Microbes in the environment

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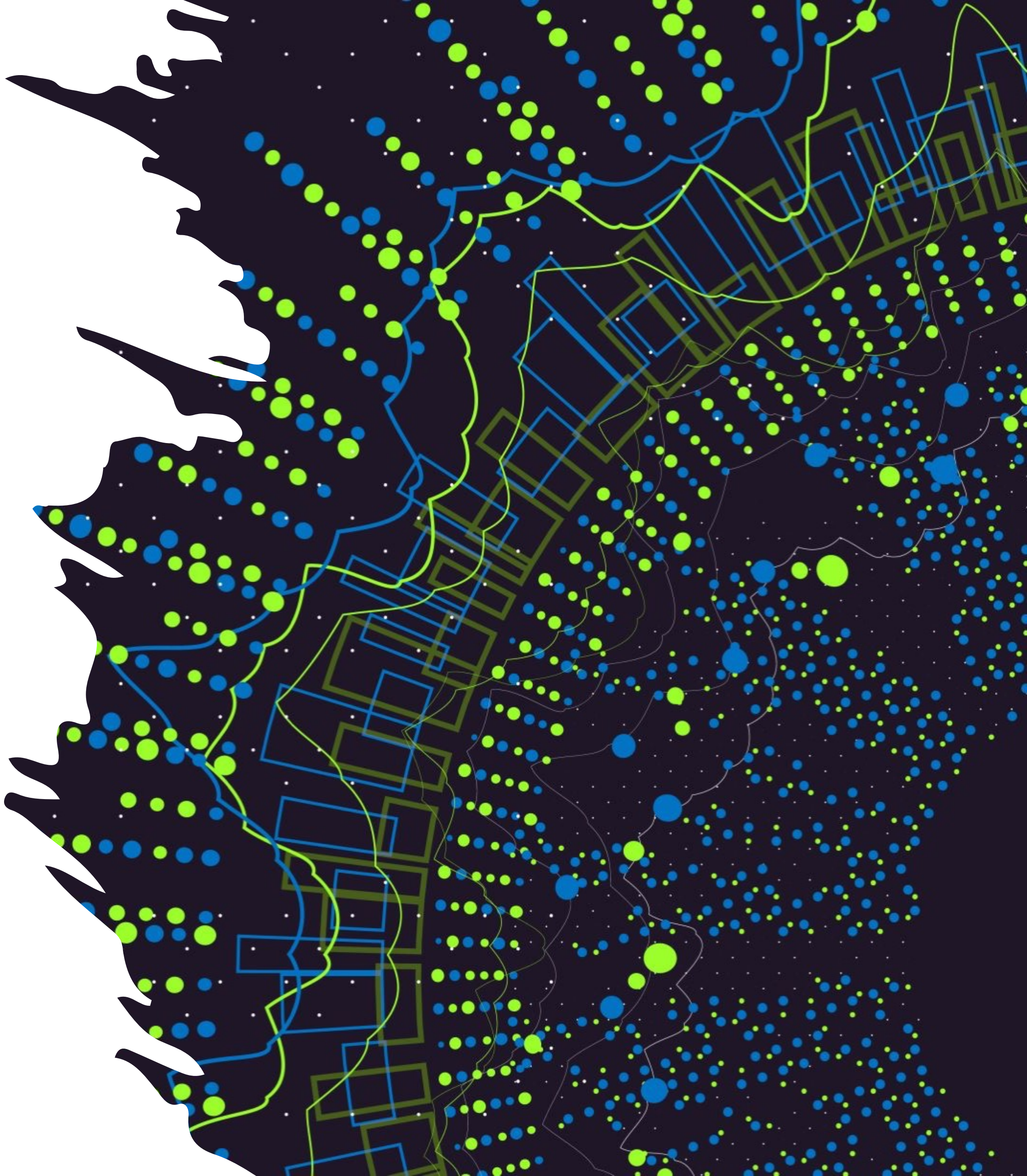
Associate Professor

MIT



Why do we care about microorganisms like bacteria?

Wherever there is a source of energy for life, microbes have evolved to take advantage of it.

The extremely diverse metabolism of microbes and their abundance in oceans, soils, animal guts, etc., have transformed the planet

Why do we care about microorganisms like bacteria?

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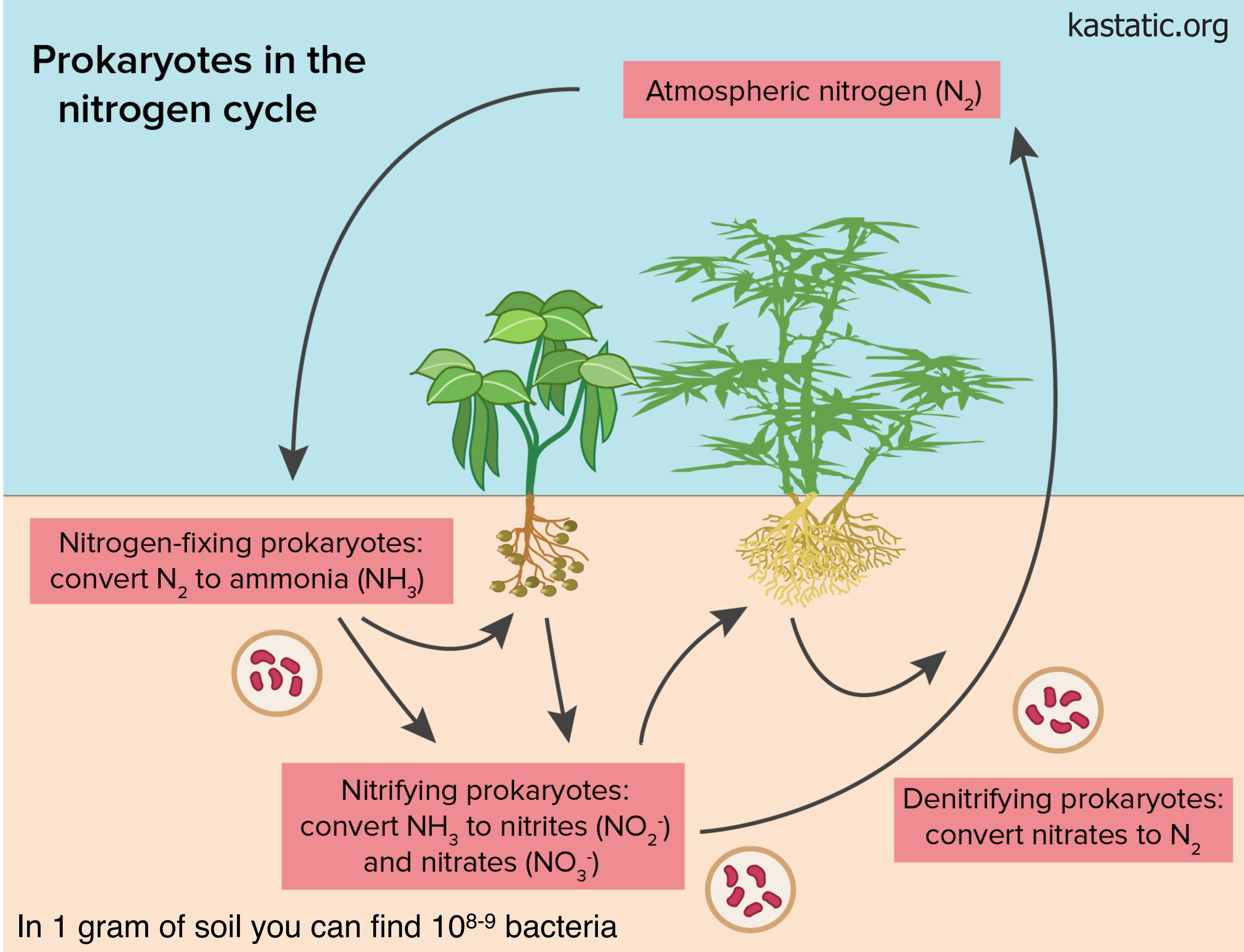
Table 1: Comparison of atmospheric compositions of Venus, Mars, Earth

