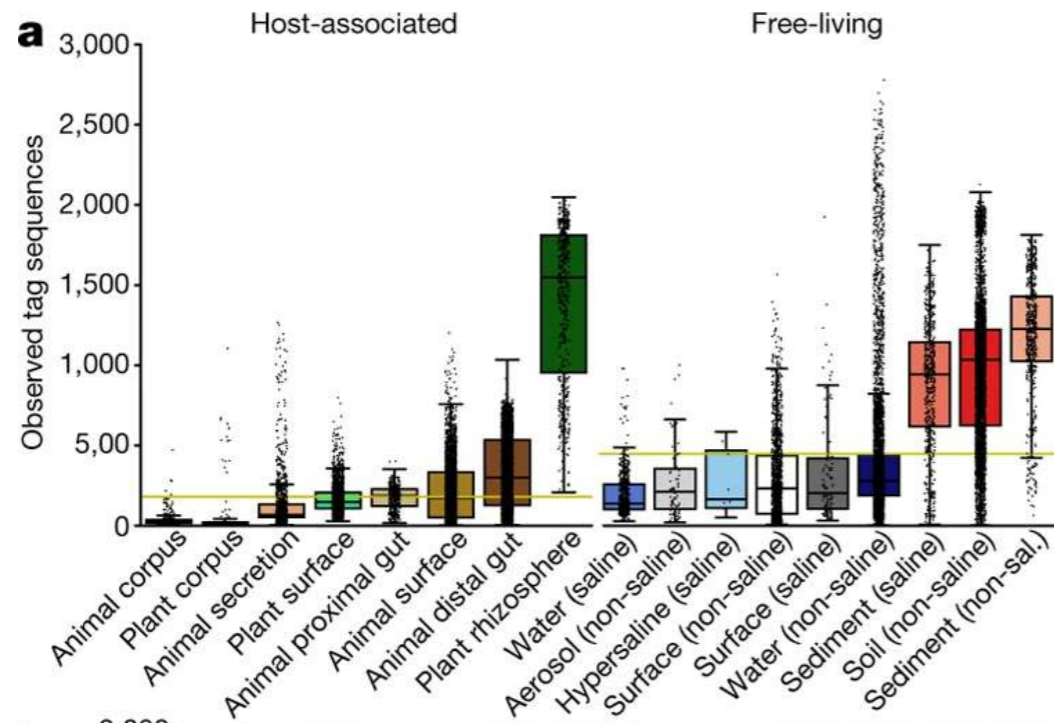
Shaffer, J.P.*, L.-F. Nothias*, L.R. Thompson* (2022). Standardized multi-omics of Earth's microbiomes reveals microbial and metabolite diversity. *Nature Microbiology* 7:2128-2150.

*These authors contributed equally. doi: 10.1038/s41564-022-01266-x.

Thompson, L., Sanders, J., McDonald, D. *et al.* A communal catalogue reveals Earth's multiscale microbial diversity. *Nature* 551, 457–463 (2017)

Environment type and provenance of samples





<https://fondationtaraocean.org/en/home/>

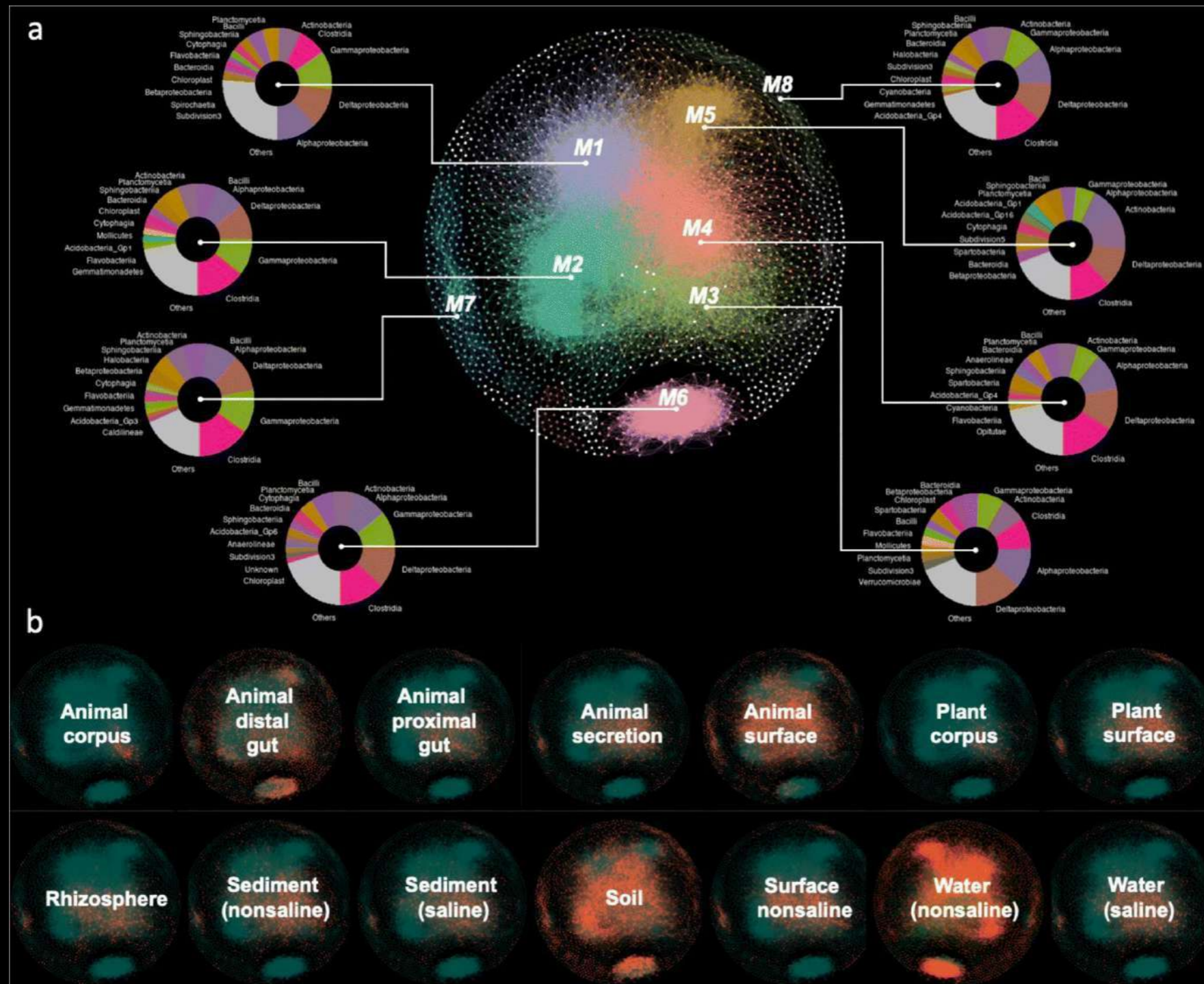
ALPHA DIVERSITY:

Diversity within a sample—-> number of different microbes (richness), but how evenly distributes in terms of total abundance (evenness)

BETA DIVERSITY:

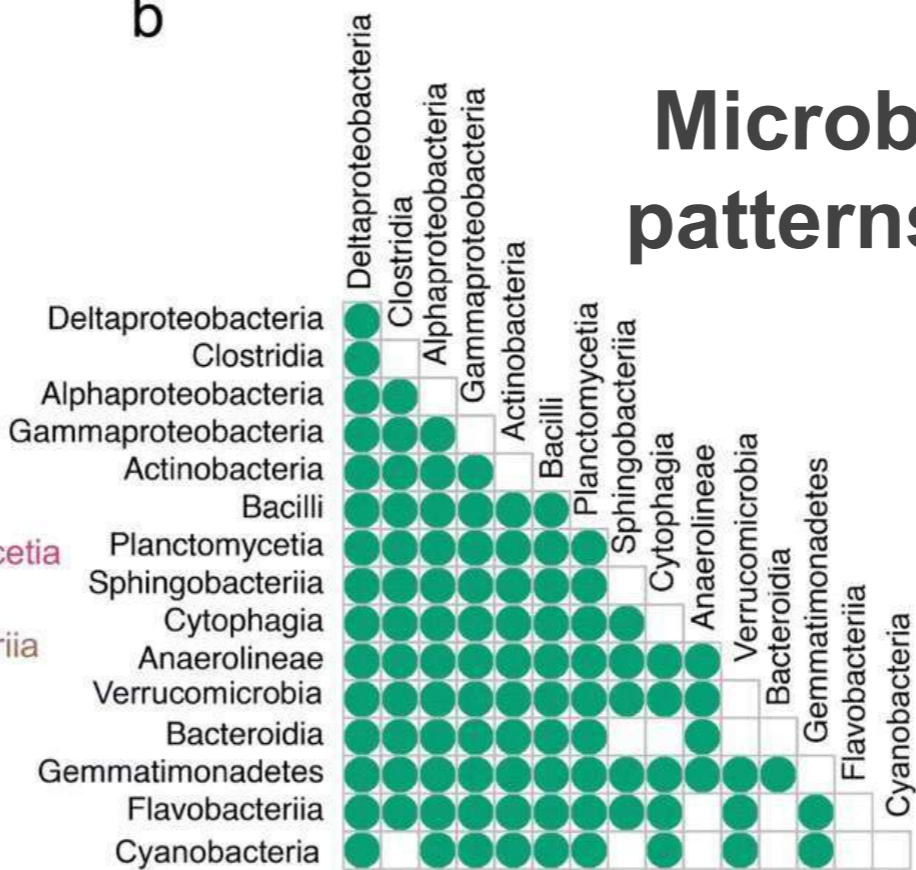
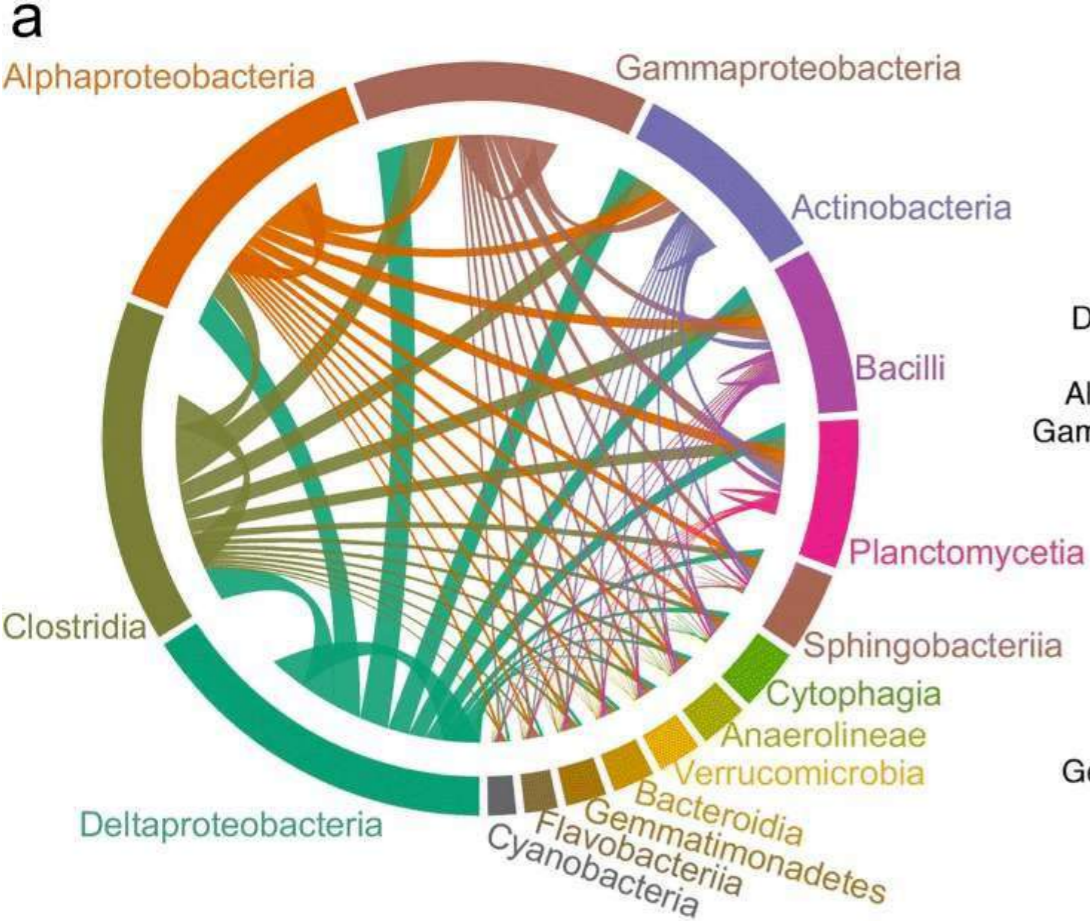
Diversity between samples

Earth microbial co-occurrence network reveals interconnection pattern across microbiomes



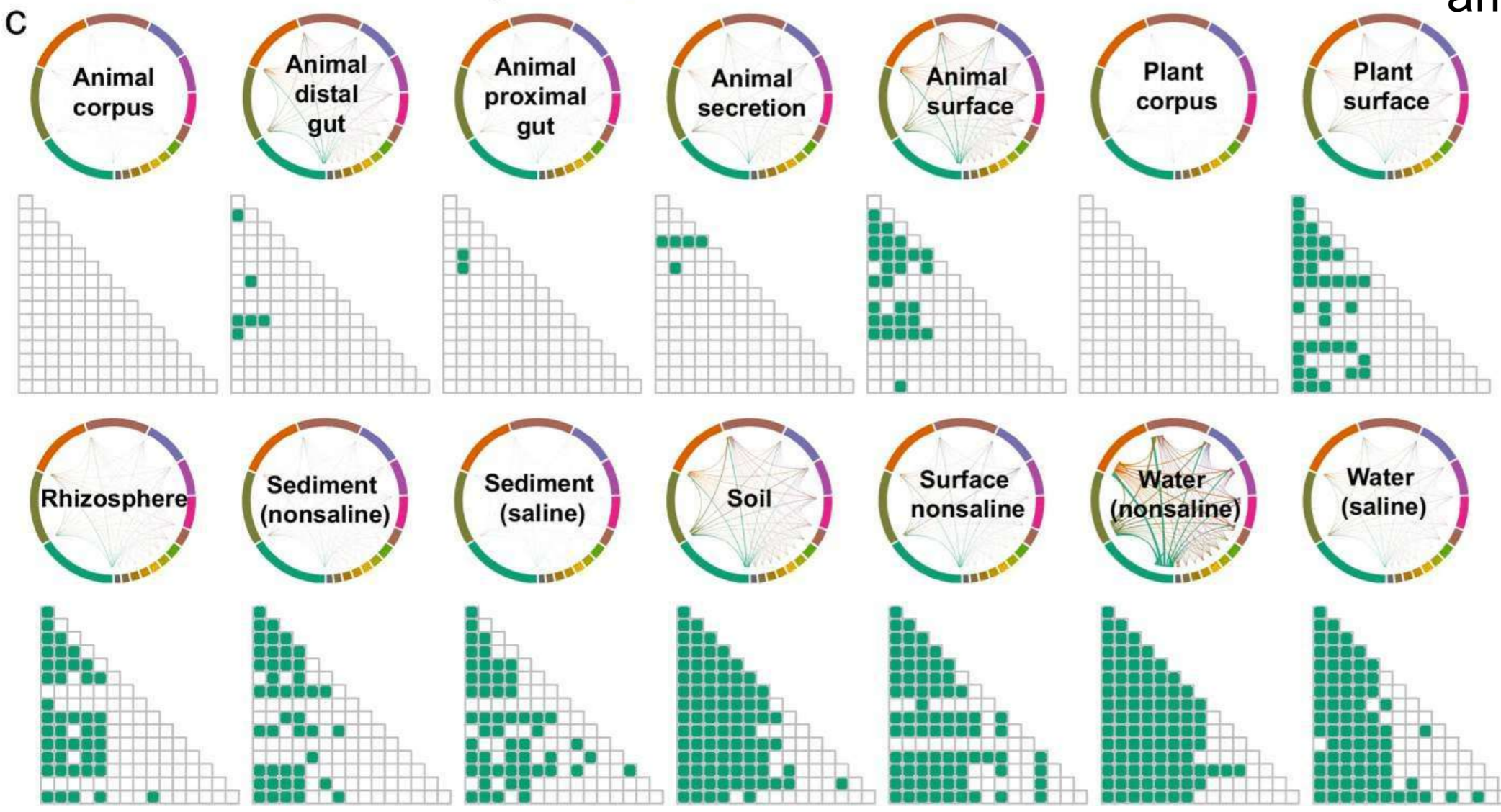
Ma et al., 2020

8 taxonomy distinct modules linked with different environments, which featured environment specific microbial co-occurrence relationships



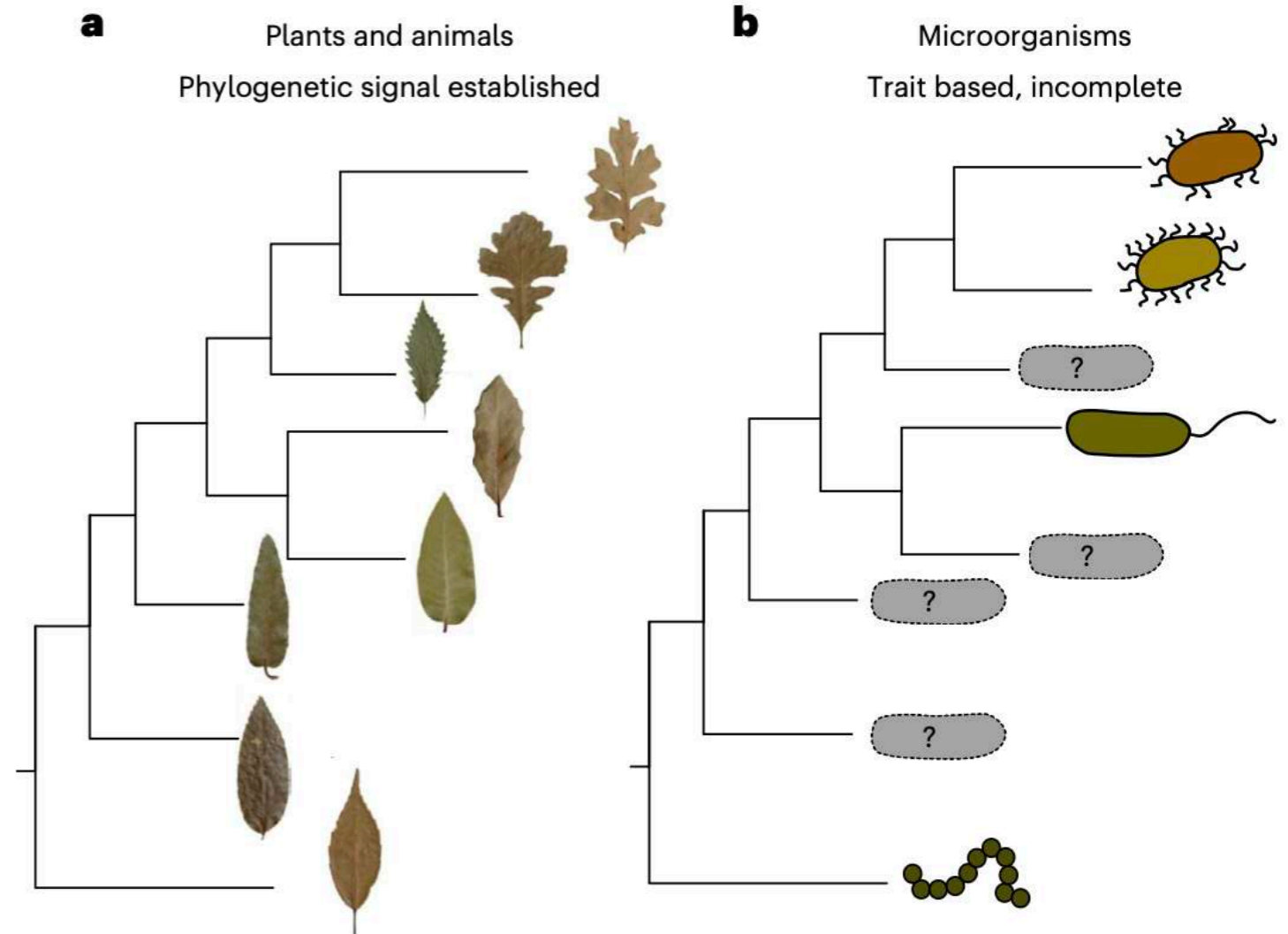
Microbial co-occurrence patterns across dominant taxa

The profiles of co-occurrence links among dominant taxa



Related microorganisms occupy similar ecological communities

- **Evolution** leads to patterns of similarity (appearance and morphology) across related organisms, a phenomenon termed '**phylogenetic signal**'
- **Related species** also tend to live in **similar** environments, a trend known as '**niche conservatism**'
- Related microorganisms are **assumed** to be similar and at least some microbial traits seem to be phylogenetically conserved
- *We reasoned that if two related microorganisms were indeed similar to one another in function and ecological niche, they should usually be found together with a similar set of microbial partners closely related microorganisms consistently occupy more similar communities as compared to less related microorganisms*
- We use the term '**community conservatism**' to refer to this phenomenon and show *that microorganisms retain signals of their community preferences over billions of years*