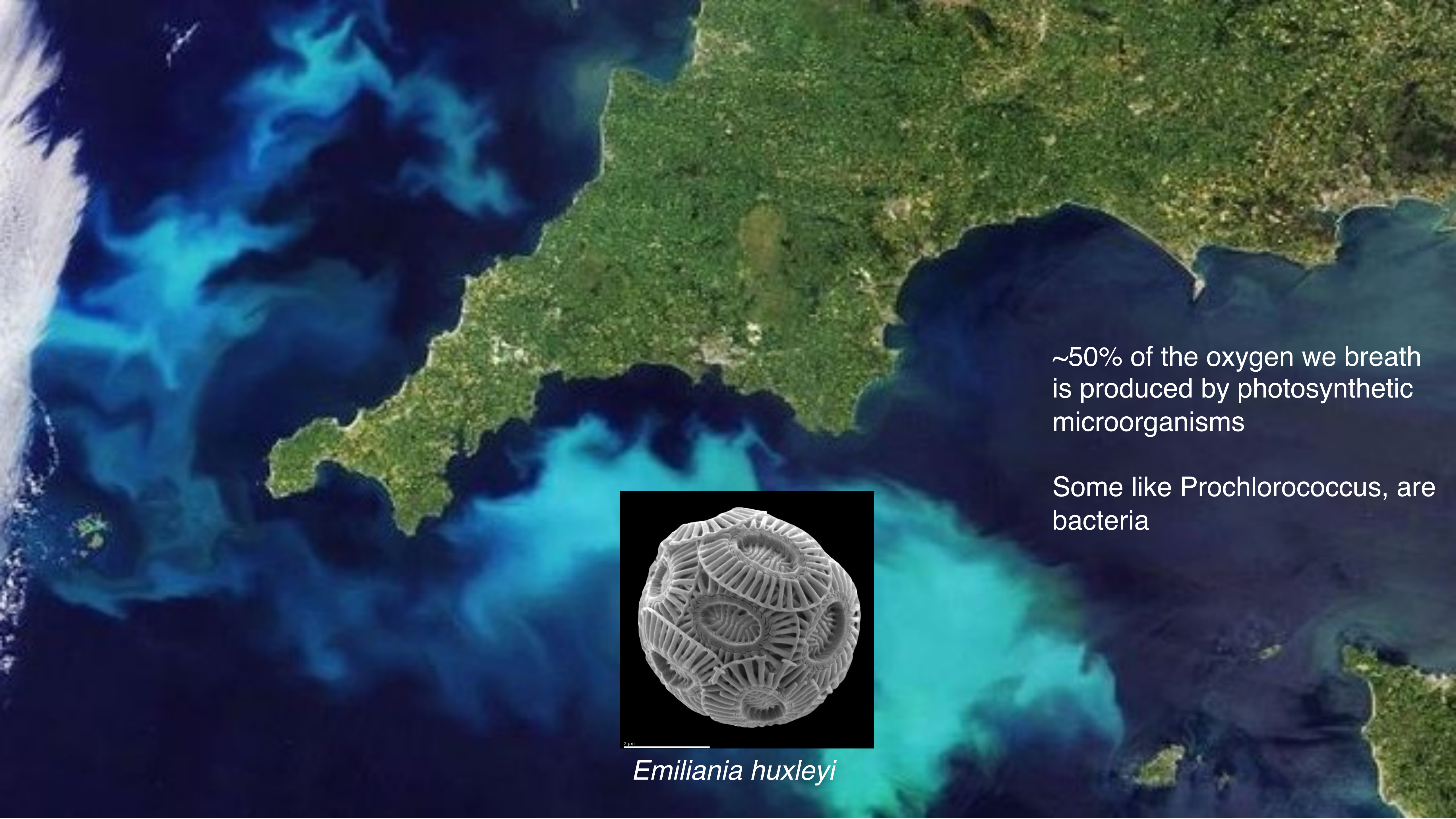
	pressure (bars)*	CO_2 (%)	N_2(%)	Argon-36 (%)	H_20 (%)	0_2(%)
Venus	92	96.5	3.5	0.00007	<0.00003	trace
Earth	1.013	0.033	78	0.01	<3	20
Mars	0.006	95.3	2.7	0.016	<0.0001	trace

* A bar is a measure of pressure. One bar equals 1.013 atmospheres, or the atmospheric pressure at sea level.

Only microorganisms like bacteria can fix nitrogen

Bacteria and archaea also mediate the conversion from organic N (ammonia) back to inorganic N (N2)

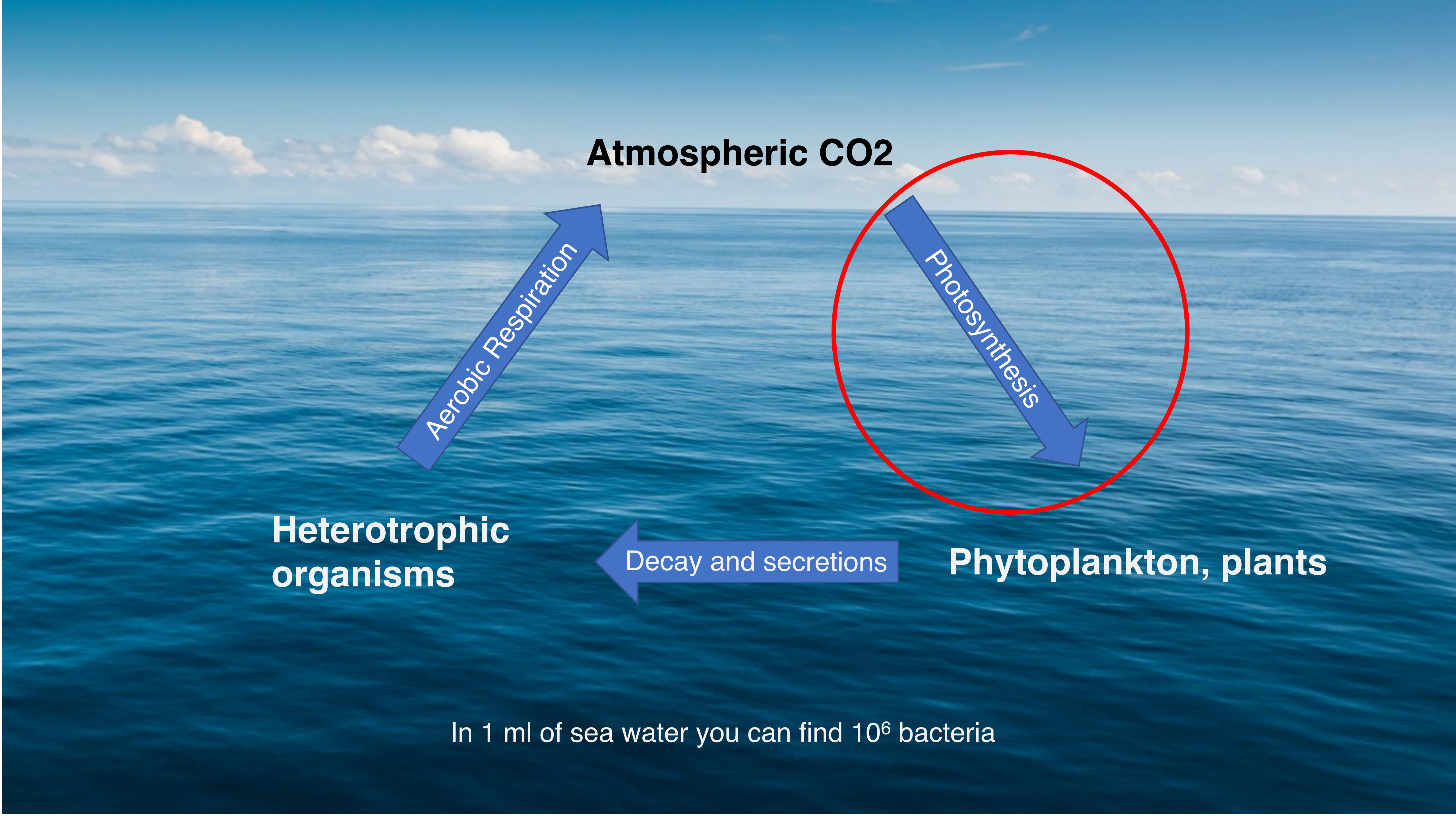




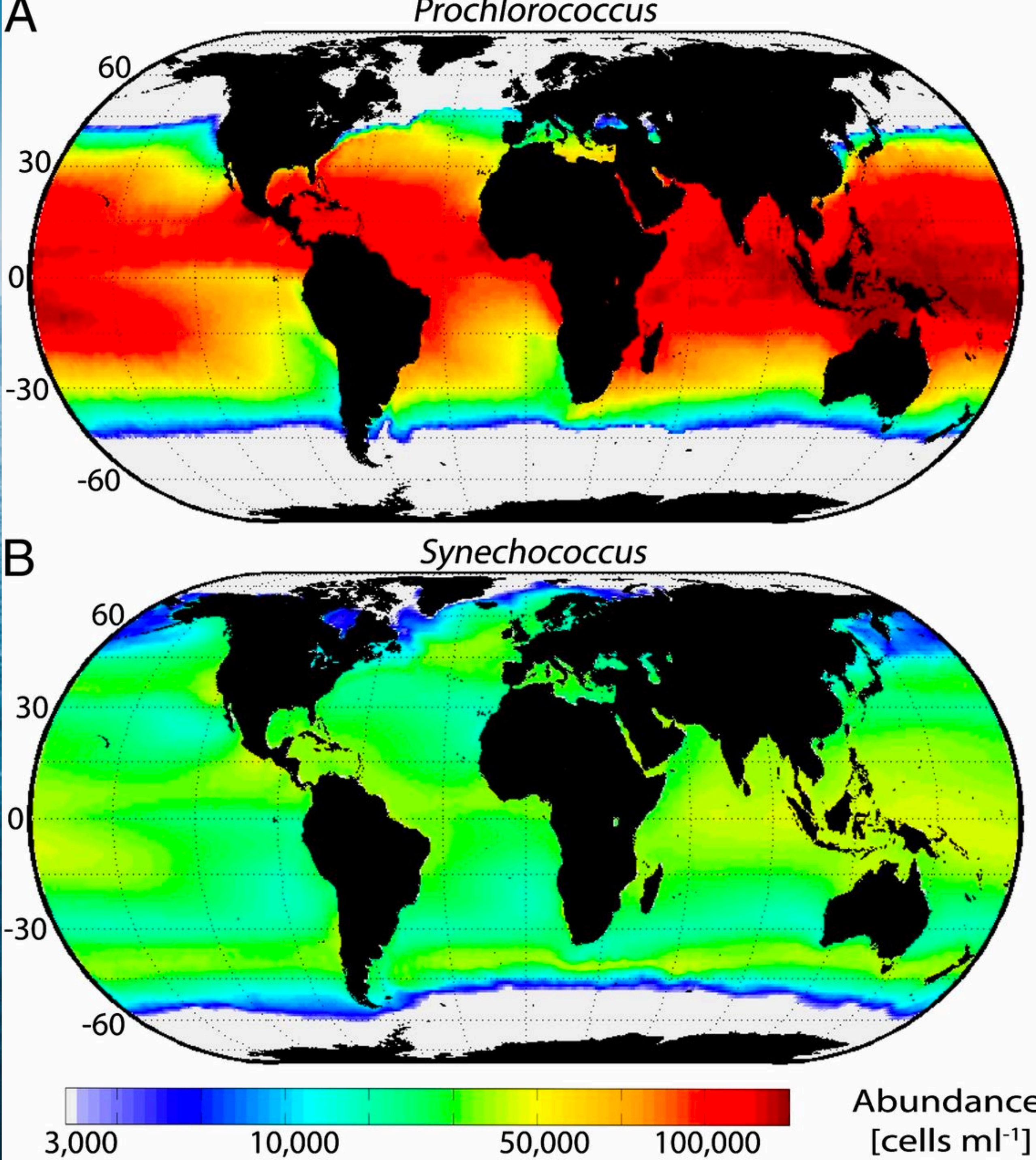
~50% of the oxygen we breath is produced by photosynthetic microorganisms