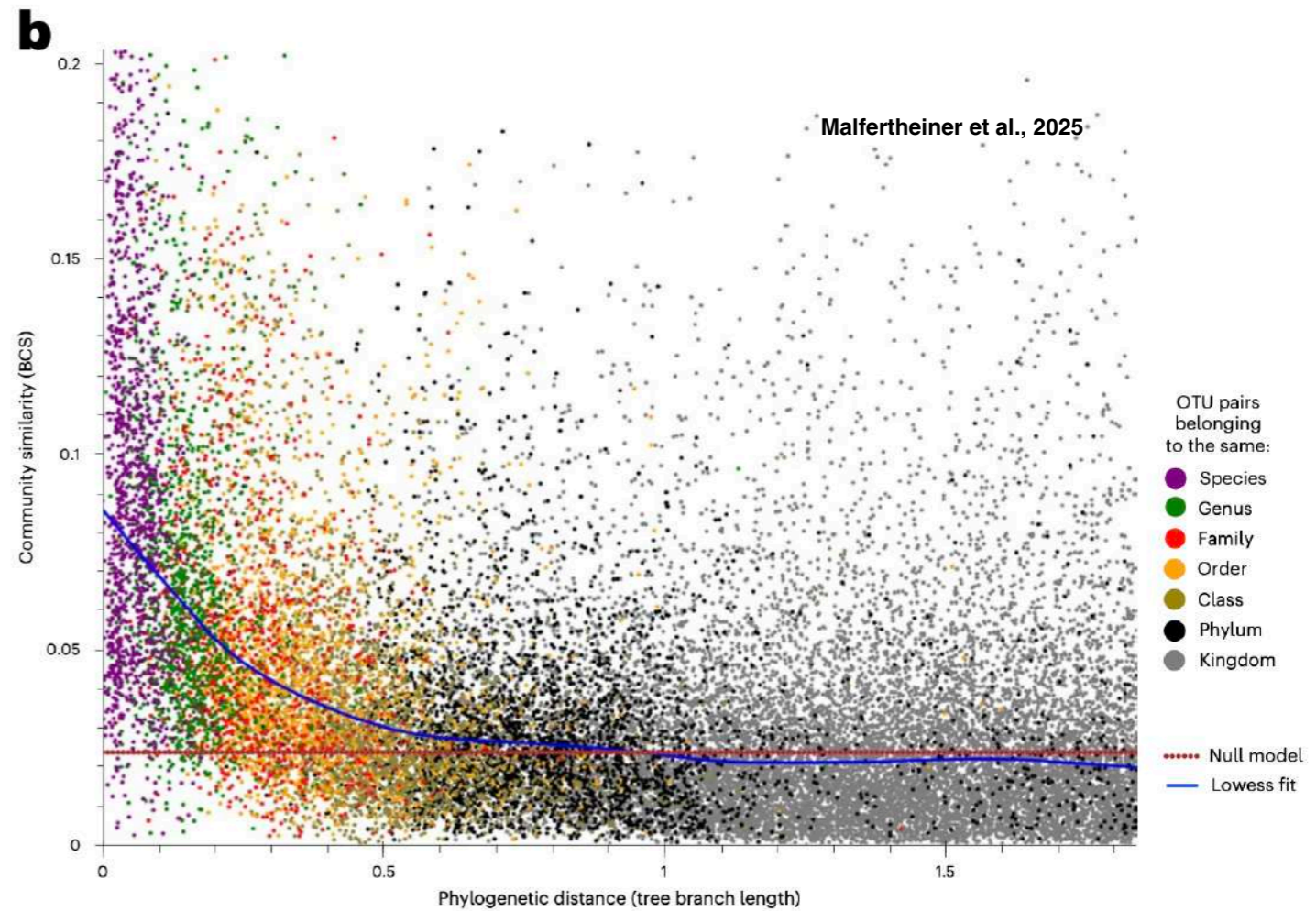
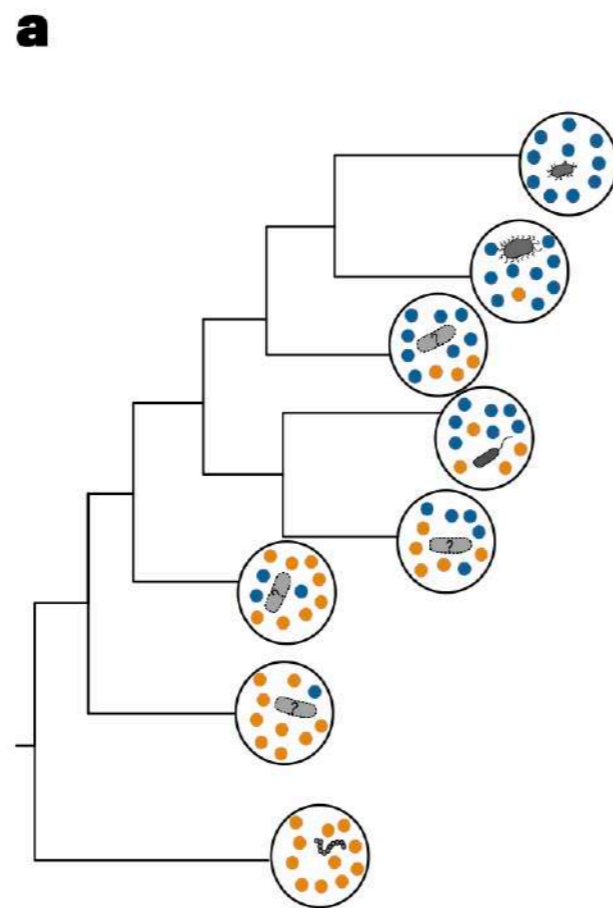


Phylogenetic signal, the trend of closely related organisms to share traits, is well established in animals and plants. Here it is shown in oak trees using leaf shape as a morphological feature.

While there are indications of traits being correlated with relatedness, a comprehensive global picture is still missing. Not all microorganisms have an associated genome, and not all traits can be deduced.

Community conservatism is widespread across microbial phyla and environments

- We analysed multiple different environments and phyla, and detected community conservatism in nearly all of them
- The shape and strength of the signal varied among lineages
- The rates of ecological divergence differ across the microbial tree of life
- Inferring phylum-specific characteristics such as **habitat generalism (the ability to thrive in a wide variety of environments) or specialism (the degree to which an organism depends on a narrow range of environmental conditions)**
- Community composition serves only as a proxy for ecological niche, and sharing a community does not necessarily mean fulfilling the same function therein.



Community similarity mirrors evolutionary relatedness.

Blue and orange dots represent different hypothetical microbial community members

Community similarity declines with increasing phylogenetic distance.

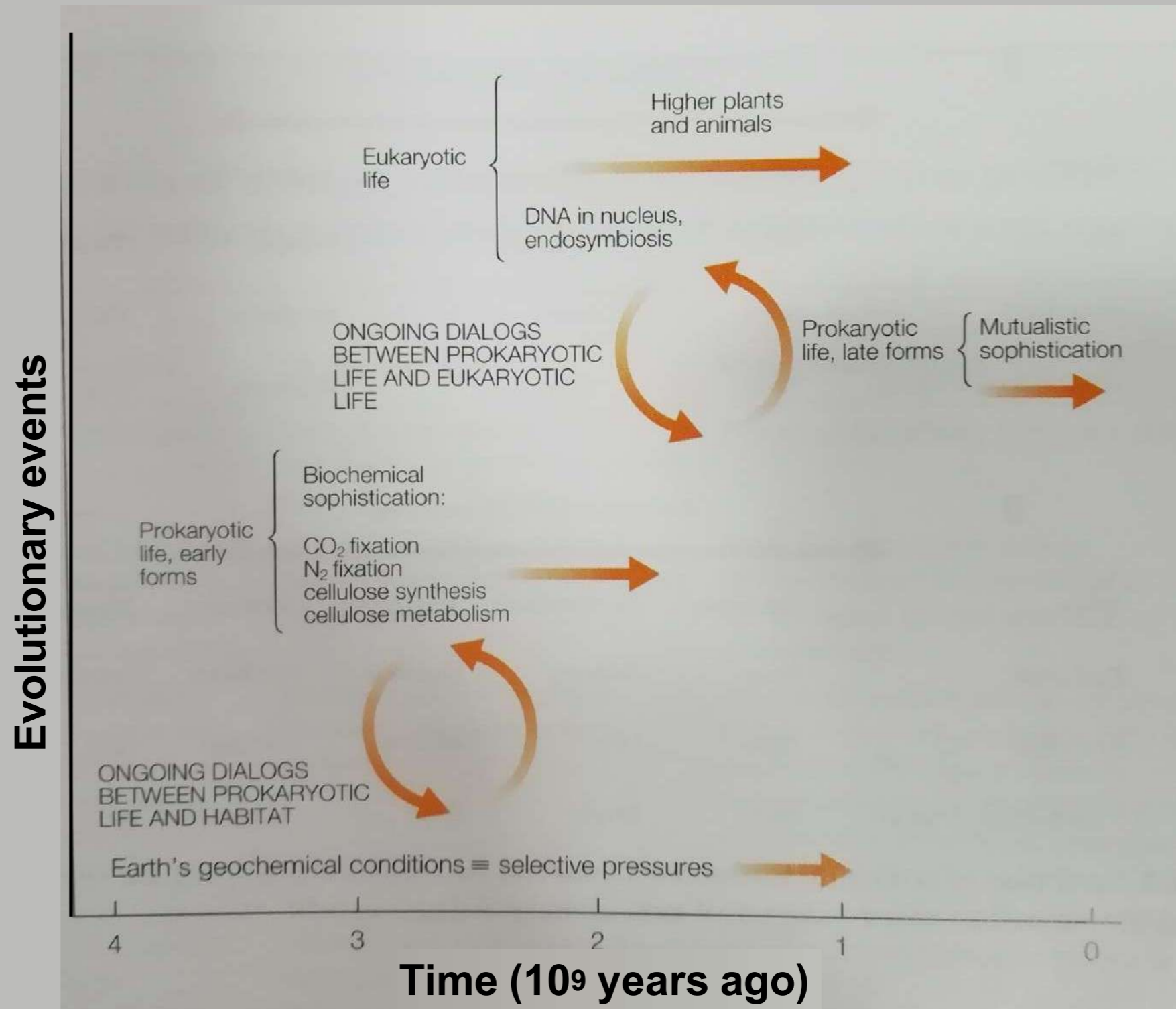
A lowess fit (blue line) and the random expectation (red dotted line) illustrate the overall trend

Ecosystem structure

- ***Primary producers***
- ***Consumers/Decomposers, Heterotrophic microbes: a general term for microbes that cannot assimilate carbon from inorganic sources (such as carbon dioxide) and instead use organic carbon compounds for anabolism***
- Water cycle <https://youtu.be/oaDkph9yQB8>
- Carbon biogeochemical cycle in soil/sediment and ocean/freshwater
- Nutrient biogeochemical cycles in soil/sediment and ocean/freshwater

Continuum of microbial interactions

- Evolution at the species level
- Evolution of interactions and behaviours
- *Microbial interactions link microbial diversity with metabolic diversity*
- *Microbial interactions has structured the environment*



Microbial Diversity-Metabolic Diversity

- Coupling of microbial diversity and metabolic diversity keep the ecosystem functioning
- Microbes influence habitability
- Habitability influence microbes
- Habitability is a binary continuum

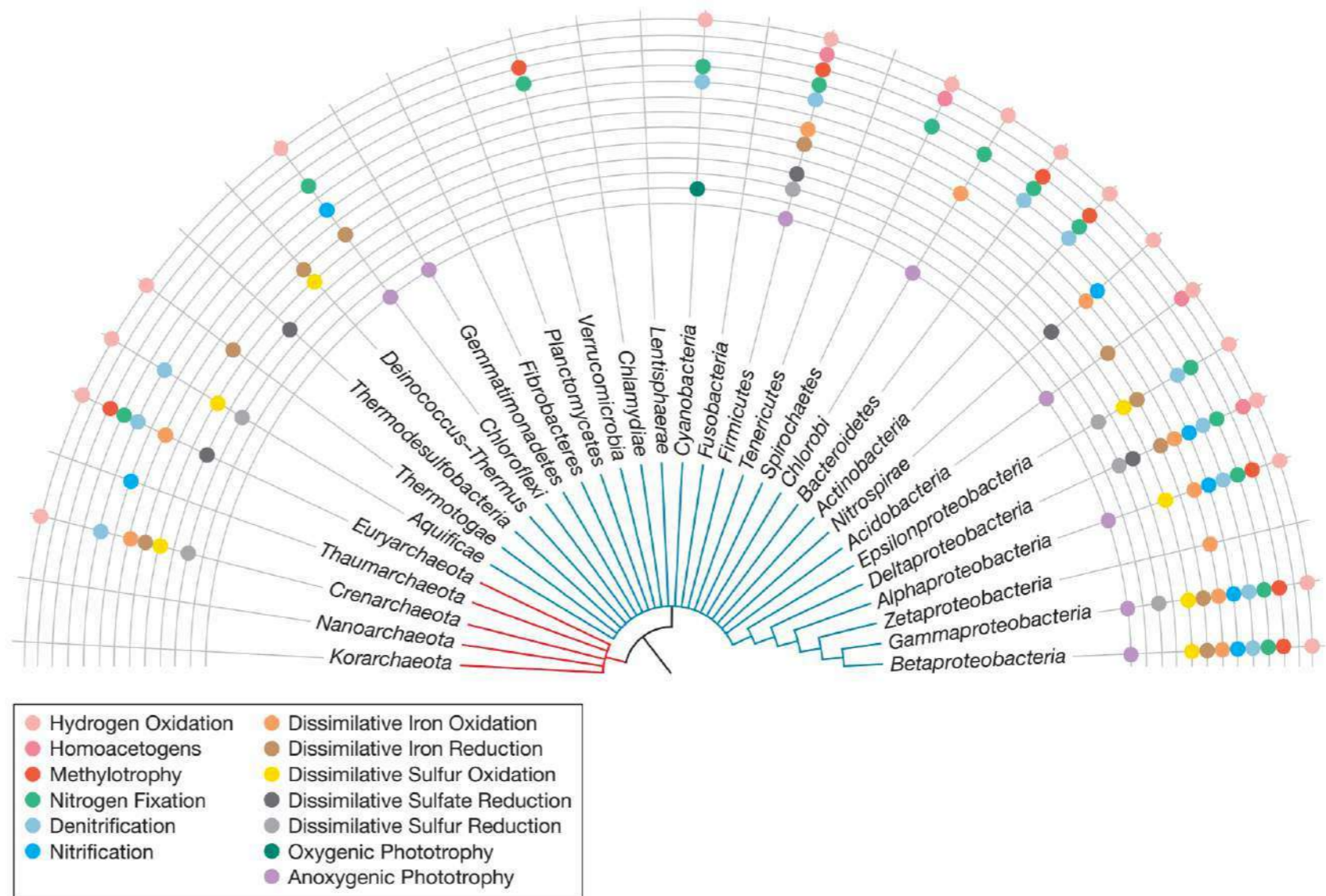


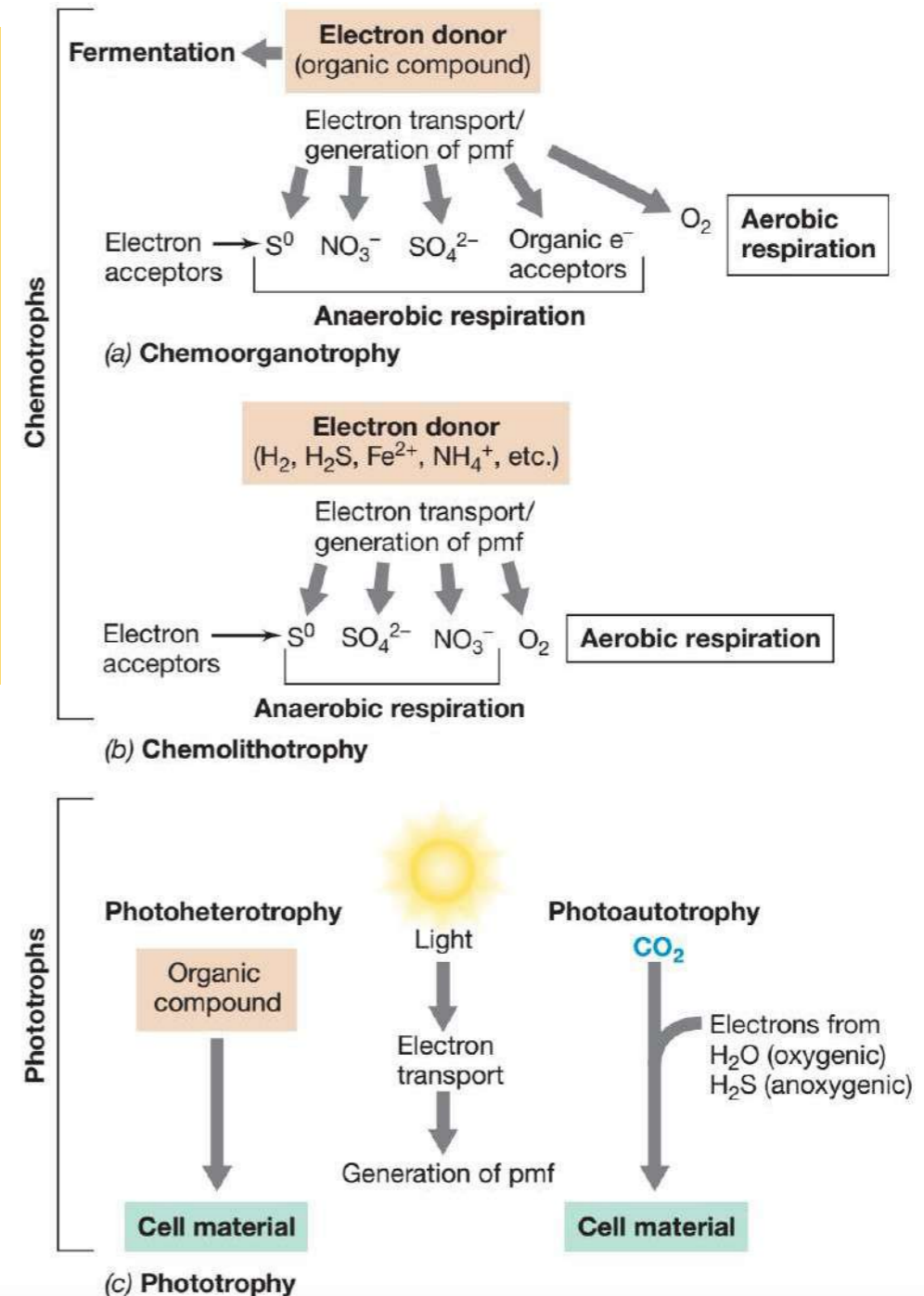
Figure 15.1 Major functional traits mapped across major phyla of *Bacteria* and *Archaea*. The dendrogram shows relationships between microbial phyla as inferred by analysis of 16S ribosomal RNA gene sequences. Blue branches are used to denote phyla of *Bacteria* and red branches phyla of *Archaea*. Colored circles indicate phyla that contain at least one species with a functional trait indicated in the color key.

Main microbial players

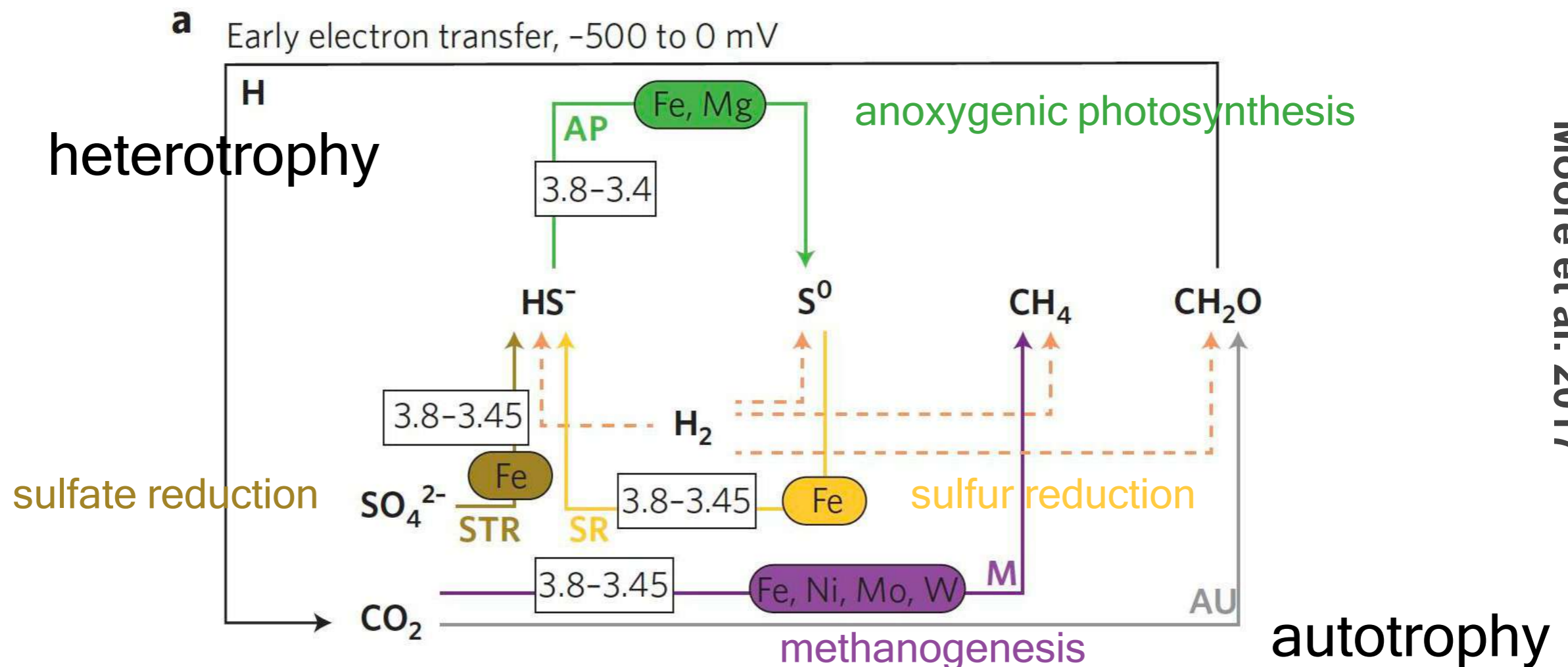
- Diverse energy sources
- Using inorganic nutrients
- Using organic nutrients
- **Primary production is coupled with decomposition in every ecosystem**