Some like Prochlorococcus, are bacteria

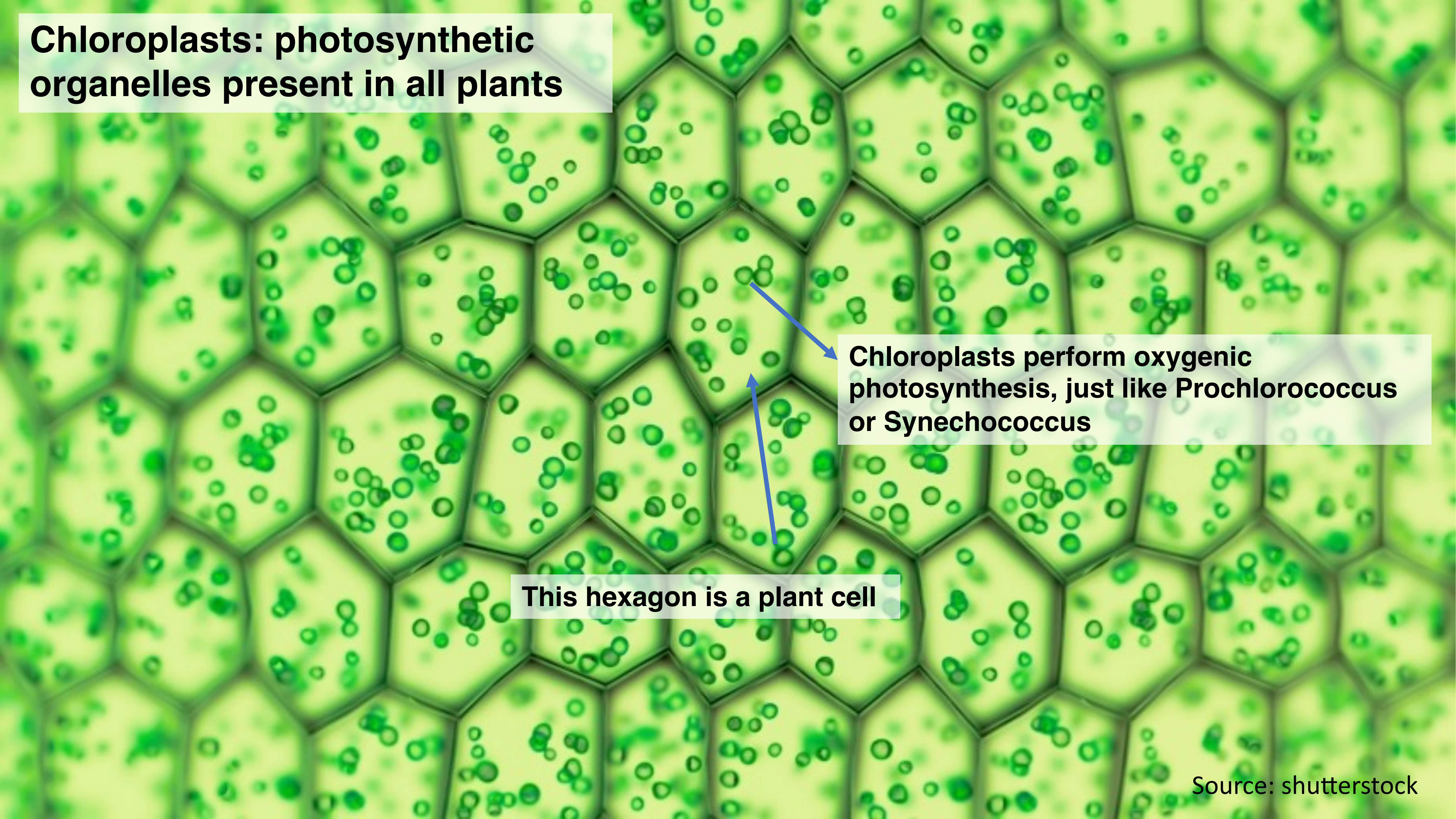
Emiliania huxleyi


Atmospheric CO2
Aerobic Respiration
Photosynthesis
Heterotrophic organisms
Decay and secretions
Phytoplankton, plants
In 1 ml of sea water you can find 10^6 bacteria

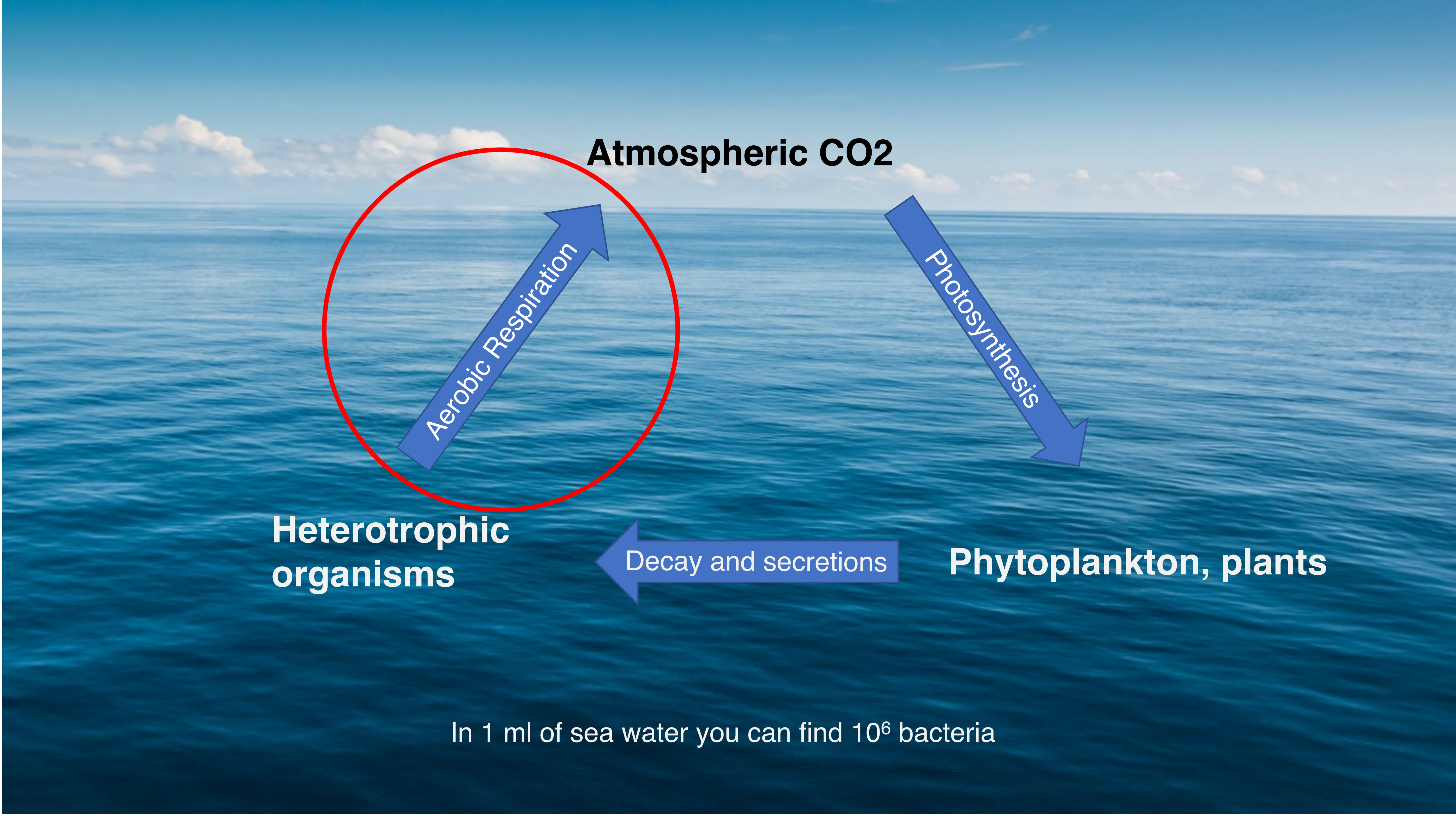
Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*
Flombaum et al. 2013