Heterotrophic microbes,
decomposers

Primary producers



Microbial metabolic pathways during Earth history: *anoxxygenic world*



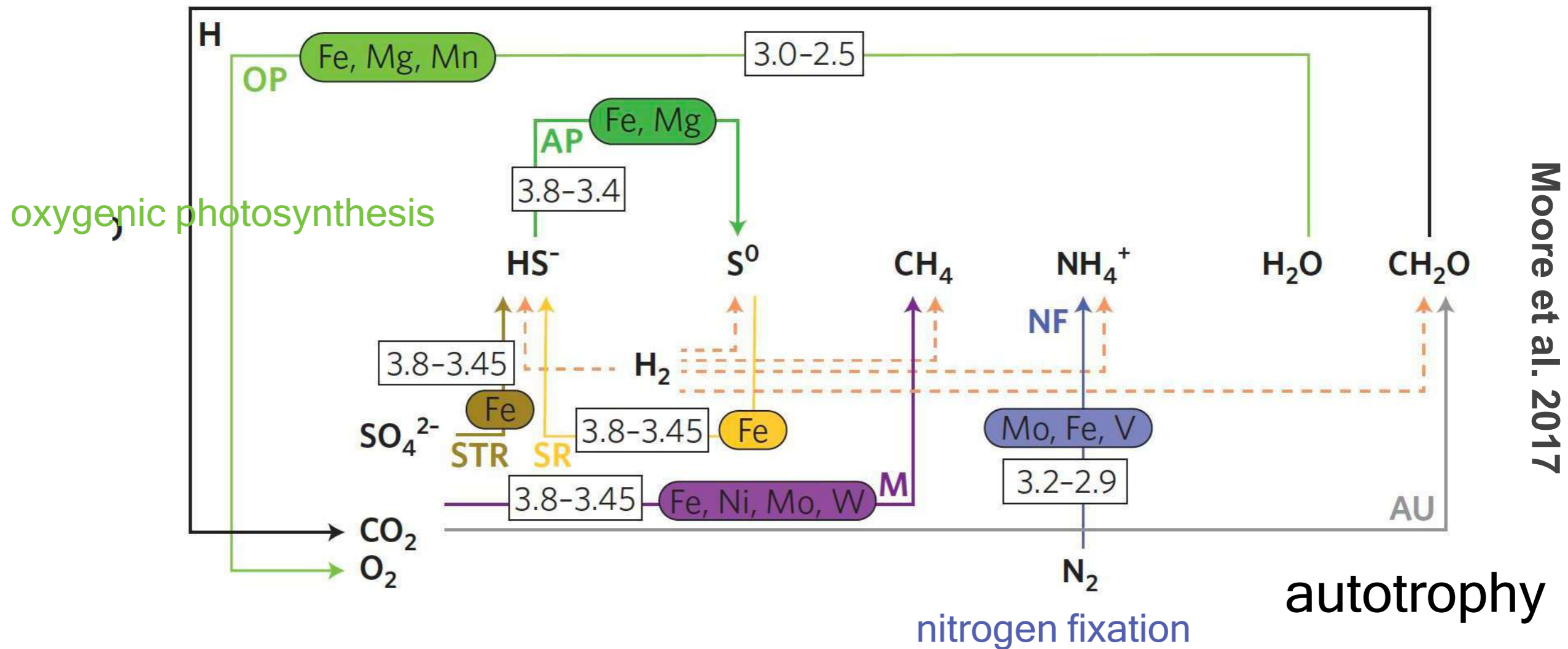
Moore et al. 2017

Molecules listed horizontally (HS⁻, S⁰, CH₄, NH₄⁺, H₂O, CH₂O, Exred) are reduced substrates, molecules listed vertically (SO₄²⁻, CO₂, NO₃⁻, O₂, Exox) are oxidized substrates, and N₂ is an intermediate and atmospheric reservoir of unreactive nitrogen

Microbial metabolic pathways during Earth history: *oxygenic world*

heterotrophy

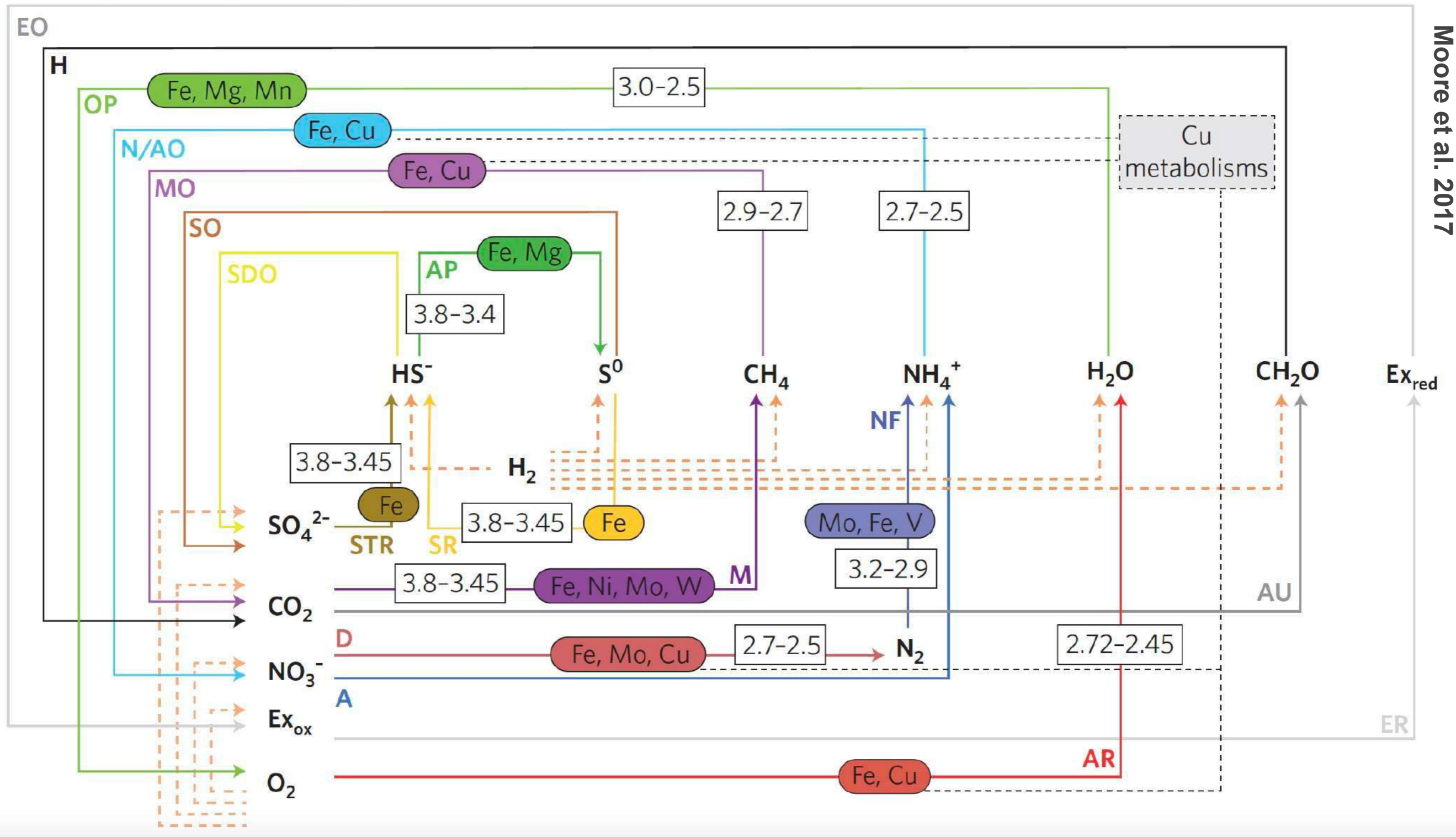
b Exploiting the atmosphere and ocean, -500 to 800 mV



Moore et al. 2017

Present microbial metabolic pathways

d Closing the carbon cycle, -500 to 1,200 mV



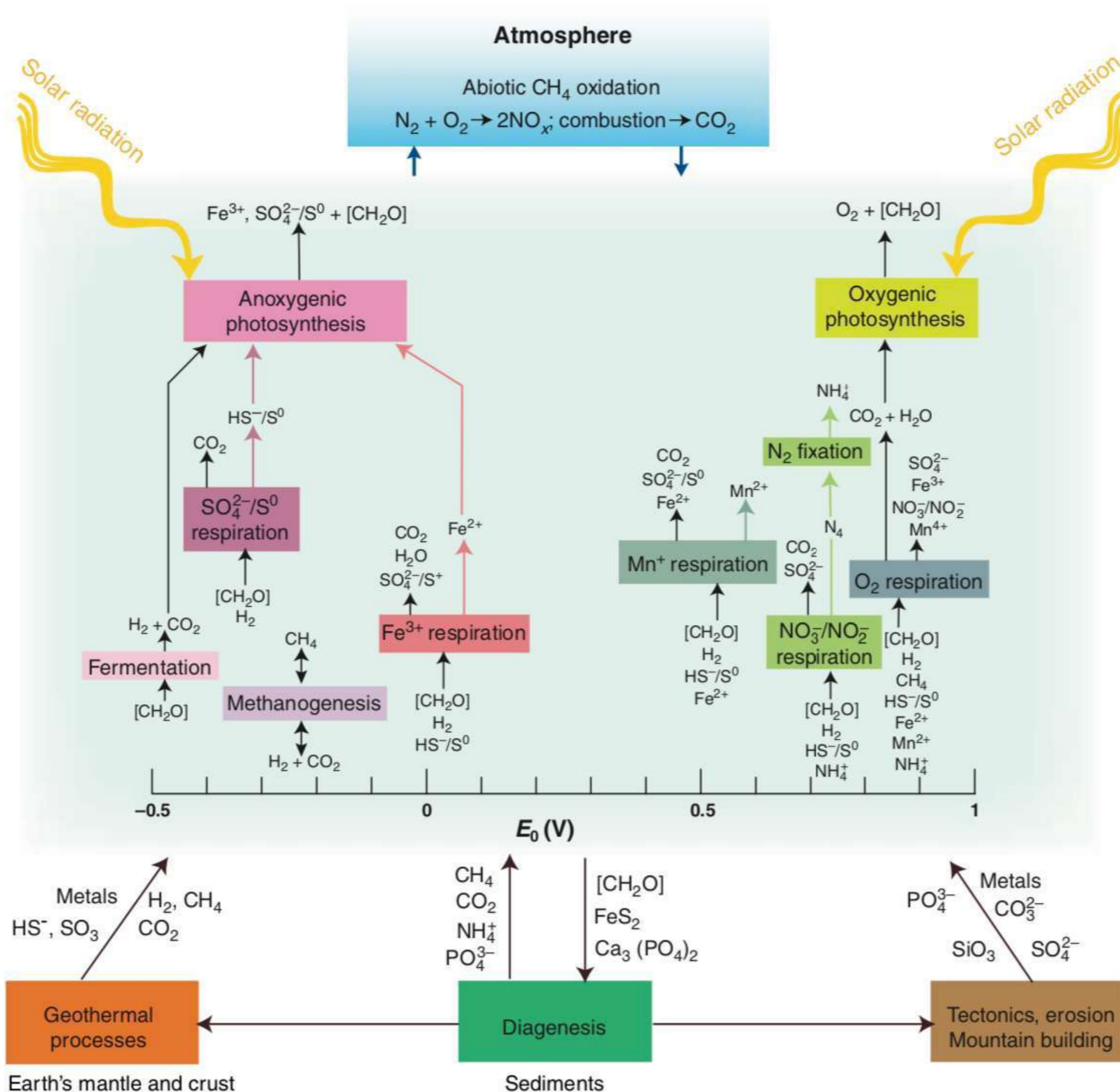
Moore et al. 2017

A, ammonification; AP, anoxygenic photosynthesis; AR, aerobic respiration; AU, autotrophy; D, denitrification; EO, other elements oxidation; ER, other elements reduction (EO and ER include Fe and Mn oxidation and reduction); H, heterotrophy; M, methanogenesis; MO, methane oxidation/methanotrophy; N/AO, nitrification/ammonia oxidation; NF, nitrogen fixation; OP, oxygenic photosynthesis; SDO, sulfide oxidation; SO, sulfur oxidation; SR, sulfur reduction; STR, sulfate reduction

Microbial microscale actions structure planet-scale functioning

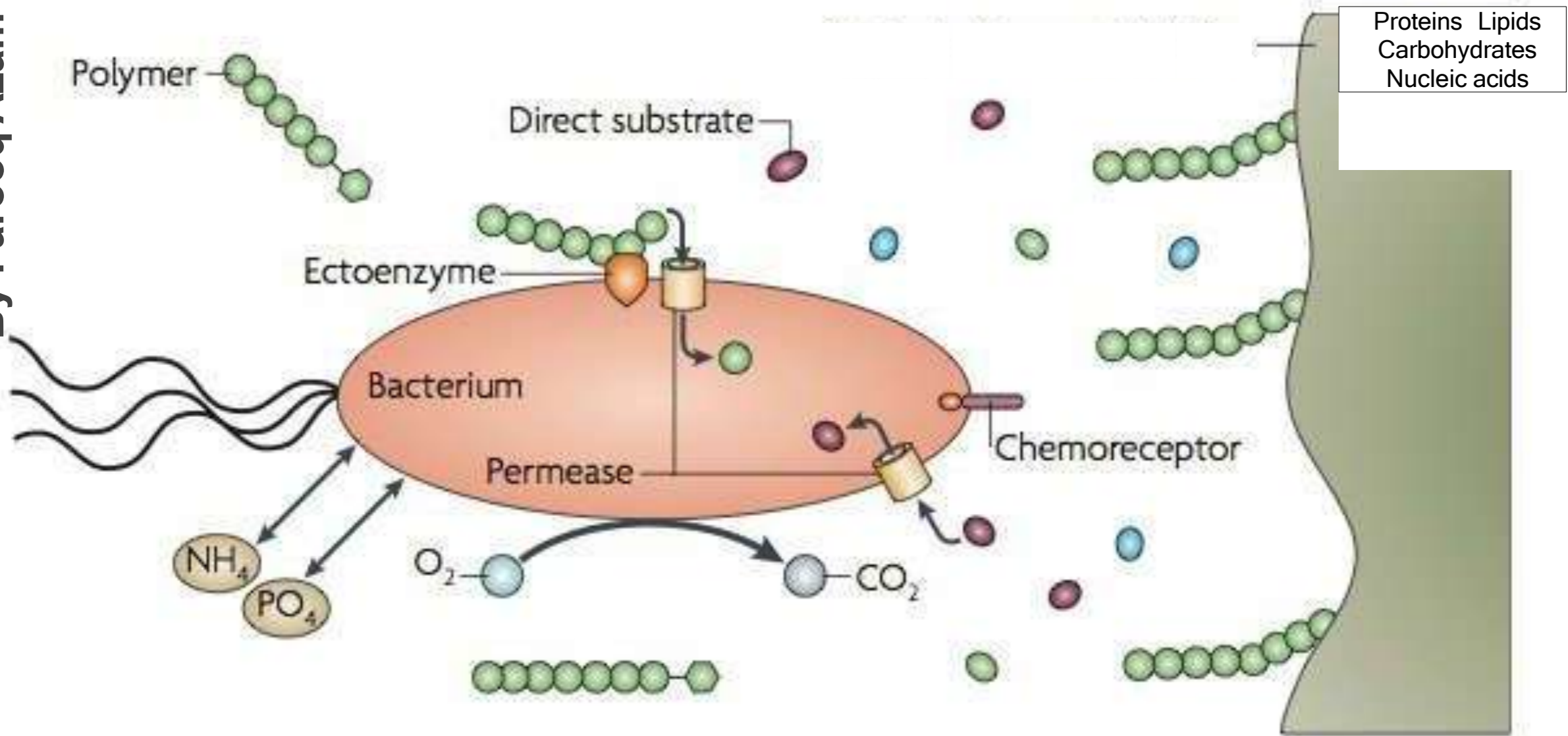
Biosphere model of energy fluxes and elemental cycles

Falkowski et al., 2008



Microbial adaptive strategies at the microscale

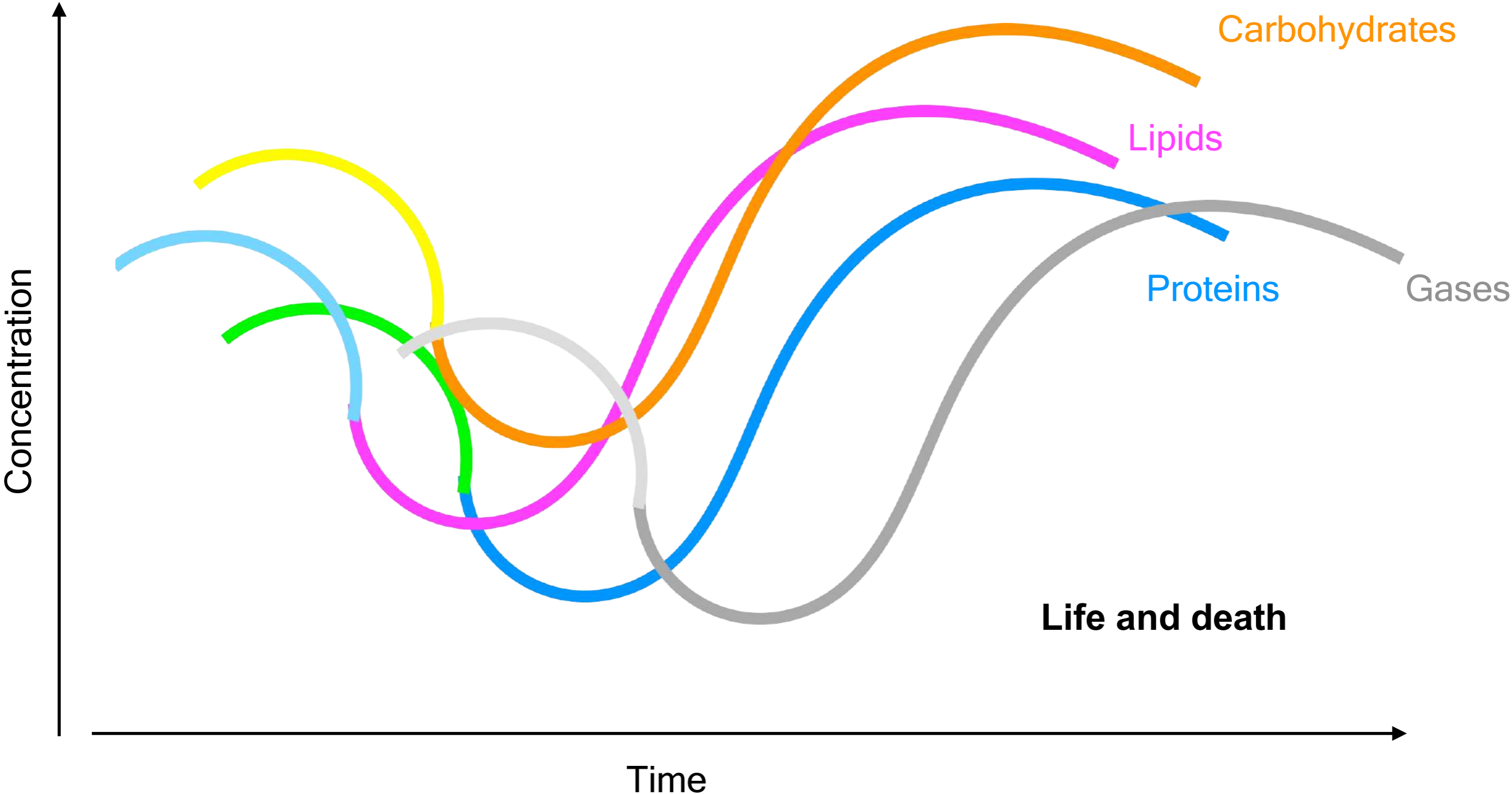
By Farooq Azam



Azam and Malfatti, 2007 Nature Reviews Microbiology 10:782

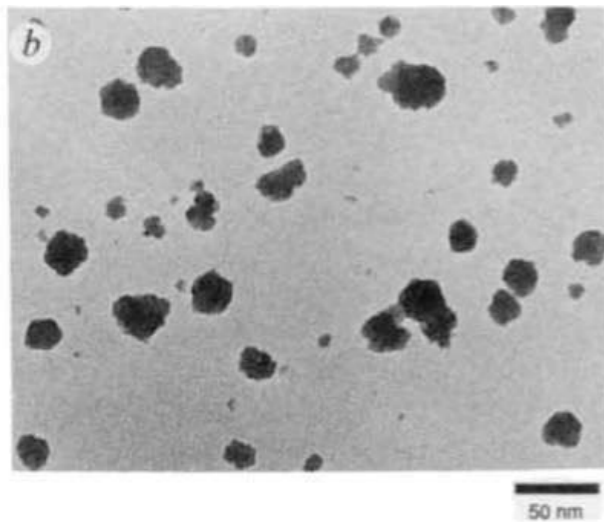
- Heterotrophic microbes, **decomposers**
- Interaction with the continuum of organic matter
- Significance of spatial coupling hydrolysis-uptake (permease) on the cell
- Cell surface hydrolases; 10^2 - 10^4 x variability in cell-specific activity
- Degree of efficiency in hydrolysis-uptake coupling

Biotransformations create chemically complex dynamics at the microscale



Physical continuum of organic matter: in “Aquasphere”

Colloids (10^8 mL⁻¹)



Wells & Goldberg, 1991

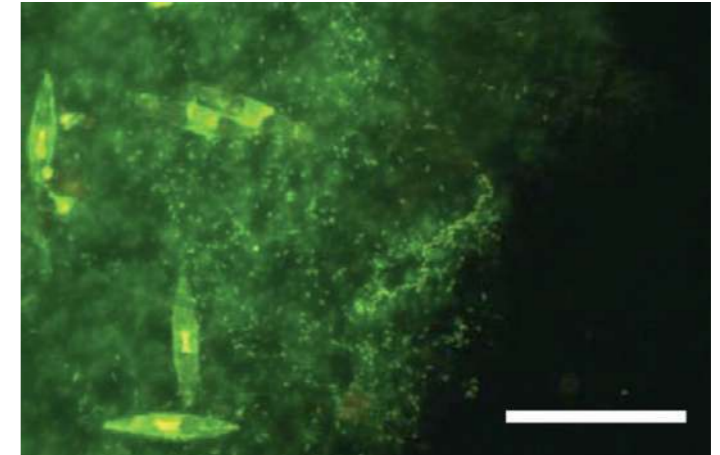
Koike et al., 1990

Coomassie Stained Particles (CSP)



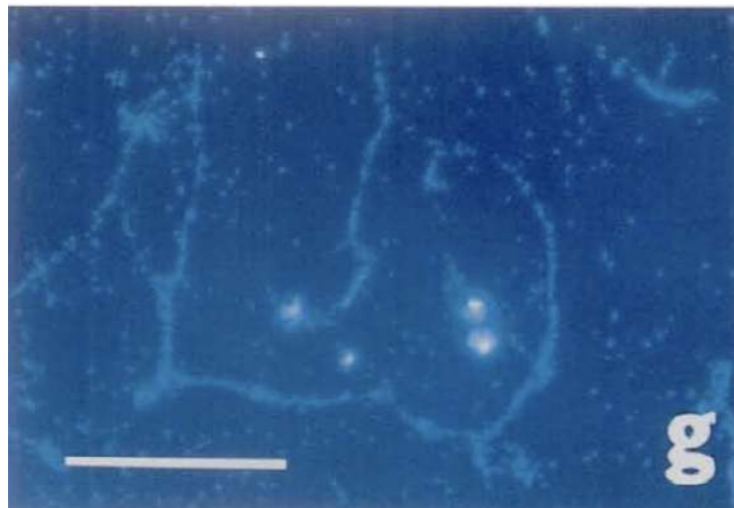
Long & Azam, 1996

Filter Fluorescing Particles (FFP)



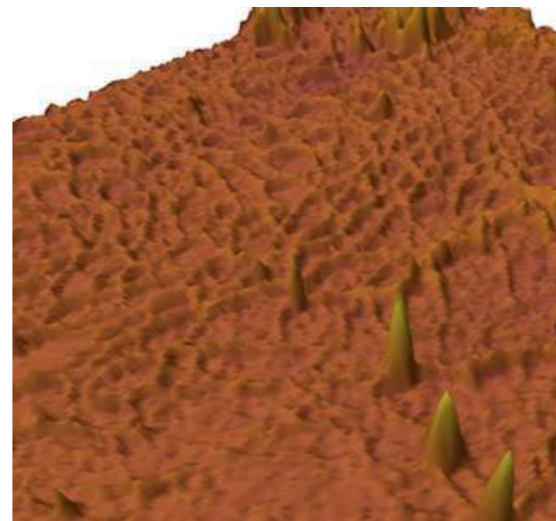
Samo, Malfatti & Azam 2008

Transparent Exopolymeric Particles (TEP)



Alledregge et al., 1993

Gel network from Adriatic Sea



Malfatti - AFM - unpub.

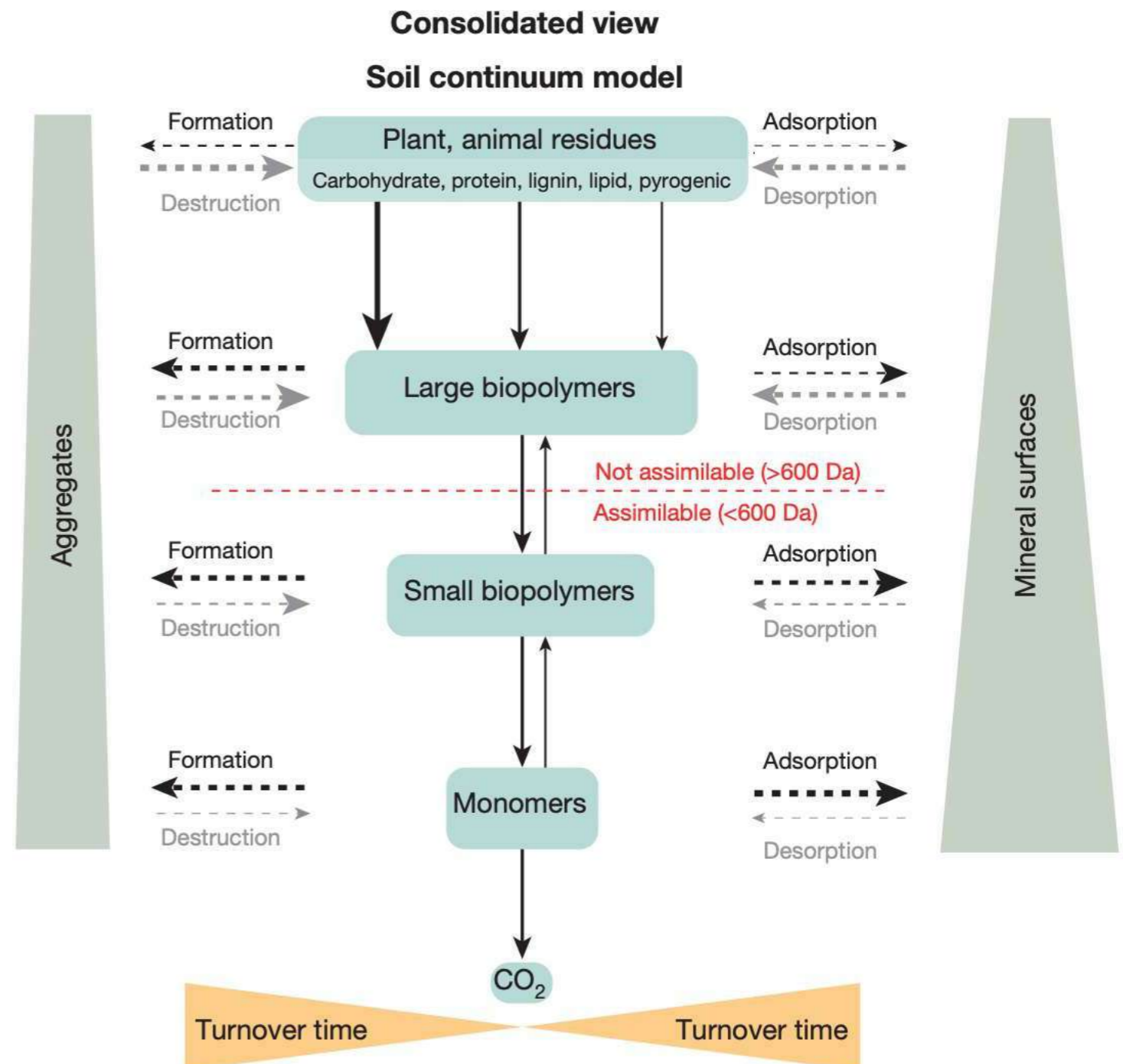


Nino Caressa

- Heterogeneous and patchy size continuum
- Chemically diverse and diverse reactivity
- Labile-recalcitrant continuum (=microbial utilization)

Physical continuum of organic matter: in “Soil-Geosphere”

- At any time within a living soil, a continuum exists of many **different organic compounds** **at various stages of decay**, moving down a thermodynamic gradient from large and energy rich compounds to smaller energy-poor compounds



Natural control of microbial growth

TABLE 20.1 Resources and conditions that govern microbial growth in nature

Resources

Carbon (organic, CO₂)

Nitrogen (organic, inorganic)

Other macronutrients (S, P, K, Mg)

Micronutrients (Fe, Mn, Co, Cu, Zn, Mn, Ni)

O₂ and other electron acceptors (NO₃⁻, SO₄²⁻, Fe³⁺)

Inorganic electron donors (H₂, H₂S, Fe²⁺, NH₄⁺, NO₂⁻)

Conditions

Temperature: cold → warm → hot

Water potential: dry → moist → wet

pH: 0 → 7 → 14

O₂: oxic → microoxic → anoxic

Light: bright light → dim light → dark

Osmotic conditions: freshwater → marine → hypersaline

Microbial metabolic pathways shaping Earth ecosystem

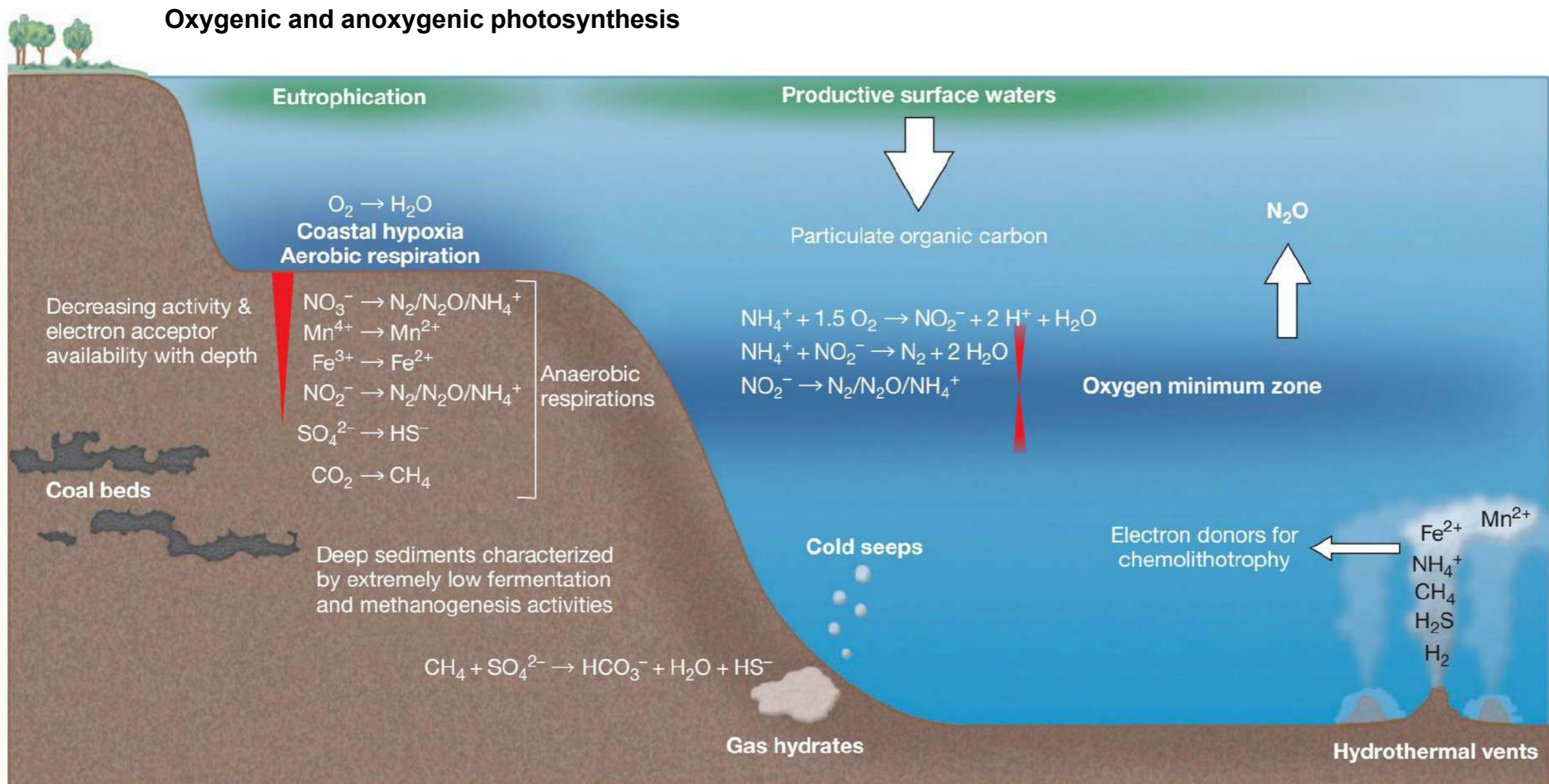
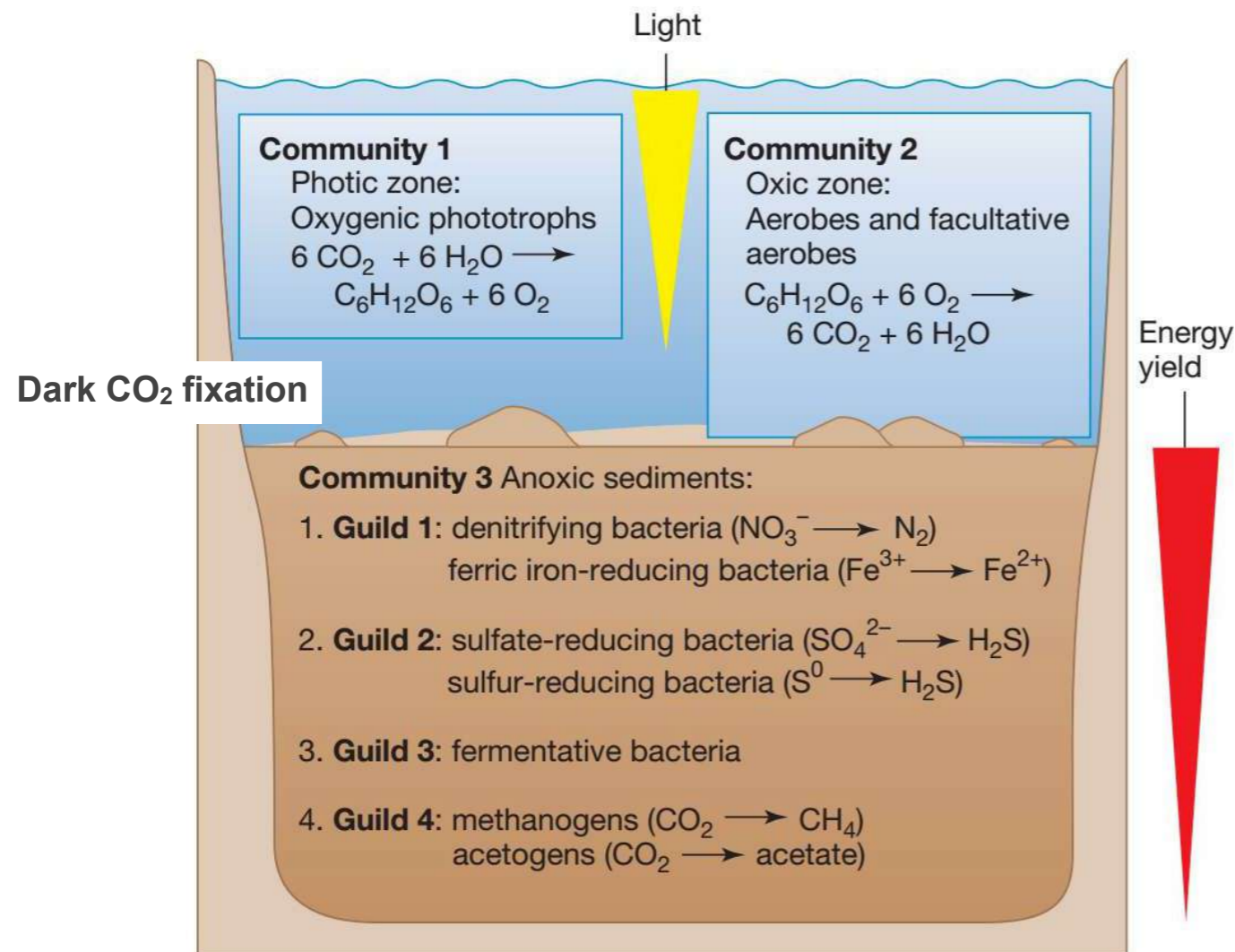


Figure 20.20 Diversity of marine systems and associated microbial metabolic processes. Decreasing electron acceptor availability with depth into the sediment or with increasing distance into an oxygen minimum zone is indicated by red wedges. Sulfate becomes limiting only at greater depths in marine sediments. The indicated metabolic diversity is covered in Chapter 14.

Community-coupling in the ocean



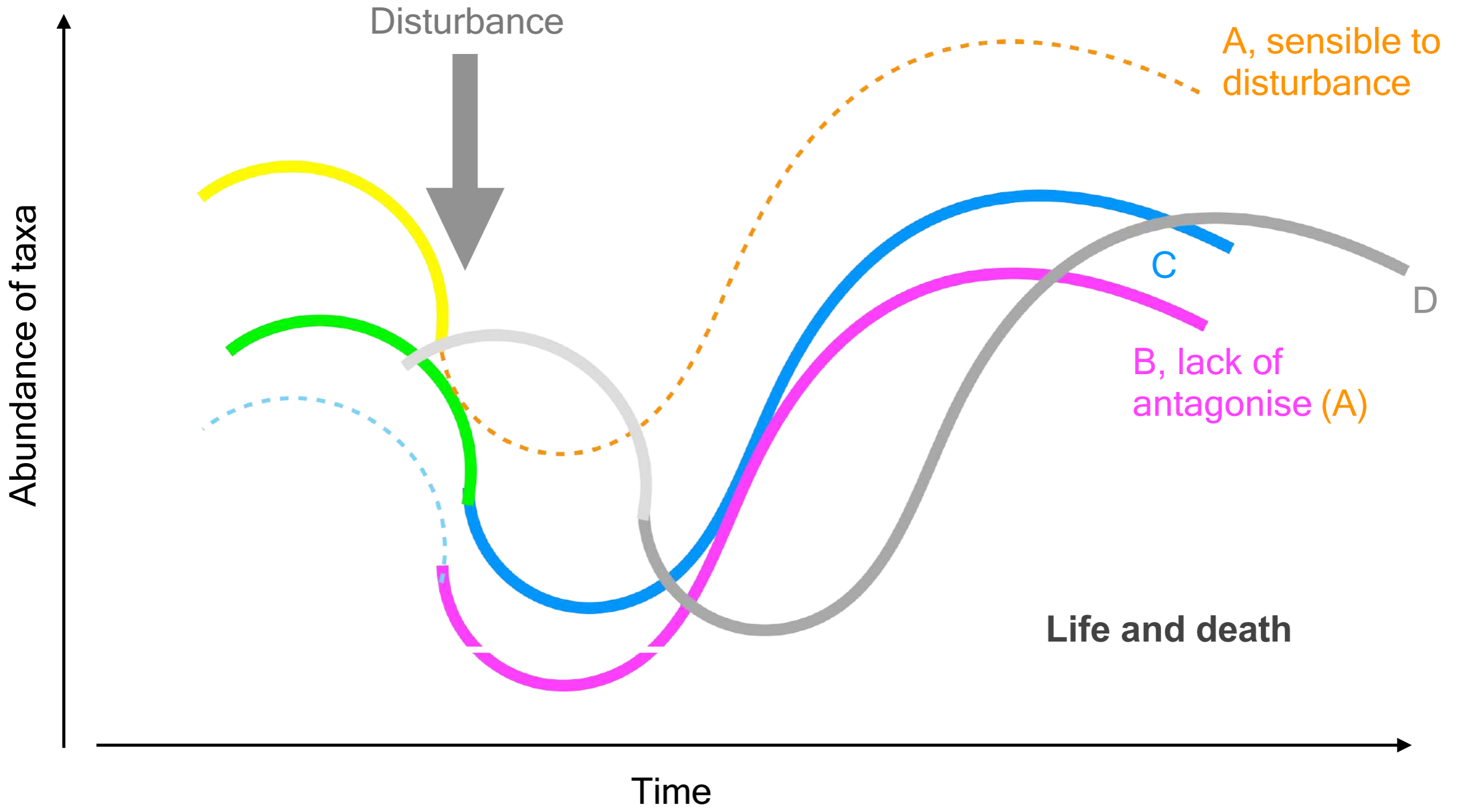
Upper ocean primary production and deep ocean chemo-lithoautotrophy (aka: dark CO₂ fixation) are fueling organic matter degradation communities

Figure 20.2 Populations, guilds, and communities. Microbial communities consist of populations of cells of different species. A freshwater lake ecosystem would likely have the communities shown here. The reduction of NO_3^- , Fe^{3+} , SO_4^{2-} , S^0 , and CO_2 are examples of anaerobic respirations. The region of greatest activity for each of the different respiratory processes would differ with depth in the sediment. As more energetically favorable electron acceptors are depleted by microbial activity near the surface, less favorable reactions occur deeper in the sediment.