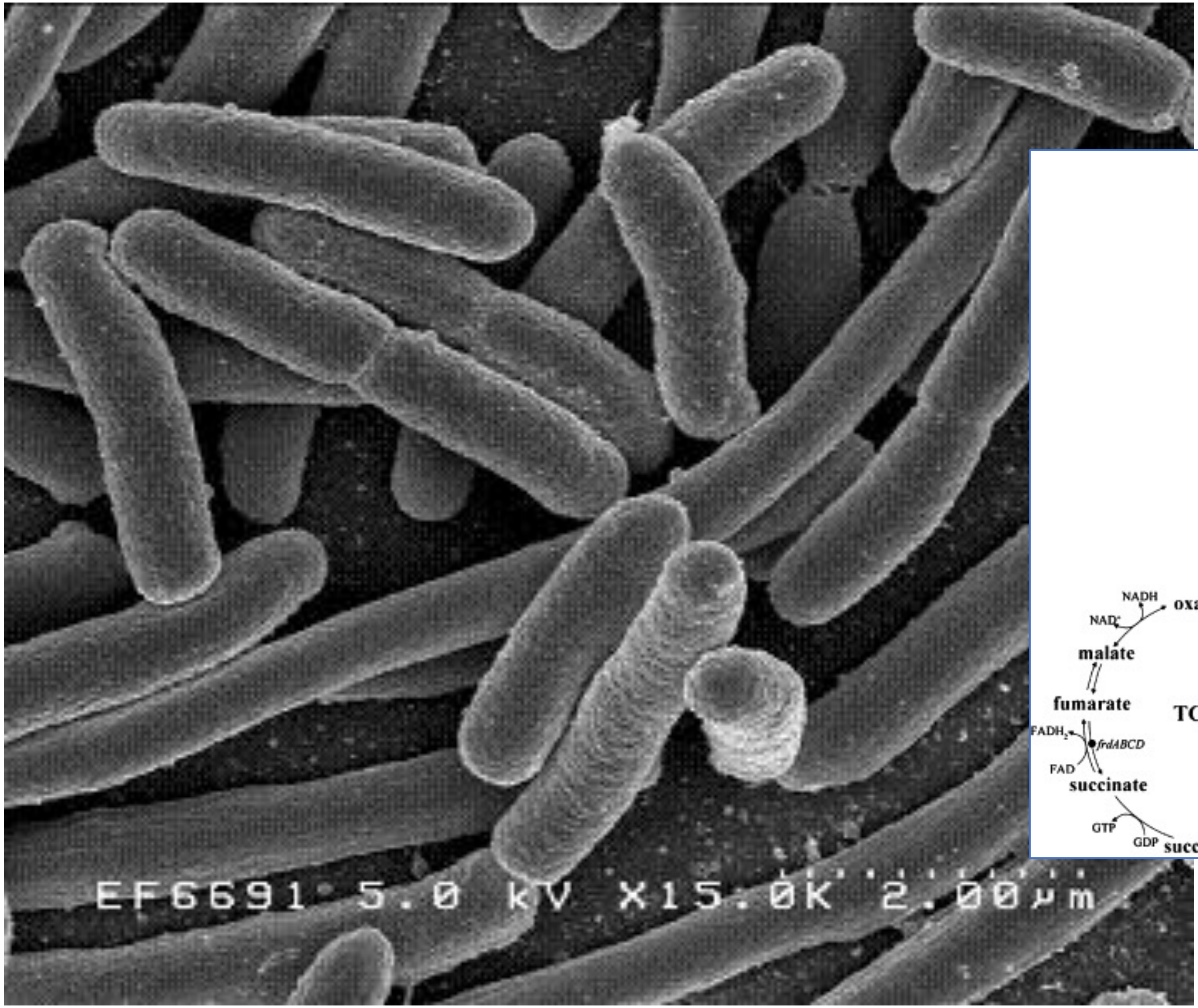
Chloroplasts: photosynthetic organelles present in all plants

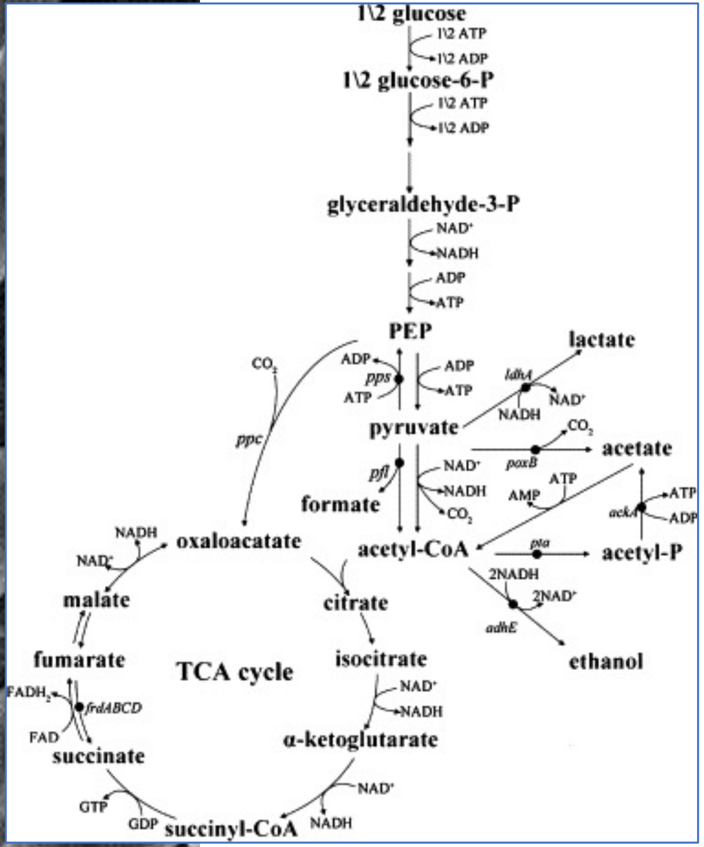


Source: shutterstock

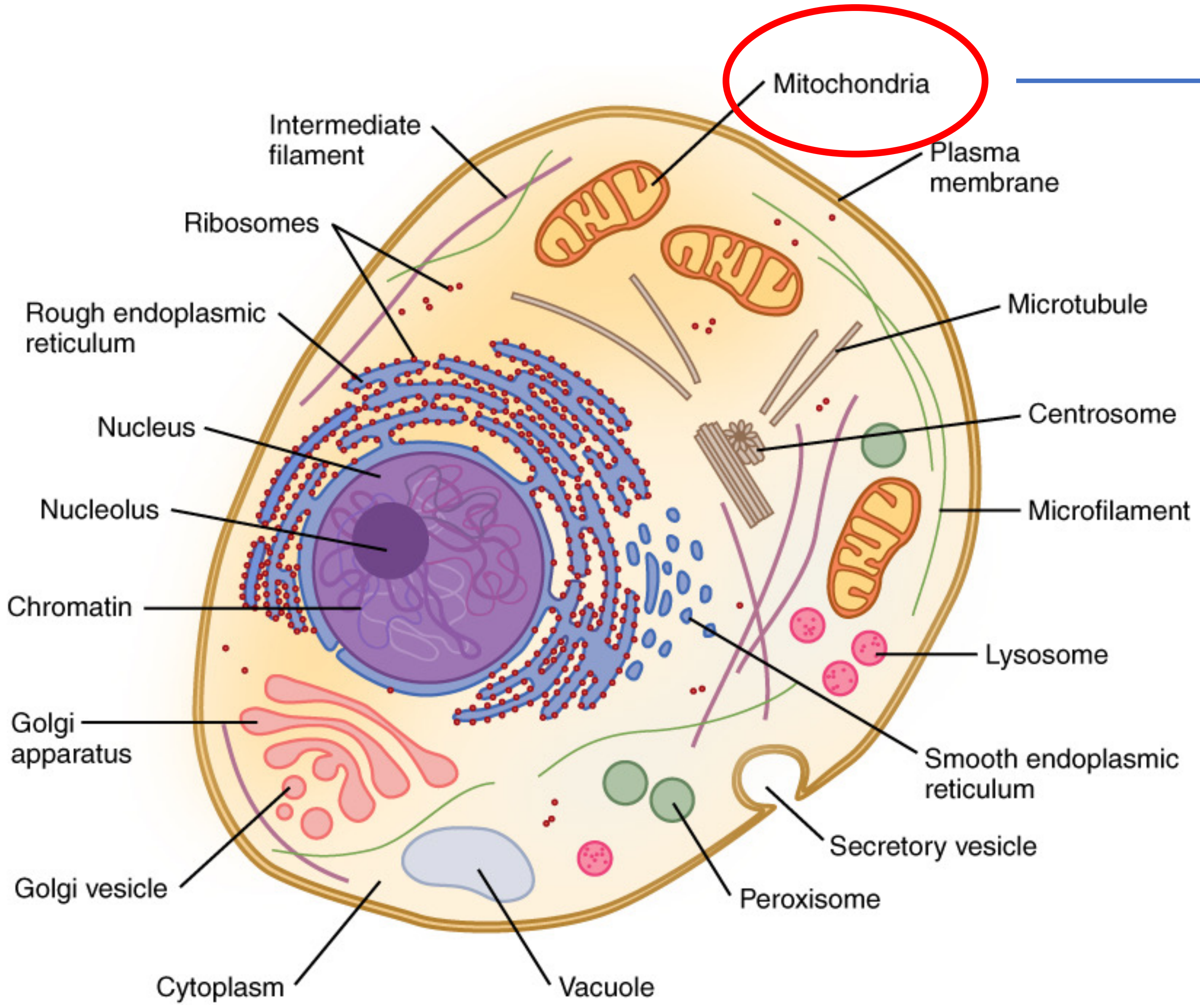

Atmospheric CO2
Aerobic Respiration
Photosynthesis
Heterotrophic organisms
Decay and secretions
Phytoplankton, plants
In 1 ml of sea water you can find 10⁶ bacteria

Your usual E. coli cell is a heterotroph and can respire C quite well





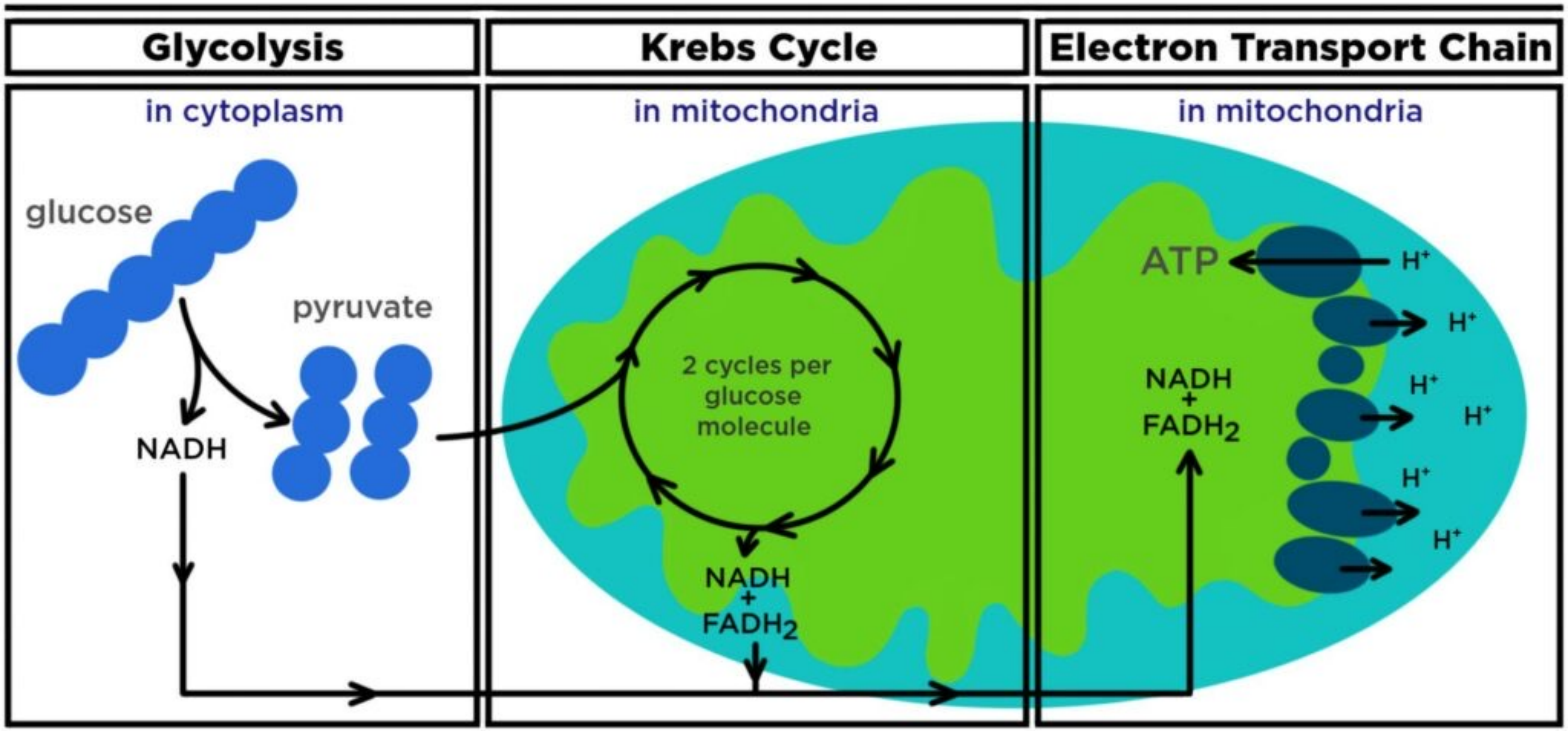
What about Eukaryotes, e.g. animals and plants?