Community Structure and Succession

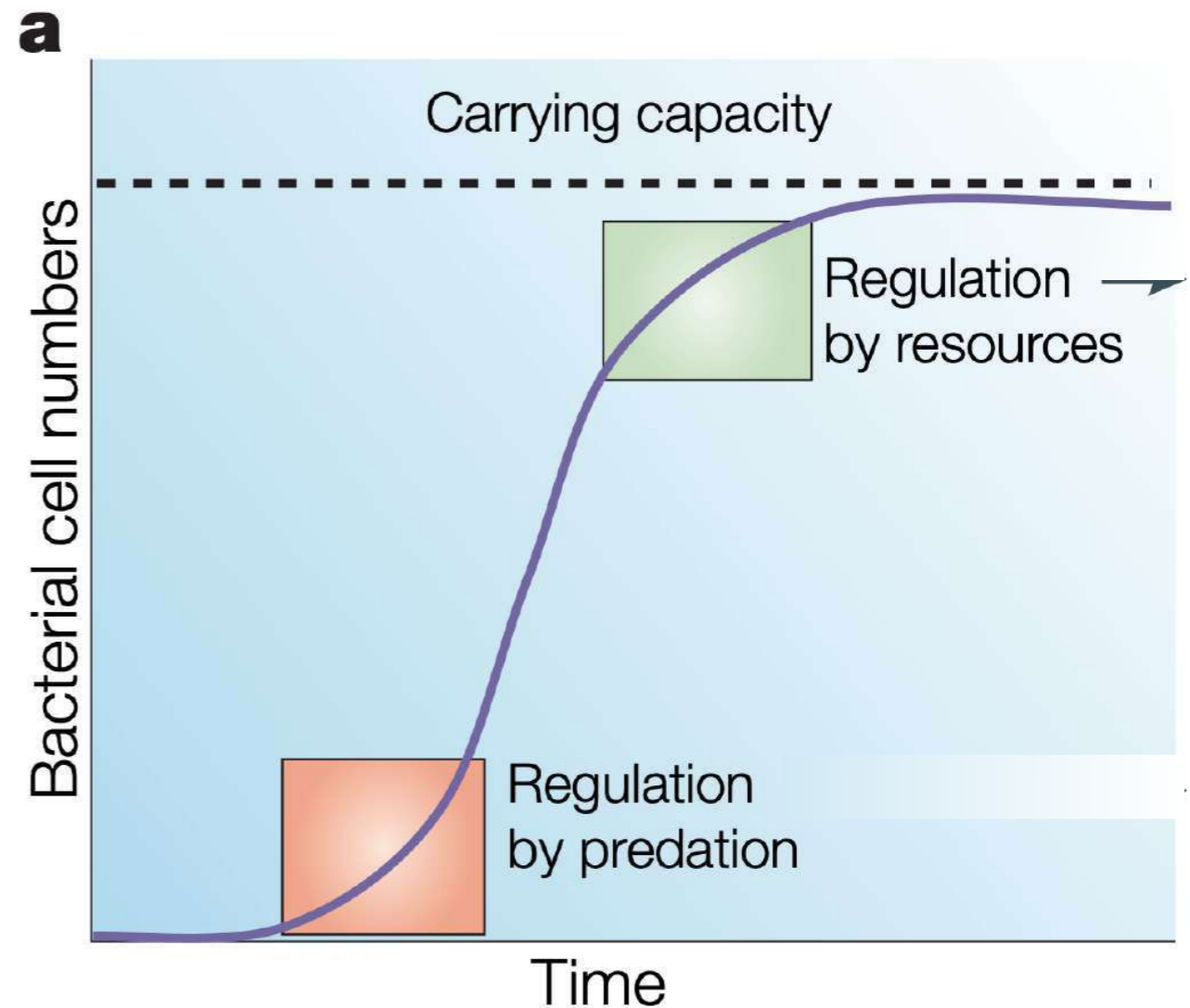
- **Community structure** refers to the **composition** (which microbes are present), **abundance**, and **diversity** of microbial species in a given environment
- **Succession** is the natural **progression or change** in microbial community structure over time, often **following a disturbance** (*e.g.*, oil spill, seasonal shift, land use change)
- Microbial succession can occur rapidly and is driven by resource availability, environmental conditions, and species interactions
- **Example:** In compost, early colonizers (fast-growing bacteria) are replaced by thermophiles as temperature rises during decomposition

Microbial succession



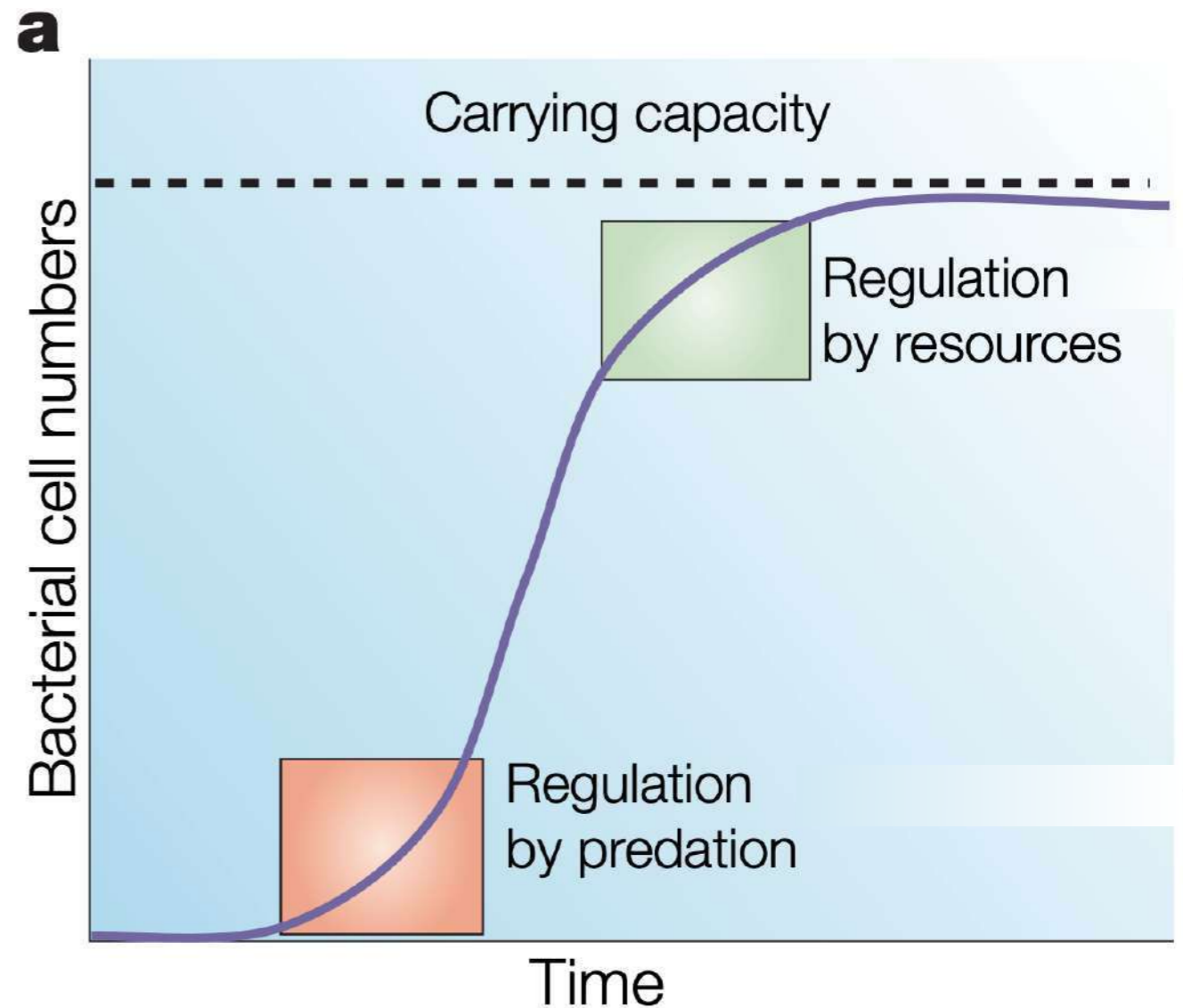
Carrying capacity

- Carrying capacity, the average [population density](#) (cell numbers) or population size of a [species](#) below which its numbers tend to increase and above which its numbers tend to decrease because of shortages of resources
- The carrying capacity is different for each species in a [habitat](#) because of that species' particular food, shelter, and social requirements
- The **carrying capacity** of a biological [species](#) in a particular habitat refers to the maximum number of individuals (of that species) that the [environment](#) can carry and sustain, considering its geography or physical features



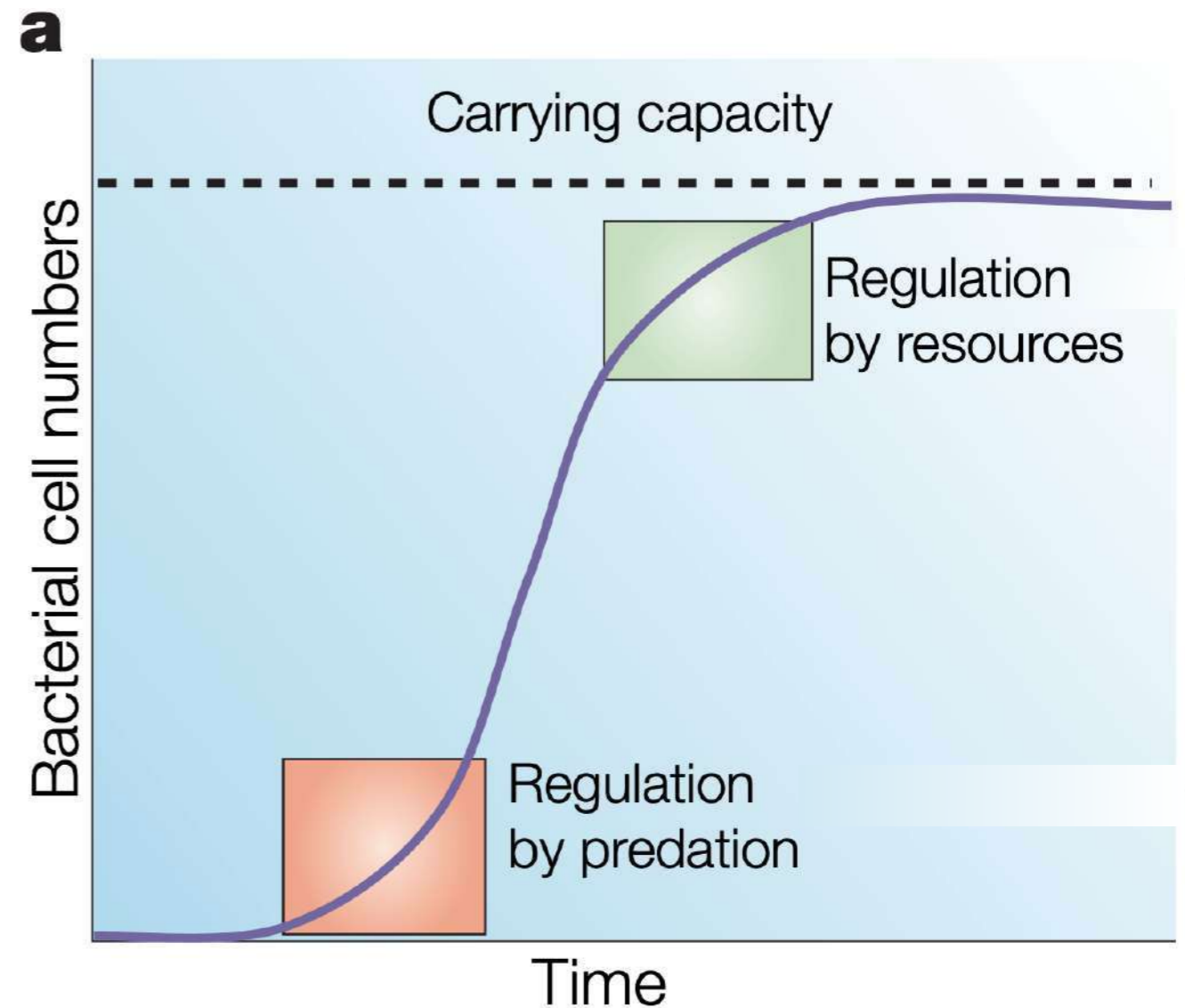
Top-down control

- **Top-down:** Ecological scenario in which the abundance or biomass of organisms is mainly determined **by mortality owing to predation**
- **Viruses and protists (less studied antagonistic reactions and bacterial predators)** can directly impact bacterial communities either through their **host specific lysis and size selective grazing respectively** or indirectly through the alteration of organic pools by mortality processes



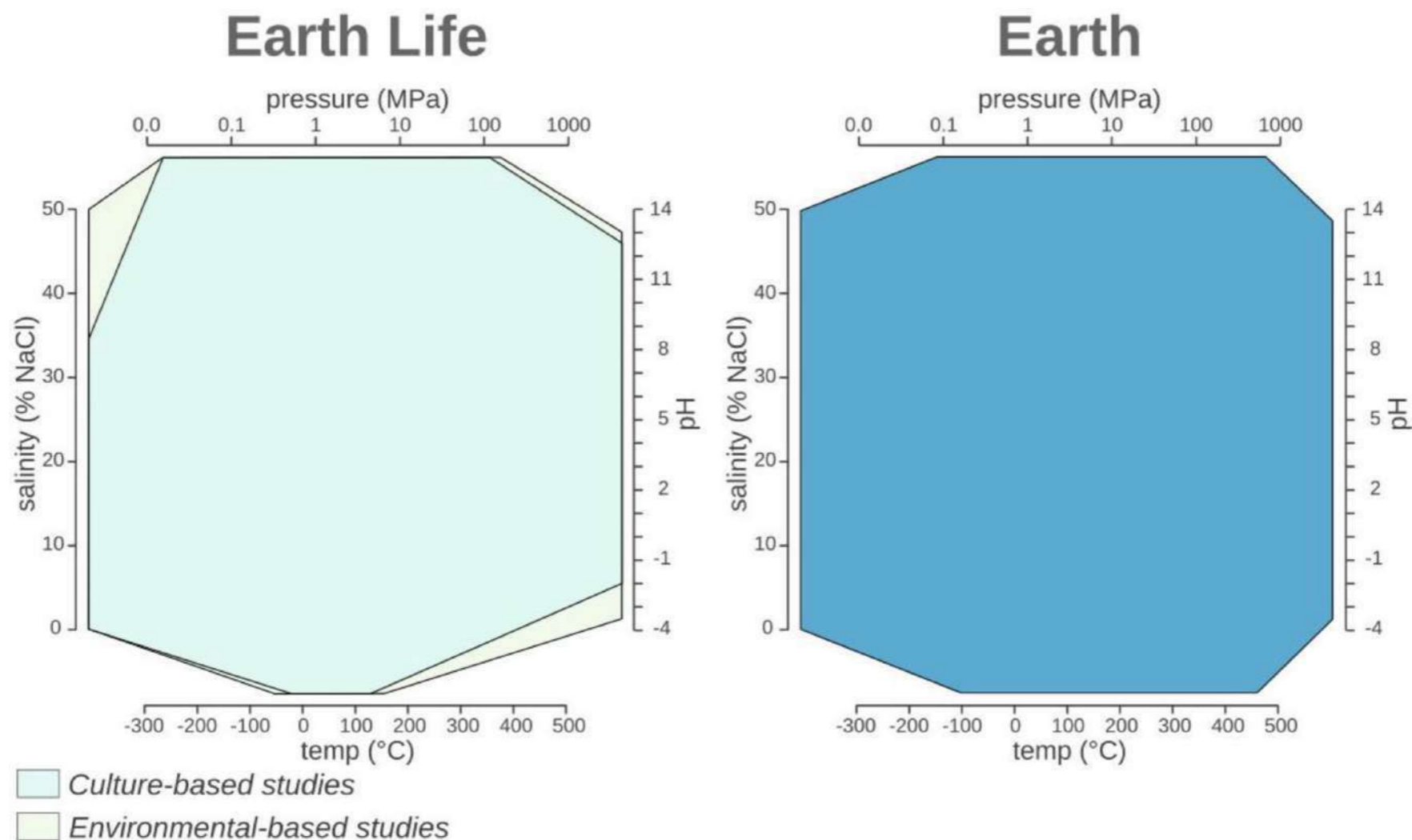
Bottom-up control

- **Bottom-up:** Ecological scenario in which the abundance or biomass of organisms is mainly determined **by a lack of resources and mortality owing to starvation**
- Bottom-up (**nutrients, organic matter** and also **energy, salinity, pH**) influence the growth and the physiological state of the microbial community



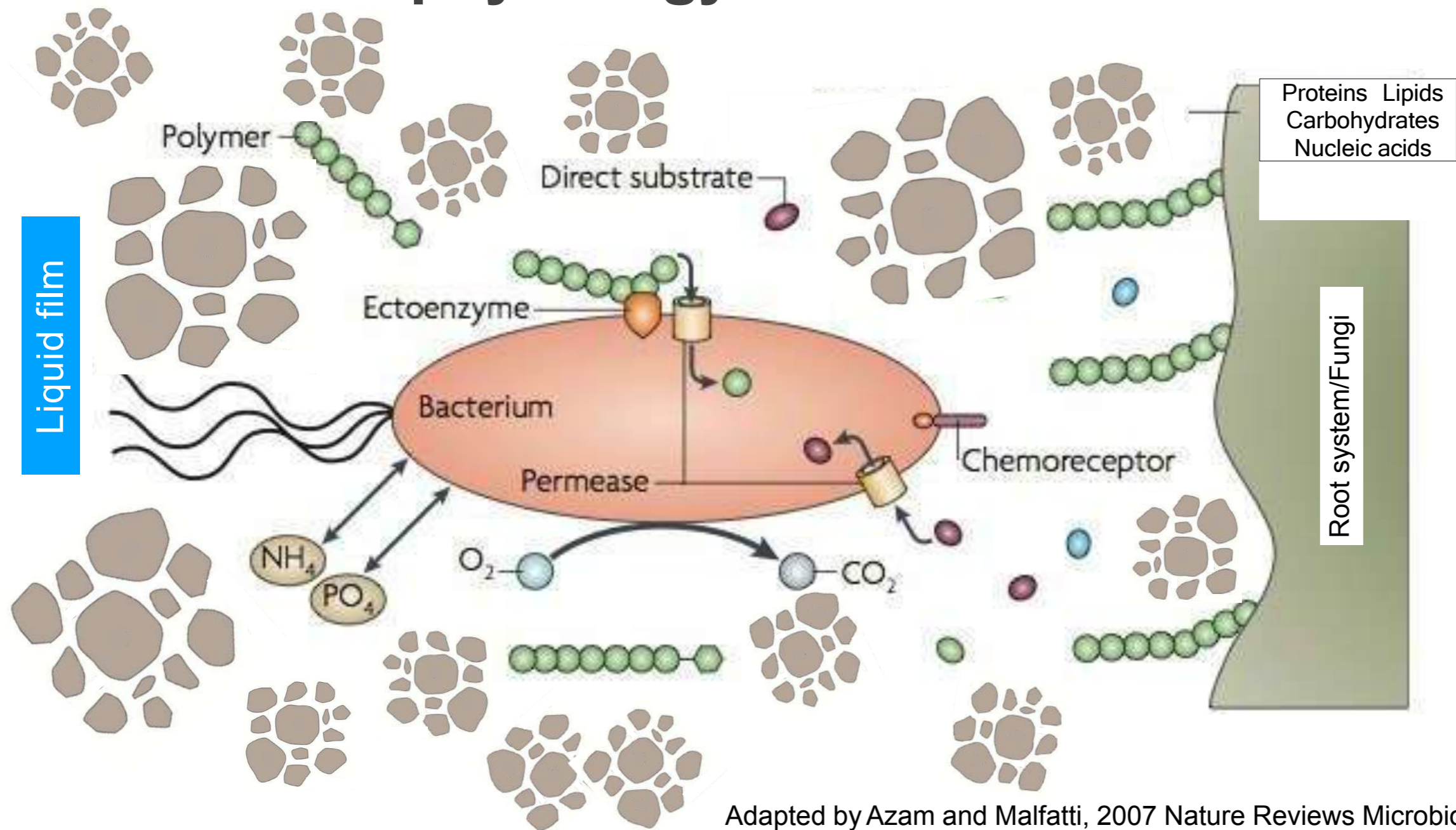
Microbial growth in the environment

- Bottom-up (nutrient supply) and Top-down (protistan grazing, viral lysis, and antagonistic reaction and bacterial predators) processes are known to influence and control microbial community composition and diversity in time and space



Merino et al. 2019

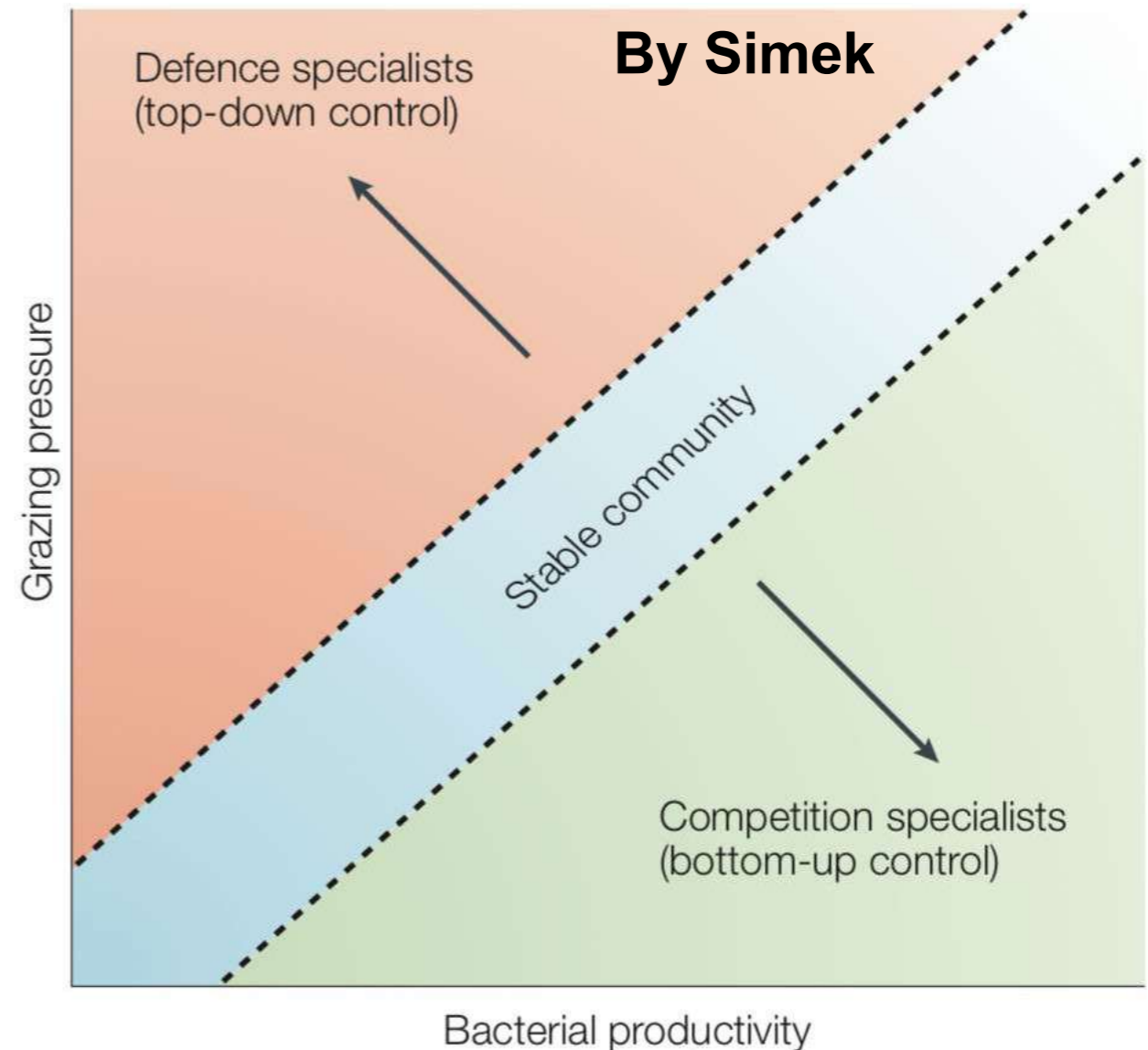
Microscale bottom-up control on microbial growth, physiology and metabolism