Mitochondrion is the "powerhouse" of the cell. It performs cellular respiration producing energy (ATP) for the cell

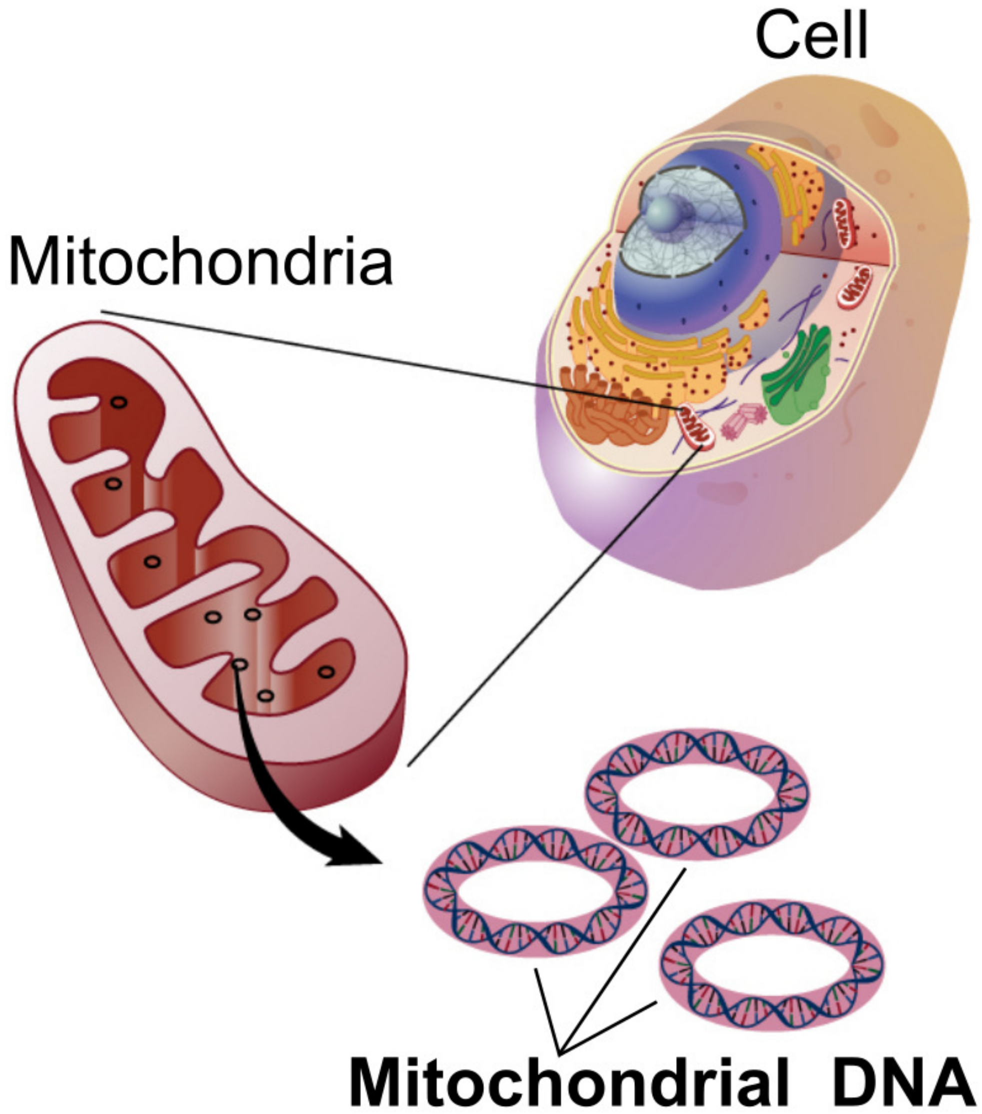
Mitochondria perform cellular respiration, just like an E. coli cell …