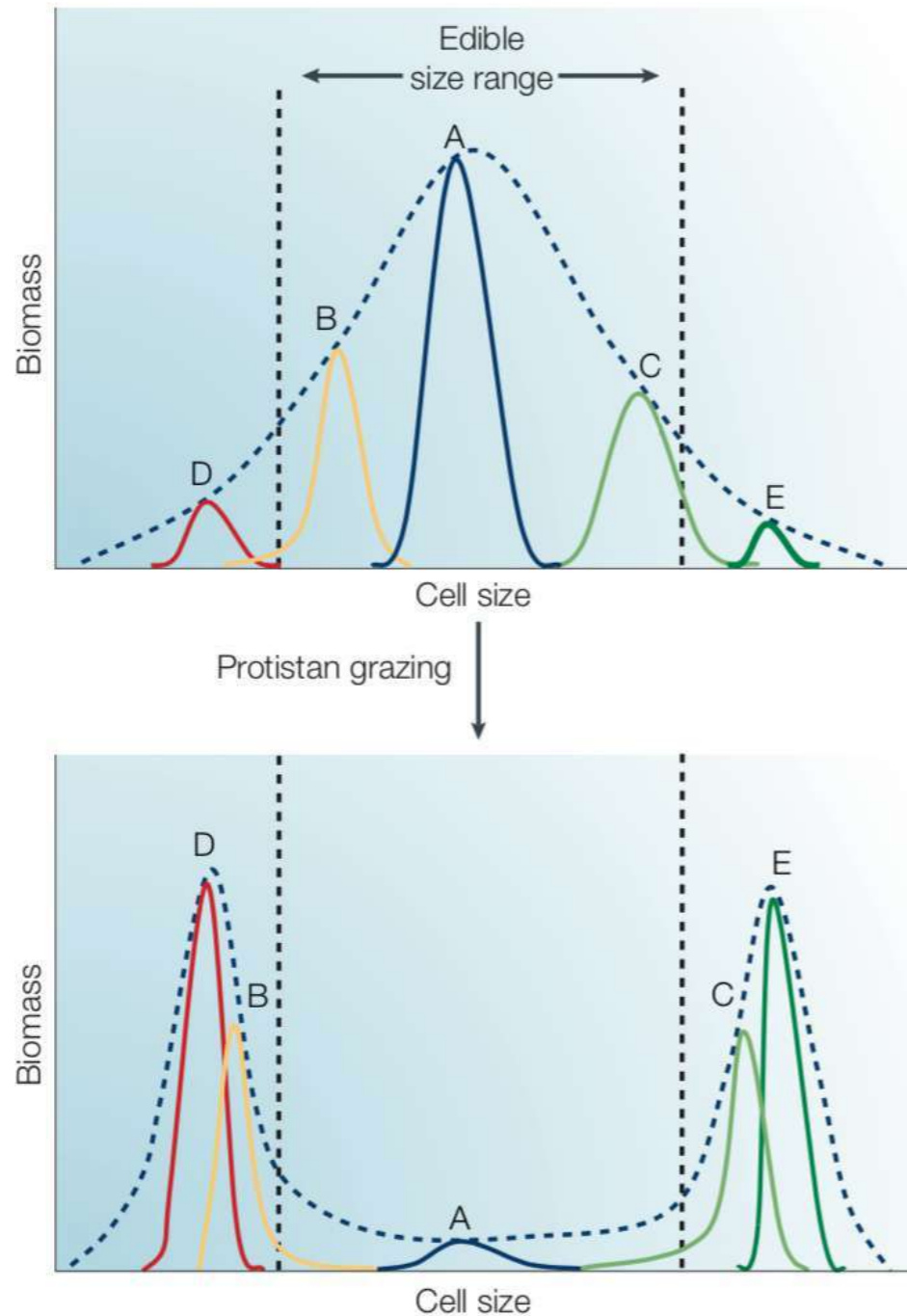
- Cell machinery respond to stress
- Changing behavior (motility), enter into dormancy
- Changing expression for limited nutrient

Stable microbial community

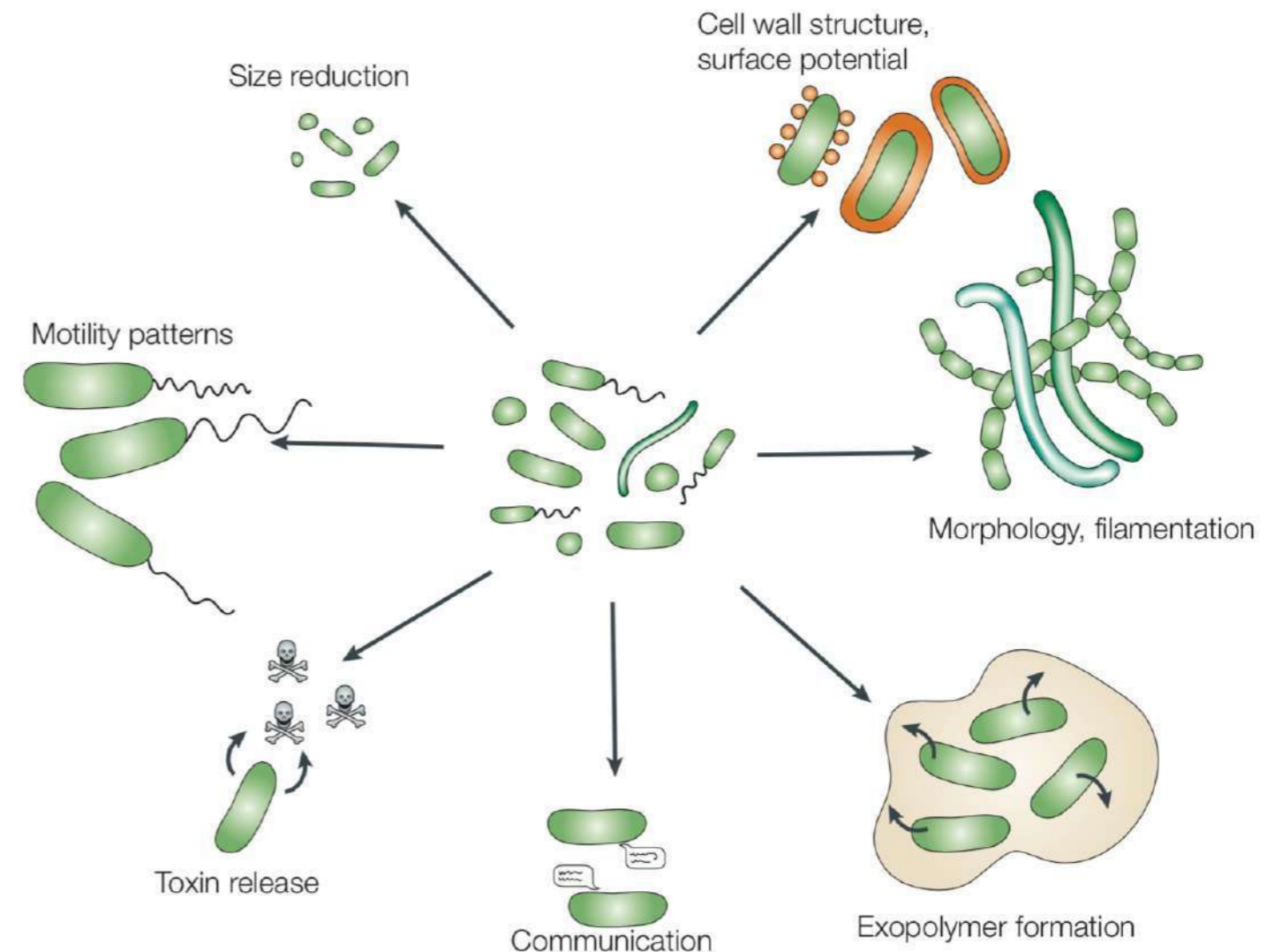
- **Stable communities** of microbial species will exist at **different levels of microbial productivity** if there is an approximate **balance between bacterial production and protistan bacterivory**
- **Changes** in species composition of the microbial assemblage are triggered by rapid shifts from 'top-down' to 'bottom-up' control
- Depending on the direction of such shifts, bacterial species are **favoured that are able either to minimize predation losses ('defence specialists')** or to **respond most rapidly to favourable changes in growth conditions ('competition specialists')**



Microbial strategies to resist to predators

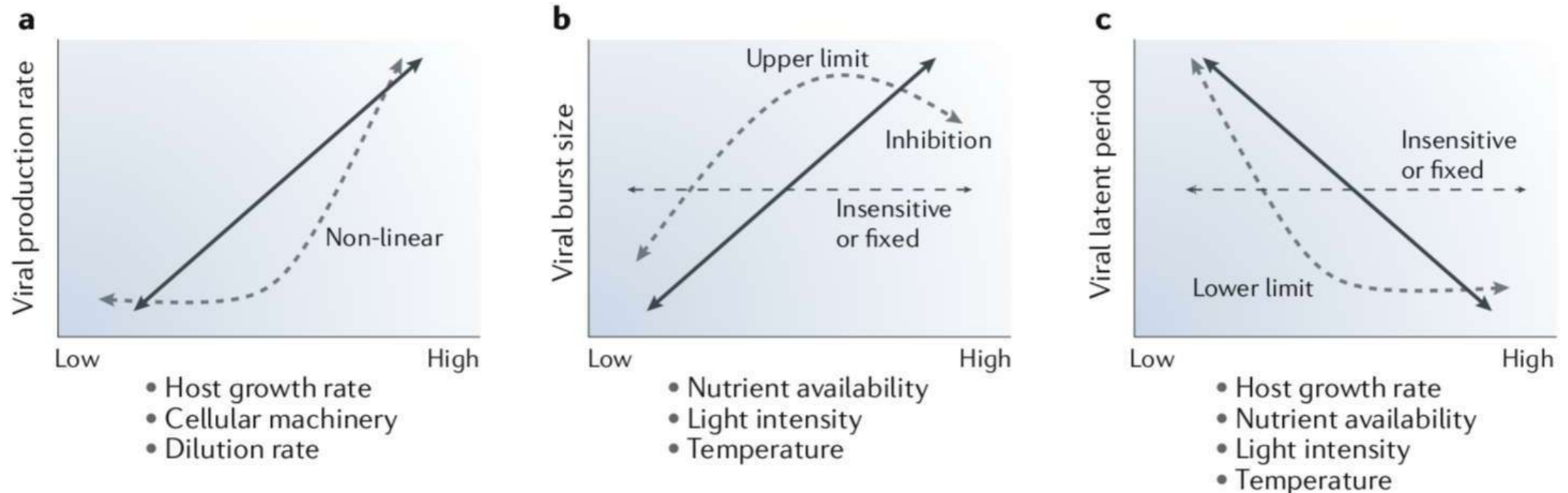


Cell surface and cell shape can influence size-dependent grazing



The effect of predation on microbial community structure effect on cell size

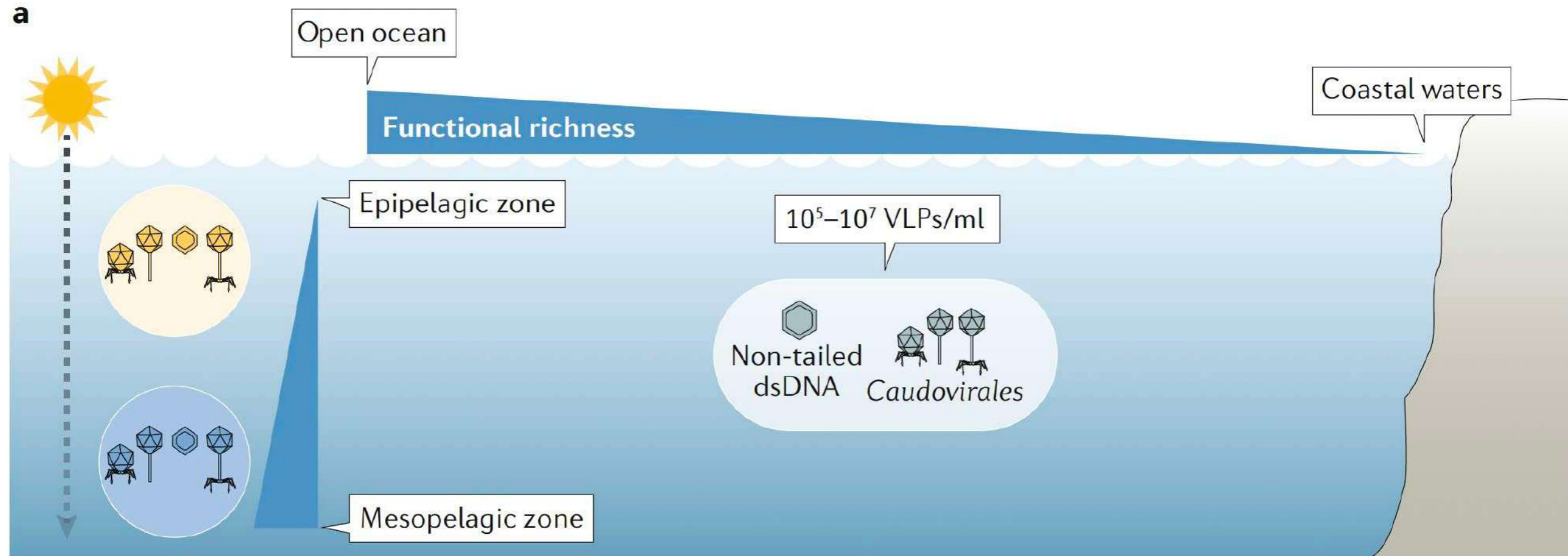
Viral dynamics with host and nutrient status



The **host growth rate and cellular machinery** (that is, ribosomes and enzymes) can be **manipulated by environmental variables** (for example, temperature, light intensity or nutrient availability)

Nutrient availability has the potential to alter viral production directly through limitation of substrates needed to build progeny virions or indirectly through the host growth rate, which in turn affects production yields or rates, respectively

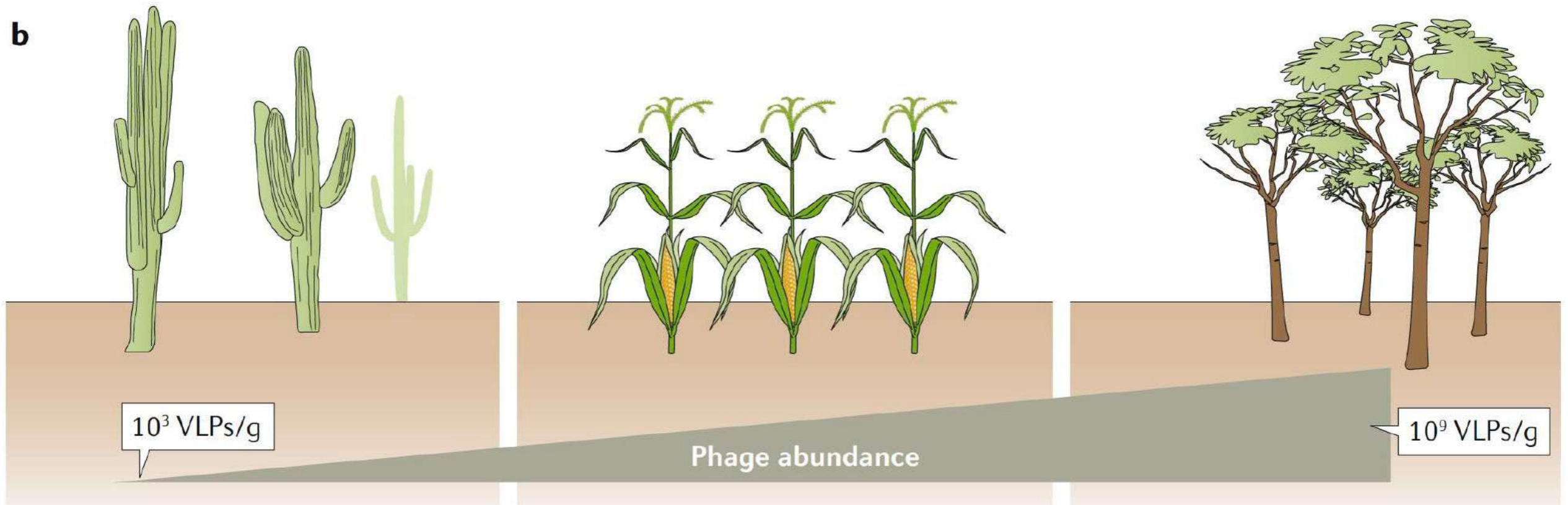
Phages in the marine environment



Dion et al., 2020

- Phages are extremely abundant, with a virus- to-bacteria ratio often ranging from 1:1 to 100:1
- Quantitative transmission electron microscopy of marine samples indicated that non- tailed phages are much more represented than tailed phages, which was also confirmed by metagenomic data
- Phages from the mesopelagic zone were distinct from phages isolated from the epipelagic zone in terms of gene content, life history traits and temporal persistence
- Functional richness was found to decrease from deep to surface water and with distance from the shore for surface water only

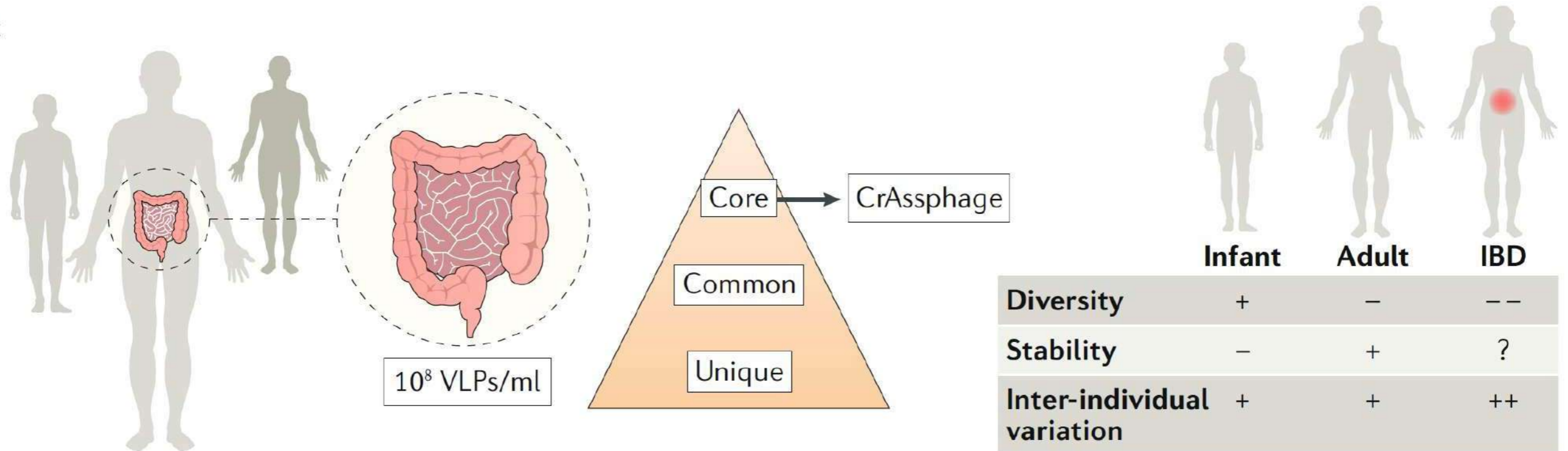
Phages in the soil environment



- Phage abundance in the soil is highly variable and correlates with biome type (for example, desert, agricultural or forest soils), pH and bacterial abundance
- Viral abundance is the lowest in hot deserts, intermediate in agricultural soils and the highest in forest and wetland soils
- Viral abundance also positively correlates with bacterial abundance in the soil and negatively correlates with pH, with phage counts decreasing at higher pH

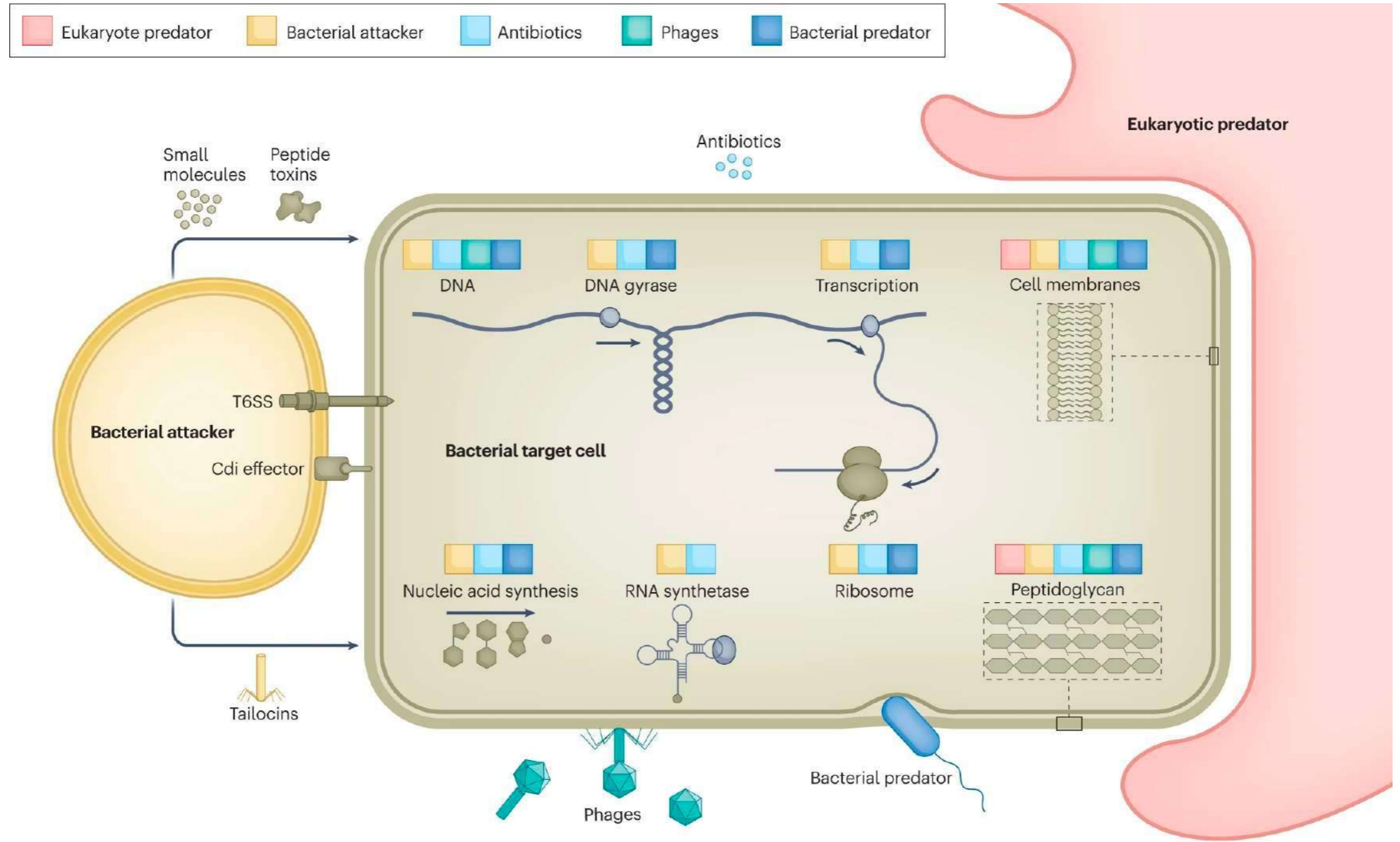
The human gut phage community

c



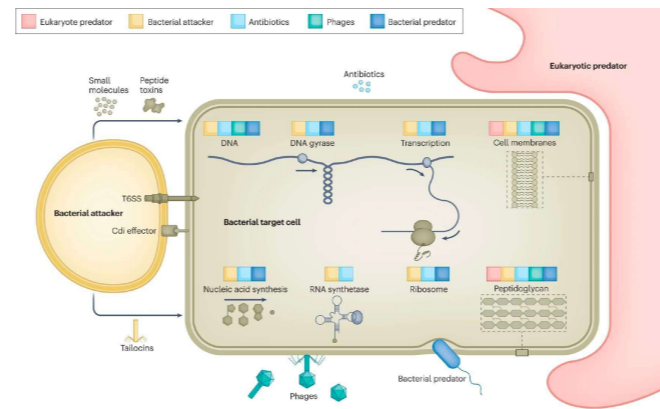
- The phage community in the human gut is mainly composed of members of the Caudovirales and Microviridae, and the majority of these phages remain unclassified
- Phage composition is unique to individuals, with global metagenomic analyses indicating that some phages are globally distributed
- The gut phage community is also stable over time, but rapid changes are observed in early life
- Changes in the diversity and composition of the human virome were also reported to be related to the gut health status, particularly in the case of inflammatory bowel disease (IBD)
- A set of widespread phages exists, named the core phage community, which includes crAssphage, likely the most prevalent human gut phage

Microbes under attack



Smith et al. 2023

Most attacks target core cellular processes and functions of the bacterial cell. Coloured squares indicate whether a given threat type typically acts on a particular target.



Most attacks target core cellular processes and functions of the bacterial cell. Coloured squares indicate whether a given threat type typically acts on a particular target.

Bacterial competitors antagonize a target bacterium via diverse mechanisms, including both contact-dependent weaponry (the type VI secretion system (T6SS); Cdi effectors) and diffusible weaponry (small molecules, peptide toxins and tailocins).

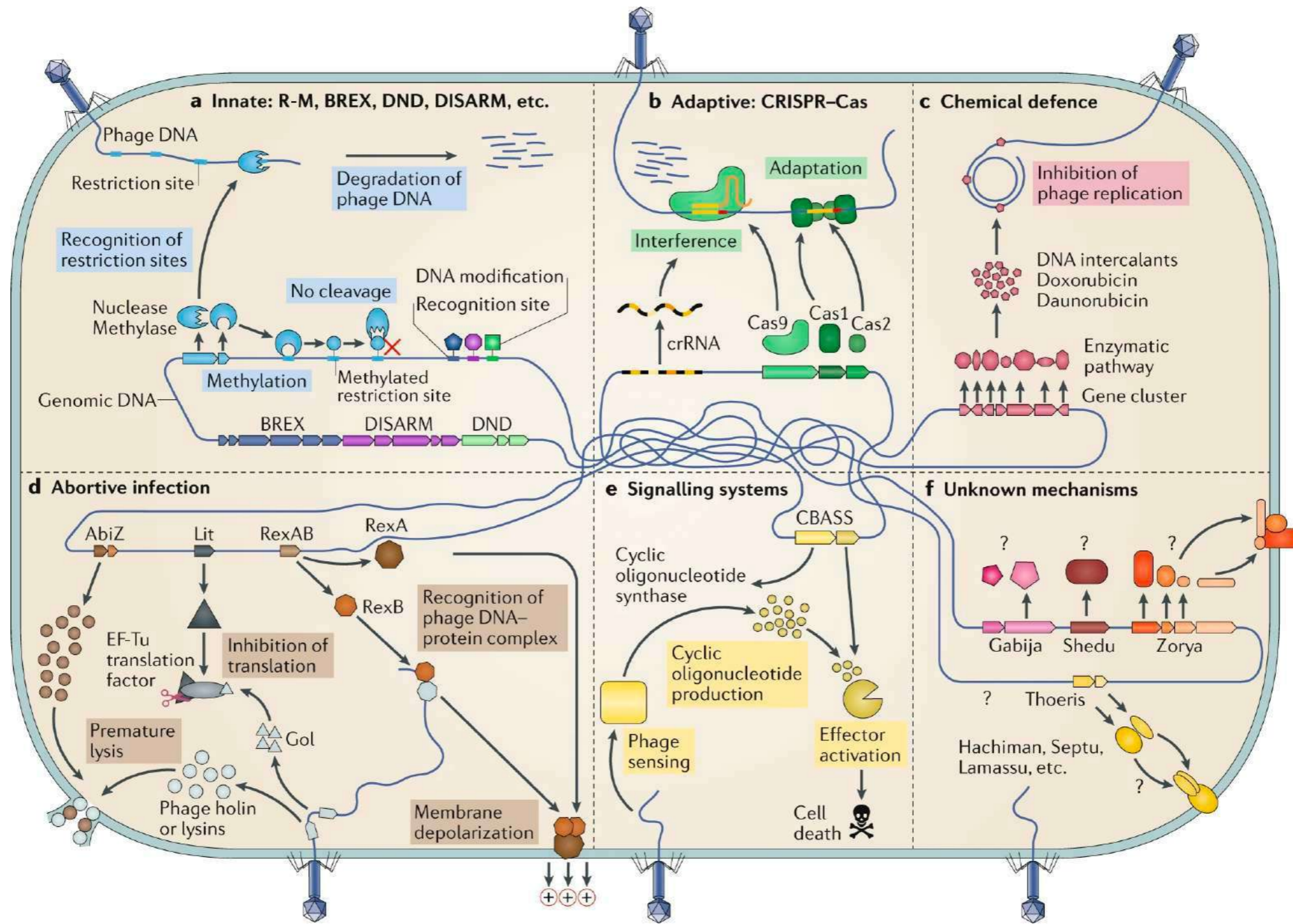
The majority of clinical antibiotics are also derived from bacteria and other microorganisms.

Following infection of a bacterial cell, phages attack cell walls and membranes to release their progeny via cell lysis.

Some bacterial predators, such as *Bdellovibrio* species and similar organisms, invade the host cell periplasm, injecting toxins that digest various cytoplasmic components.

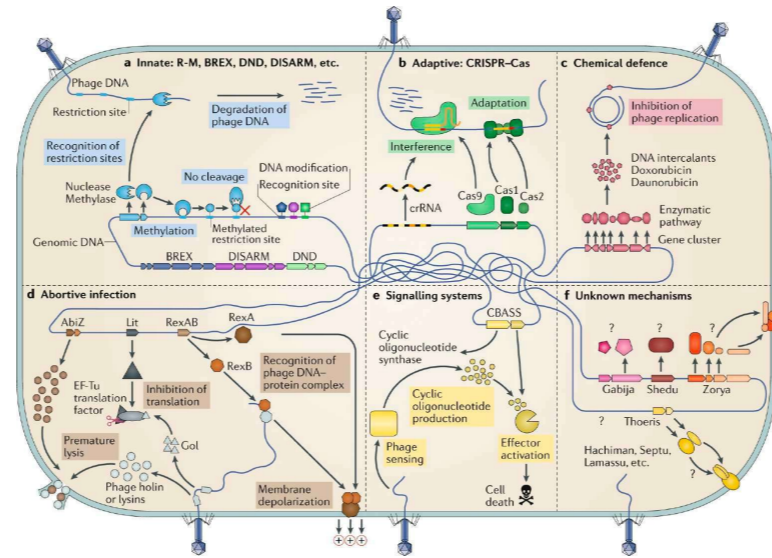
Many eukaryotic predators engulf and digest target bacteria whole in phagosome compartments.

Bacterial antiviral strategies



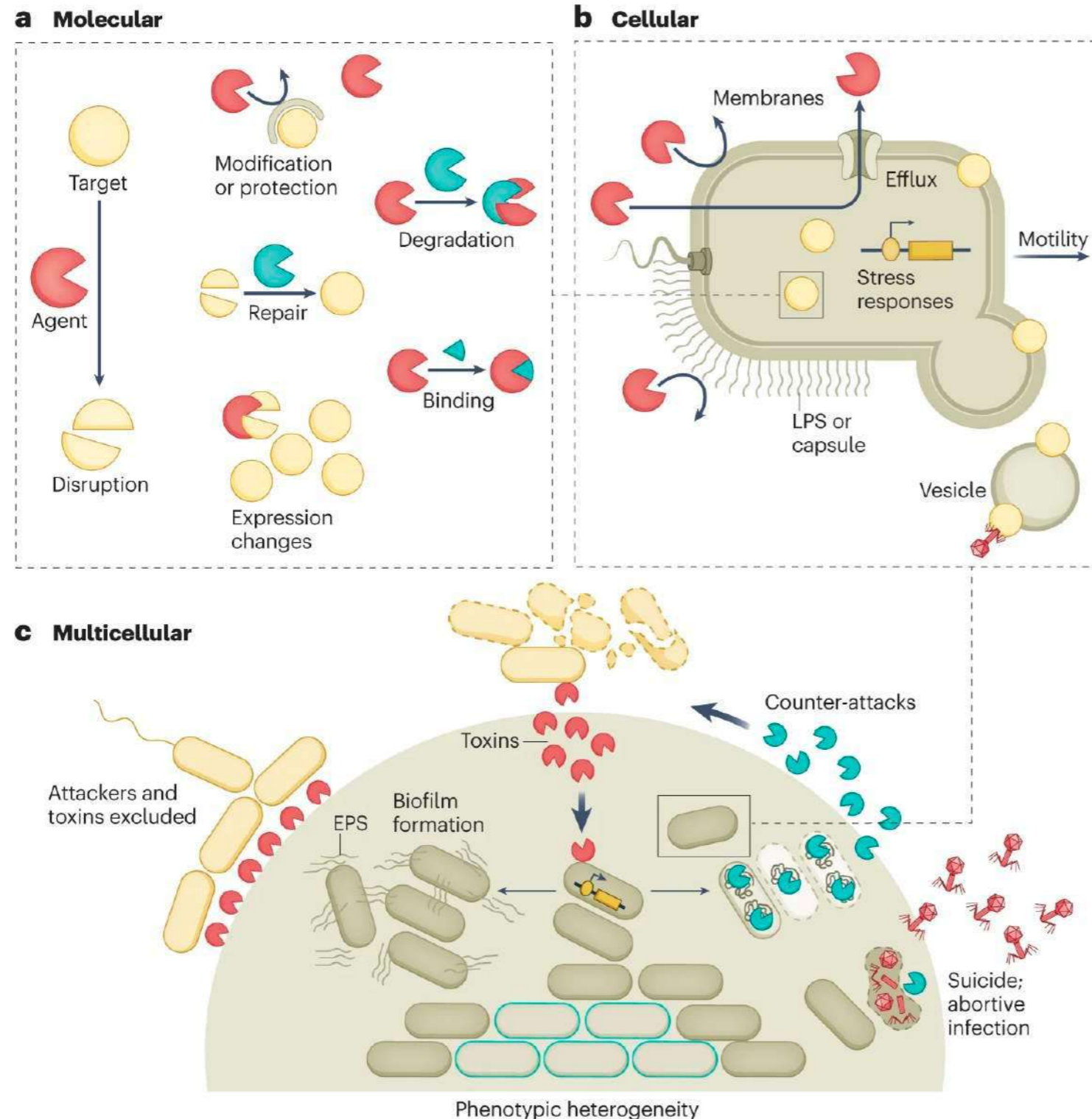
Bernheim & Sorek, 2019

Bacterial defence systems that target nucleic acids encompass both innate and adaptive immunity and chemical defence and cell lysis or cell death induction



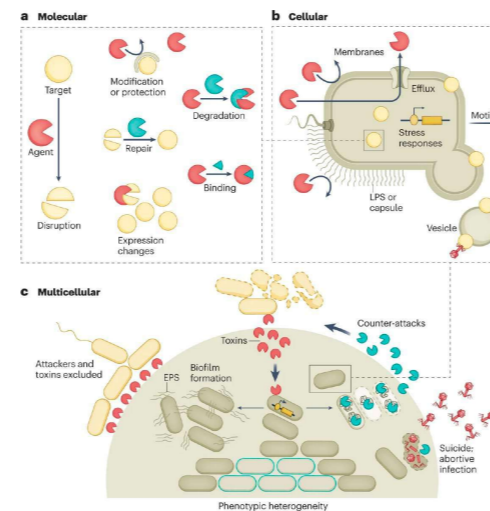
Defence systems that target nucleic acids encompass both innate and adaptive immunity. **a** | Restriction-modification (R-M) and other related systems modify specific sequence motifs in the host genome and cleave or degrade unmodified foreign DNA. **b** | CRISPR-Cas systems work in two main phases: adaptation, where a complex of Cas proteins guides the acquisition of new bacteriophage (phage)-derived spacers; and interference, where Cas proteins in a complex with a spacer-derived CRISPR RNA (crRNA) target and degrade phage nucleic acids. **c** | Chemical defence has been described in *Streptomyces* spp., in which bacteria produce a small anti-phage molecule that intercalates into phage DNA and inhibits its replication. **d** | Abortive infection mechanisms are diverse. In concert with phage-encoded holins and lysins of phage Phi31, AbiZ from *Lactococcus lactis* accelerates lysis before phage assembly is completed. Upon expression of the T4 phage protein Gol, the *Escherichia coli* Lit protein inhibits translation through cleavage of the EF-Tu elongation factor. The *E. coli* protein RexA recognizes a specific DNA-protein complex formed by the λ phage, and activates RexB, an ion channel that depolarizes the membrane, leading to cell death. **e** | CBASS (cyclic oligonucleotide-based anti-phage signalling system) senses the presence of phage and generates a cyclic oligonucleotide small-molecule signal that activates an effector leading to cell death. **f** | Multiple systems have recently been demonstrated to have anti-phage roles, but their mechanisms remain unknown. Abi, abortive infection; BREX, bacteriophage exclusion; DISARM, defence islands system associated with R-M.

Bacterial multiple lines of defence against biotic threats



At both the individual and collective level, bacteria draw upon a plethora of defensive adaptations to escape harm

Defences are arranged according to the spatial scale at which they operate



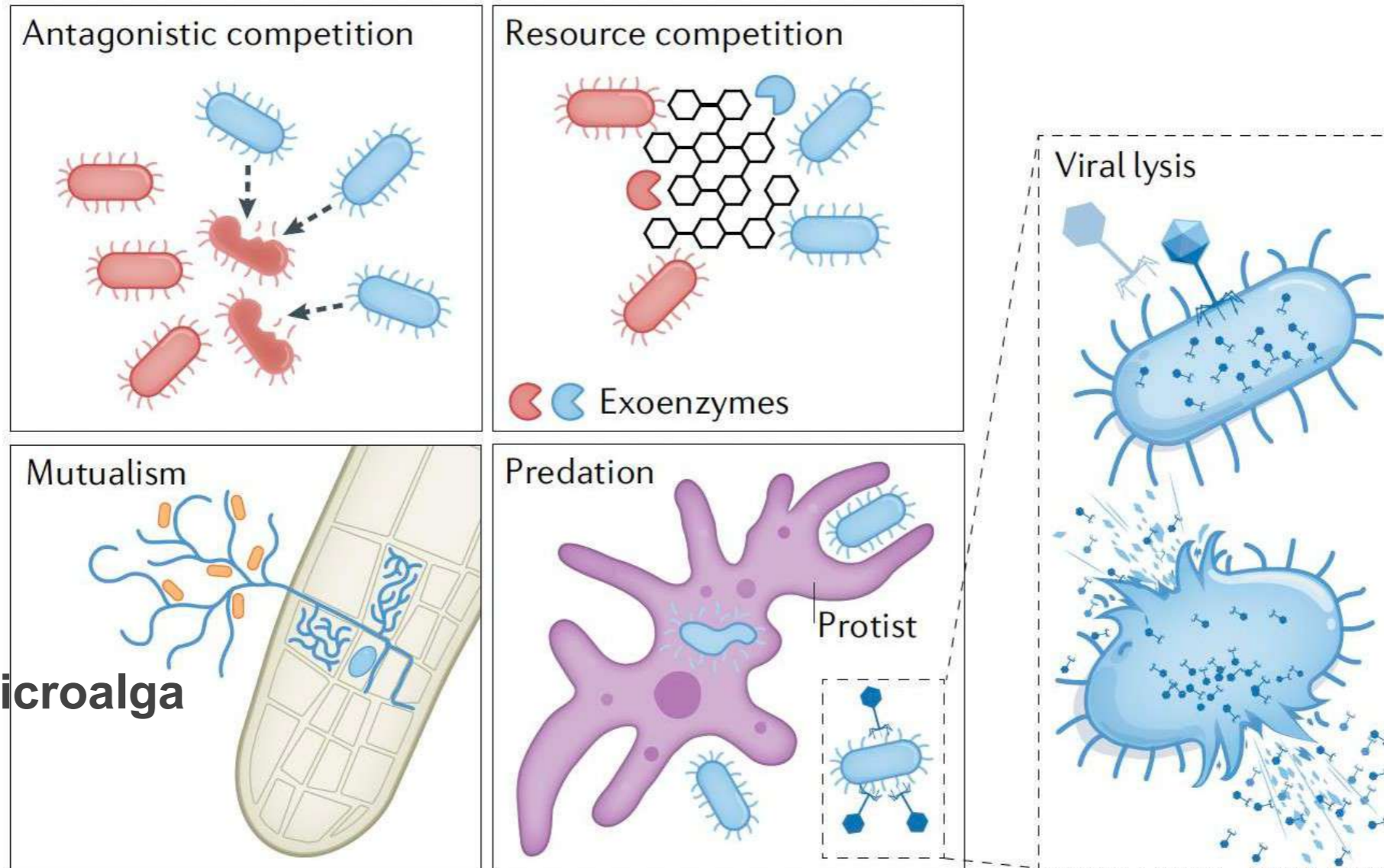
a, At the molecular level, attacks by competitors, phages and predators are mediated by harmful agents (for example, toxins, enzymes and genetic elements) that disrupt cellular functions by interacting with diverse targets. **Bacteria can mitigate disruption at a molecular level by altering the target or compensating for its disruption, or by destroying or binding to the harmful agent.**

b, At the cellular level, macromolecular barriers, including cell membranes, S-layers, lipopolysaccharide (LPS) or capsules, prevent harmful agents from entering a bacterial cell. **Efflux pumps remove harmful molecules that overcome barriers, and motile bacteria can escape harmful environments by repositioning themselves. Secreted membrane vesicles can bind and inactivate toxins and phages.**

c, At the multicellular level, bacteria **create collective barriers** (production of extracellular polymeric substances (EPSs); biofilm formation) that exclude attackers. Dense cell groups can limit toxin penetration via **reduced diffusion or collective degradation**. They may also contain resistant subpopulations (**phenotypic heterogeneity**), launch en masse counter-attacks and, in some circumstances (for example, abortive infection), **commit suicide to protect kin cells. Stress responses and other regulatory pathways enable these defences to be activated in response to specific or general threat cues.**

Biotic interactions in the soil /ocean microbiome, which shape microbial community structure and organic matter cycling —> interactions influence how organisms allocate carbon and can shape the chemical composition and flow of organic matter

a Types of biotic interaction



With microalga

Sokol, 2022

Interactions include antagonistic competition (combative interactions for resources), exploitative competition (indirect competition for resources), mutualisms (for example, interactions between mycorrhizal fungi and plant roots) and predation (for example, protists consuming bacteria or viral lysis)

Microbial mortality in sum

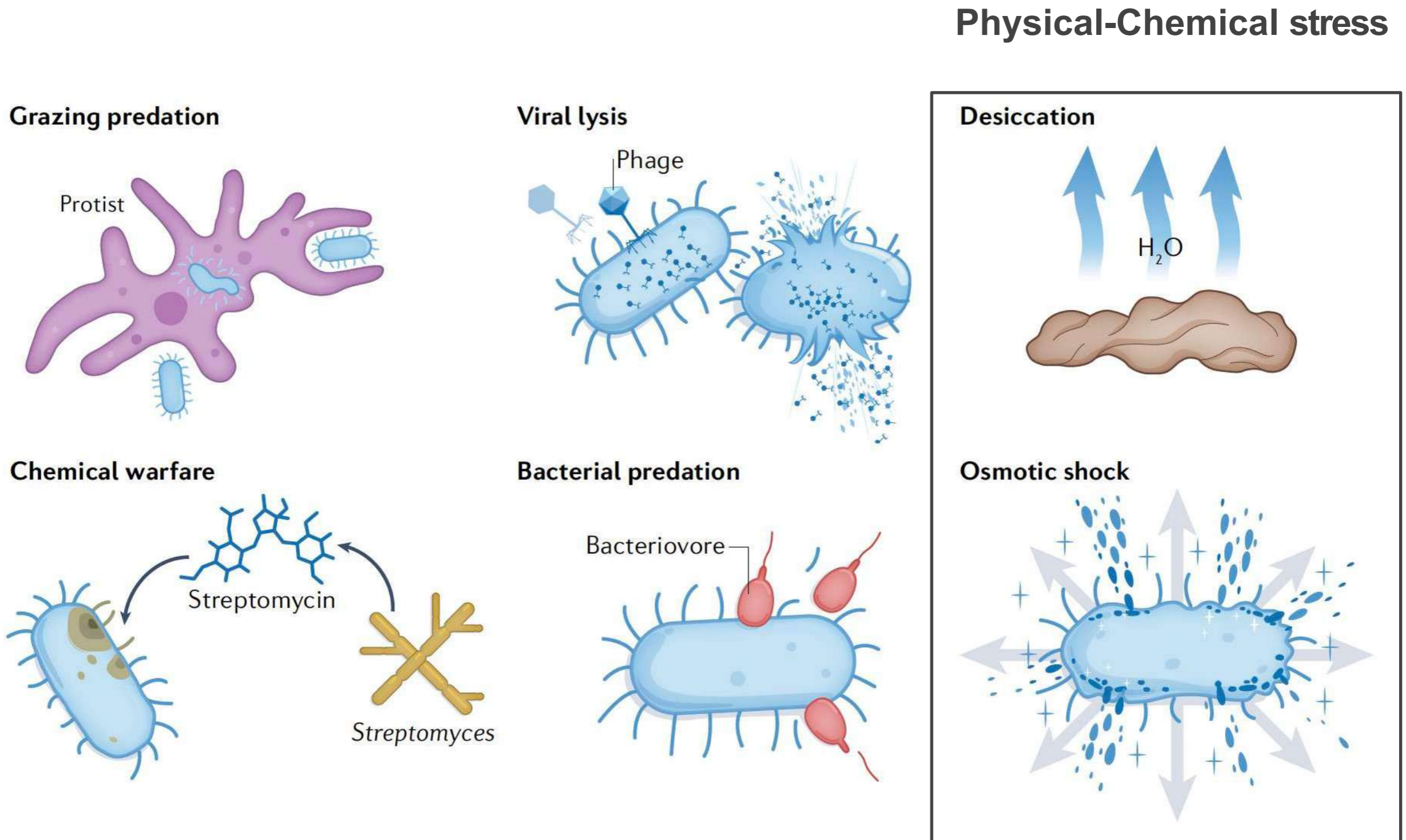
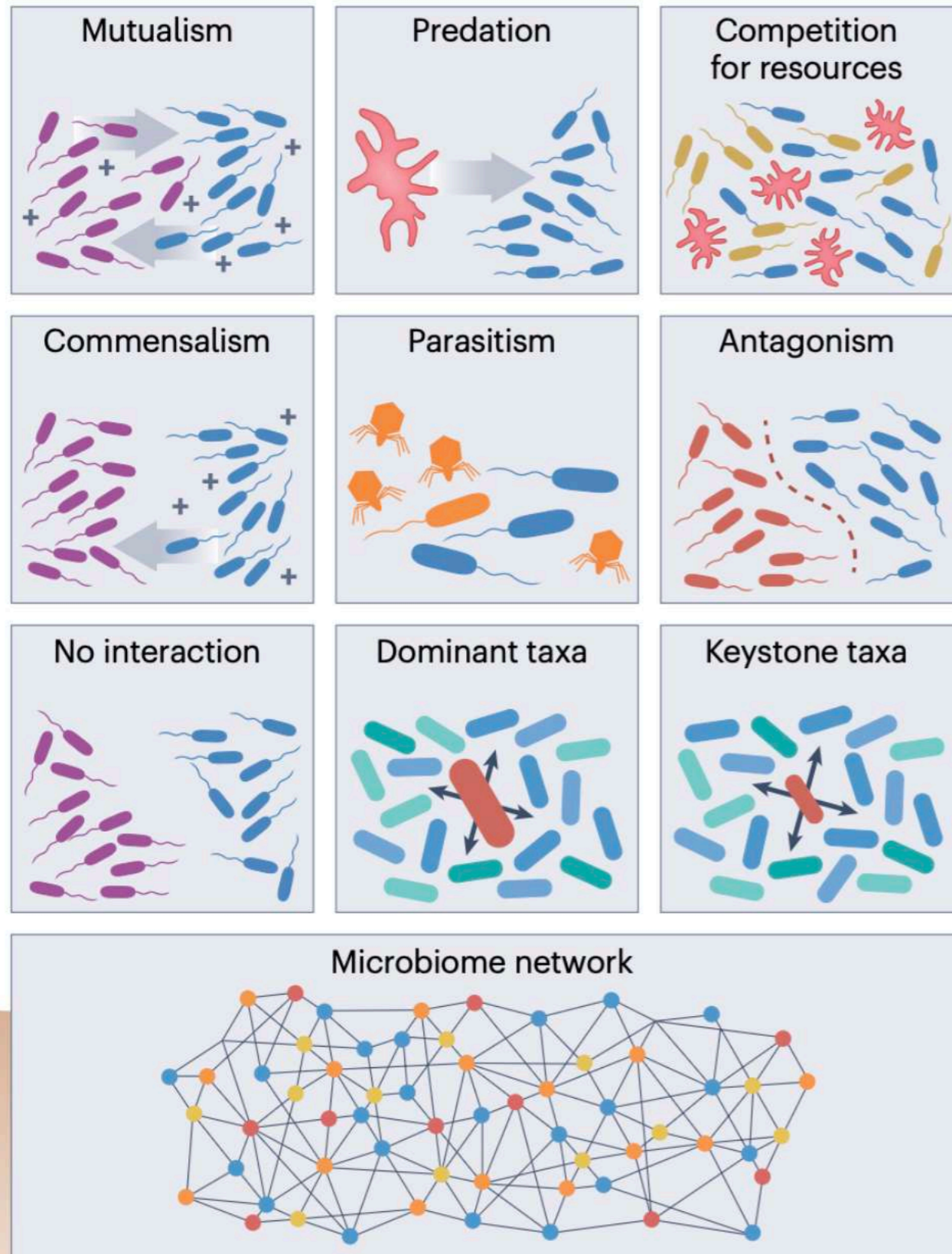


Fig. 4 | **Mechanisms of microbial mortality and theorized effects on the fate of microbial necromass.** There are different ways for a microorganism to die in soil, including grazing, bacterial predation, viral lysis, osmotic shock, desiccation and chemical warfare. The mechanism of death may affect the fate of its necromass, with direct consequences for organic matter cycling.

Microbial interactions at the microscale



Microbial interactions in the microbiome network:

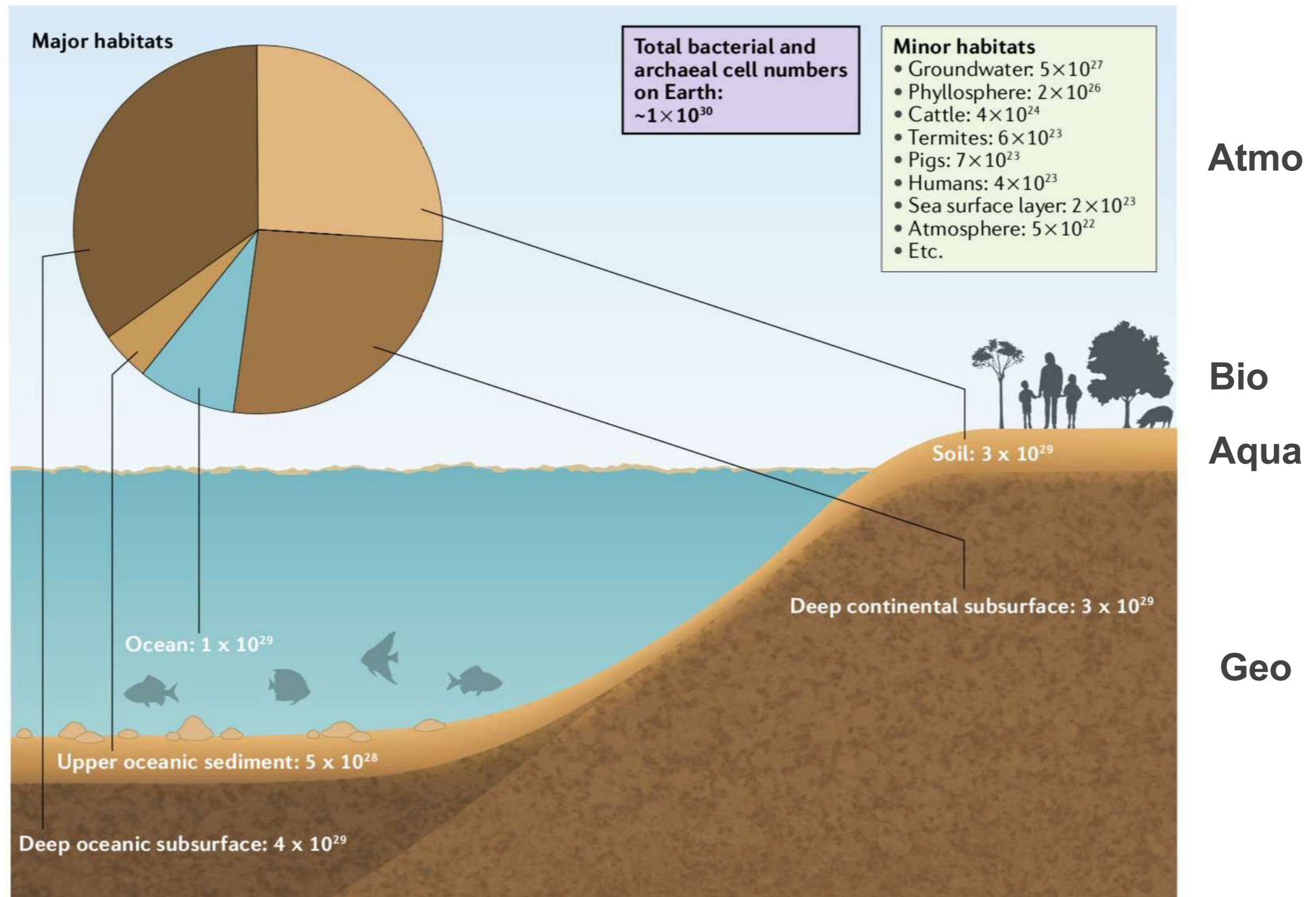
- **mutualism** (all species involved benefit from their interactions, $\langle symbiosis \rangle$),
 - **antagonism** (one organism benefits at the expense of another),
 - **predation** (one organism, the predator, kills and eats another organism),
 - **commensalism** (one species obtains food or other benefits from the other without either harming or benefiting the latter),
 - **parasitism** (one organism lives on or in the other organism and benefits from it by causing some harm)
 - **competition** for resources
-
- **Dominant taxa** are taxa more abundant than others → important role for microbiome functioning
 - **Keystone taxa** are highly connected taxa → key importance for ecosystem functioning

Microbial roles in ecosystem functioning

Functional Redundancy and Resilience

- **Functional redundancy** means **multiple species can perform the same ecological function**. This ensures stability if some species are lost
- **Resilience** is the ability of a microbial community to **resist or recover** from disturbances while maintaining its functions
- **Functional community profiling** – describing communities in terms of metabolic functions of interest suggest that certain **metabolic functions are strongly coupled to certain environmental factors** and can, in many cases, appear decoupled from the species assemblages associated with the mat a given place and time
- **Systems with high redundancy tend to be more resilient and adaptable to stressors like pollution or climate change**
- **Example:** In soil, many bacteria can fix nitrogen, so if one group is inhibited by drought, others may step in

Microbes are a pervasive force for Earth functioning



Flemming & Wuertz, 2019

Ecosystem & Ecosystem services

Ecosystems consist of organisms, their environments, and all of the **interactions among the organisms and environments**

The organisms are members of populations and communities and are adapted to habitats – > species richness and abundance

Ecosystem services:
outputs, conditions, or processes of natural systems that directly or indirectly benefit humans or enhance social welfare

<https://www.millenniumassessment.org/en/index.html>



source: *Final Recommendations of the Interagency Ocean Policy Taskforce, 2010*

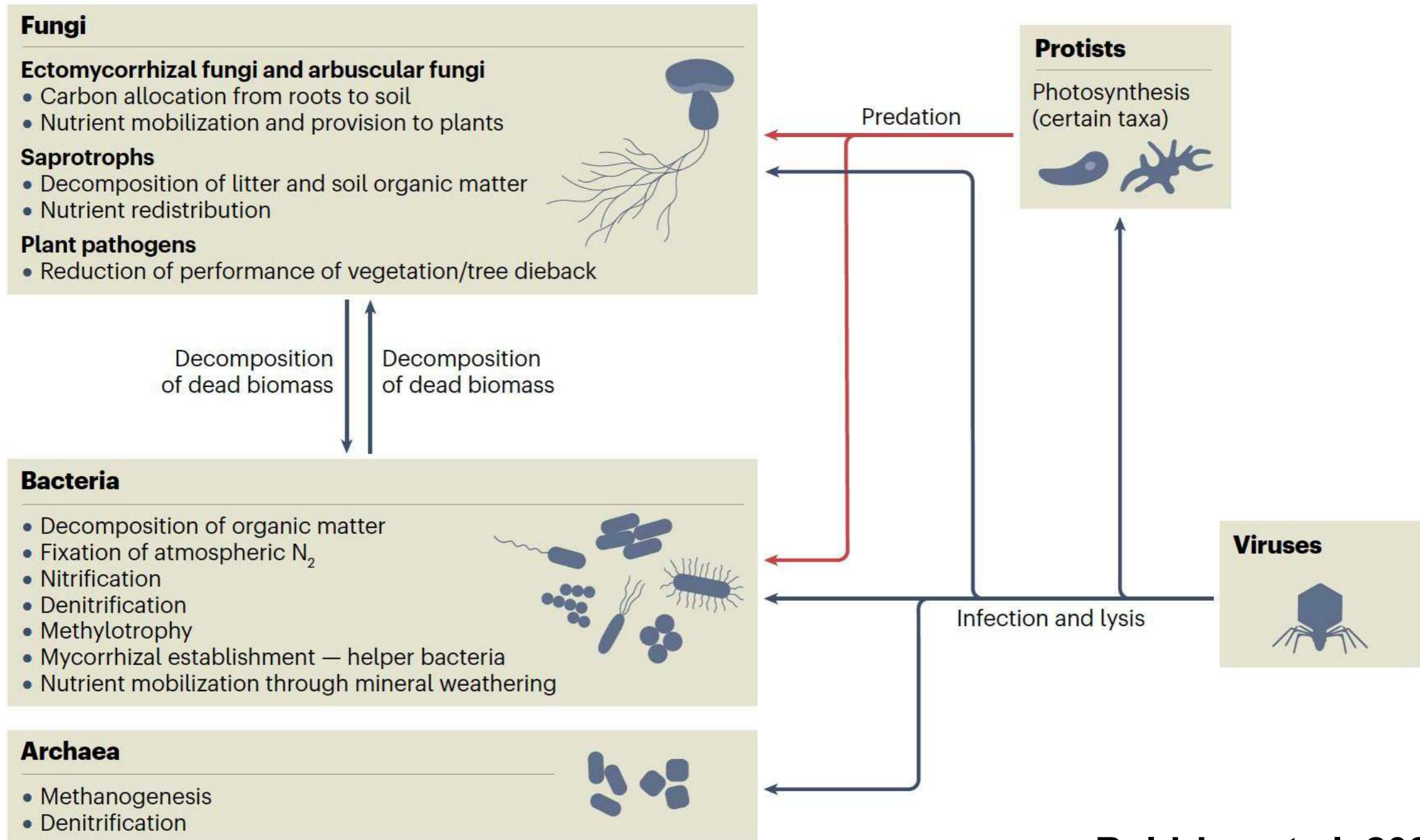
Microbes drive ecosystem services

Table 1 | Major groups of microbes and ecosystem services they provide.

Microbial group	Process	Ecosystem service	Ecosystem service category
Heterotrophic bacteria/ archaea	Organic matter breakdown, mineralization	Decomposition, nutrient recycling, climate regulation, water purification	Supporting and regulating
Photoautotrophic bacteria	Photosynthesis	Primary production, carbon sequestration	Supporting and regulating
Chemo(litho)autotrophic	Specific elemental transformations (e.g., NH_4^+ , S_2^- , Fe_2^+ , CH_4 oxidation)	Nutrient recycling, climate regulation, water purification	Supporting and regulating
Unicellular phytoplankton	Photosynthesis	Primary production, carbon sequestration	Supporting and regulating
Archaea	Specific elemental transformation (e.g., metals, CH_4 formation, NH_4^+ oxidation), often in extreme habitats.	Nutrient recycling, climate regulation, carbon sequestration	Supporting and regulating
Protozoa	Mineralization of other microbes	Decomposition, nutrient recycling, soil formation	Supporting
Fungi	Organic matter breakdown and mineralization	Decomposition, nutrient recycling, soil formation, primary production (i.e., mycorrhizal fungi)	Supporting
Viruses	Lysis of hosts	Nutrient recycling	Supporting
All	Production of metabolites (e.g., antibiotics, polymers), degradation of xenobiotics, genetic transformation, and rearrangement	Production of precursors to industrial and pharmaceutical products	Provisional
All	Huge diversity, versatility, environmental and biotechnological applications	Educational purposes, getting students interested in science	Cultural

*The last column depicts the ecosystem service category as was defined in the Millennium Ecosystem Assessment (2005).
Modified from Ducklow, 2008.*

Roles of the forest/soil/microbiome



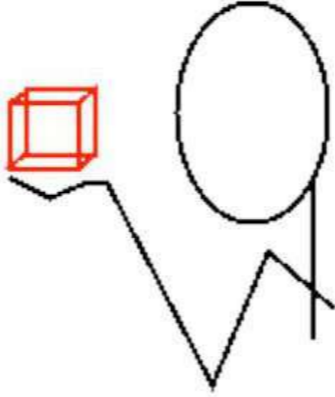
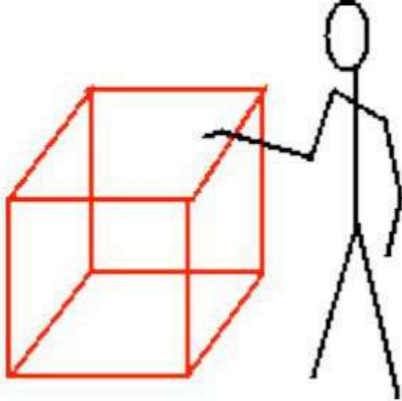
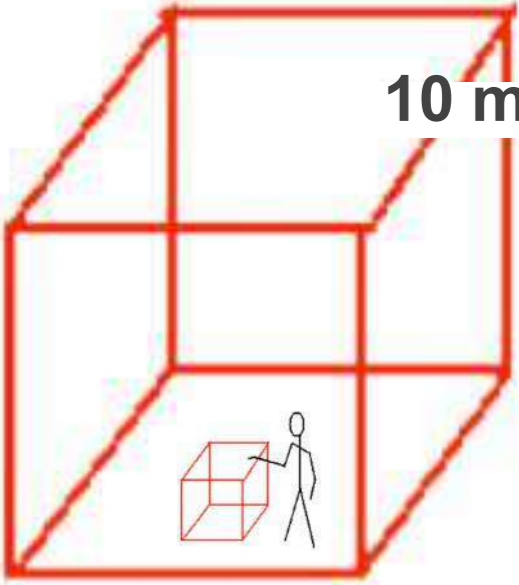








Baldrian et al. 2023

Microbial Contributions to Ecosystem Services

- Microbes play critical roles in **ecosystem services**, which are benefits that ecosystems provide to humans and nature:
 - **Nutrient cycling** (N, C, P, S)
 - **Decomposition and organic matter turnover**
 - **Water purification** through microbial breakdown of contaminants
 - **Climate regulation** via greenhouse gas flux (methane, CO₂, N₂O)
 - **Soil fertility** and plant health (e.g., rhizobia, mycorrhizae)
- **Understanding microbial contributions is vital for managing agriculture, conservation, and restoration efforts**

Feeling the microscale

<p>1 mm</p> 	<p>1 cm</p> 	<p>10 cm</p> 	<p>1 m=100 cm</p> 	<p>10 m</p> 
<p>10^{-6} m (1 micron)</p>	<p>10^{-5} m (10 microns)</p>	<p>10^{-4} m (100 microns)</p>	<p>10^{-3} m (1 mm)</p>	<p>10^{-2} m (1 cm)</p>
<p>bacteria</p>  <p>900606 15KV X20.0K 1.50um ASM Biofilms Collection, Kobayashi</p>	<p>red blood cells</p>  <p>Copyright © 2007 Texas Instrument Microscopy, Inc. / Dennis Kunkel</p>	<p>your hair</p>  <p>parasitic mite</p> 	<p>a grain of salt</p> 	<p>a marble</p> 

Microbial life provides ecosystem services

Unique goal of microbial life: survival, maintenance, generation of ATP (energy storage), reducing power, growth of new cells

Decomposition, nutrient recycling, climate regulation, water purification

Primary production, carbon sequestration

Nutrient recycling, climate regulation, water purification

..... in an ecosystem context