Cellular respiration



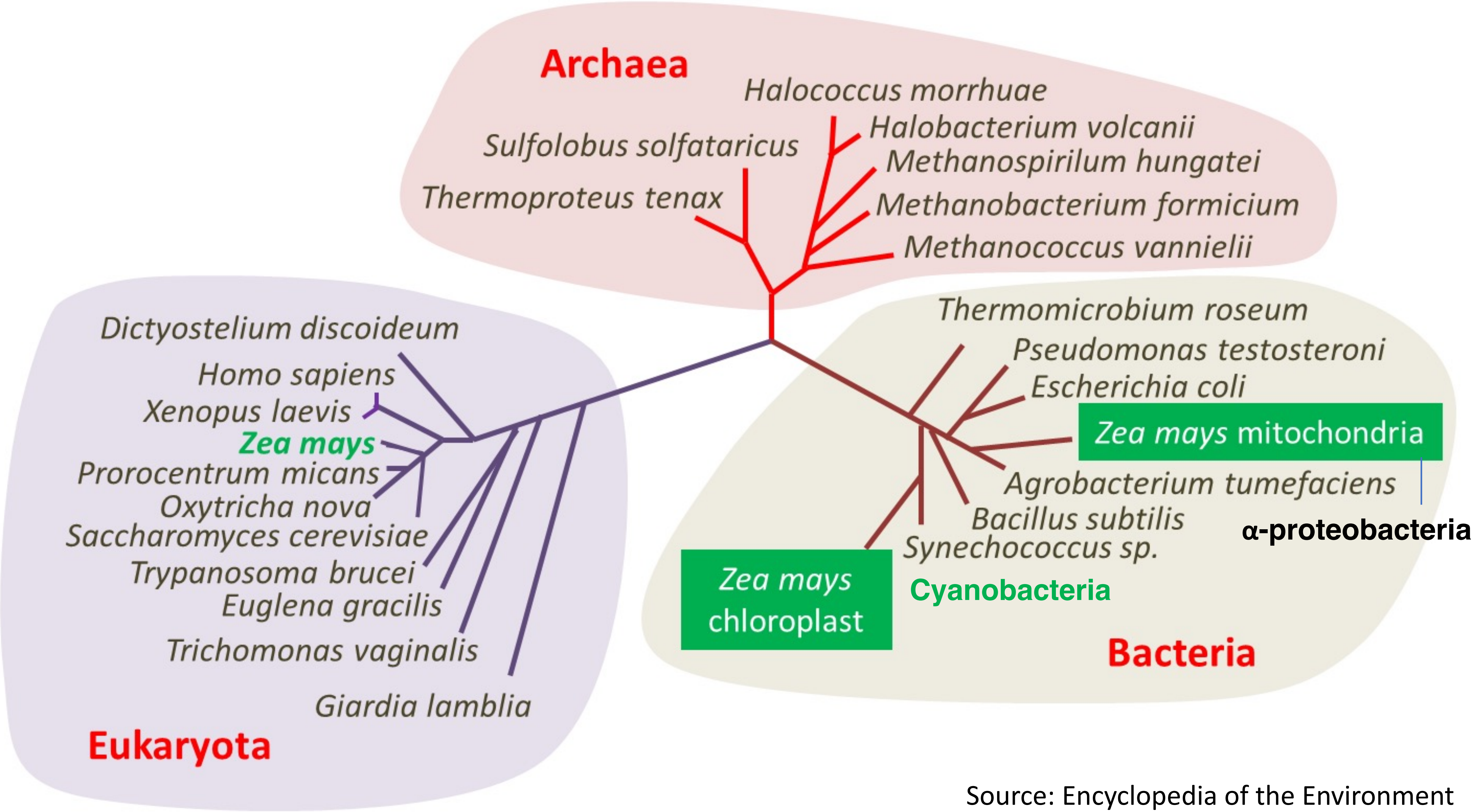
We have a specialized organelle to do what a simple bacterium like E. coli can do,
respire with O2 pyruvate to produce CO2

Source: Zmescience

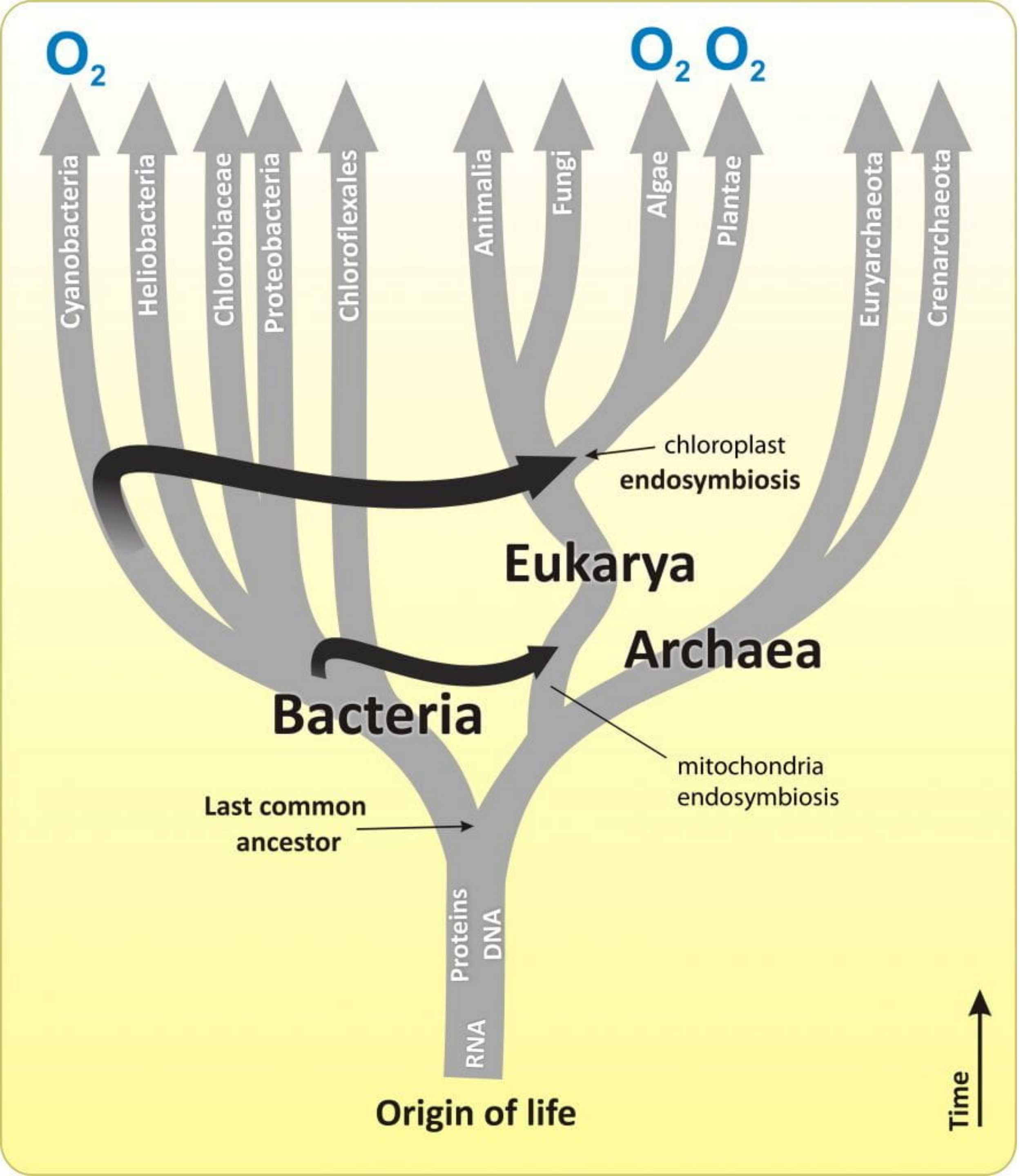


Mitochondria and chloroplasts are organelles that carry their own genomes!

Source: Wikipedia



Source: Encyclopedia of the Environment



The evolution of life on earth is intricately linked to microbes and their enormous metabolic diversity

Key metabolic reactions are performed by organelles which are descendants of bacteria

From an ecological and evolutionary points of view, life in this planet is microbial

Paulinella (ameoba)

Paulinella … have recently (in evolutionary terms) taken on a cyanobacterium as an endosymbiont.[8] … The event to permanent endosymbiosis probably occurred with a cyanobiont.

Georgia Tech Biological Sciences

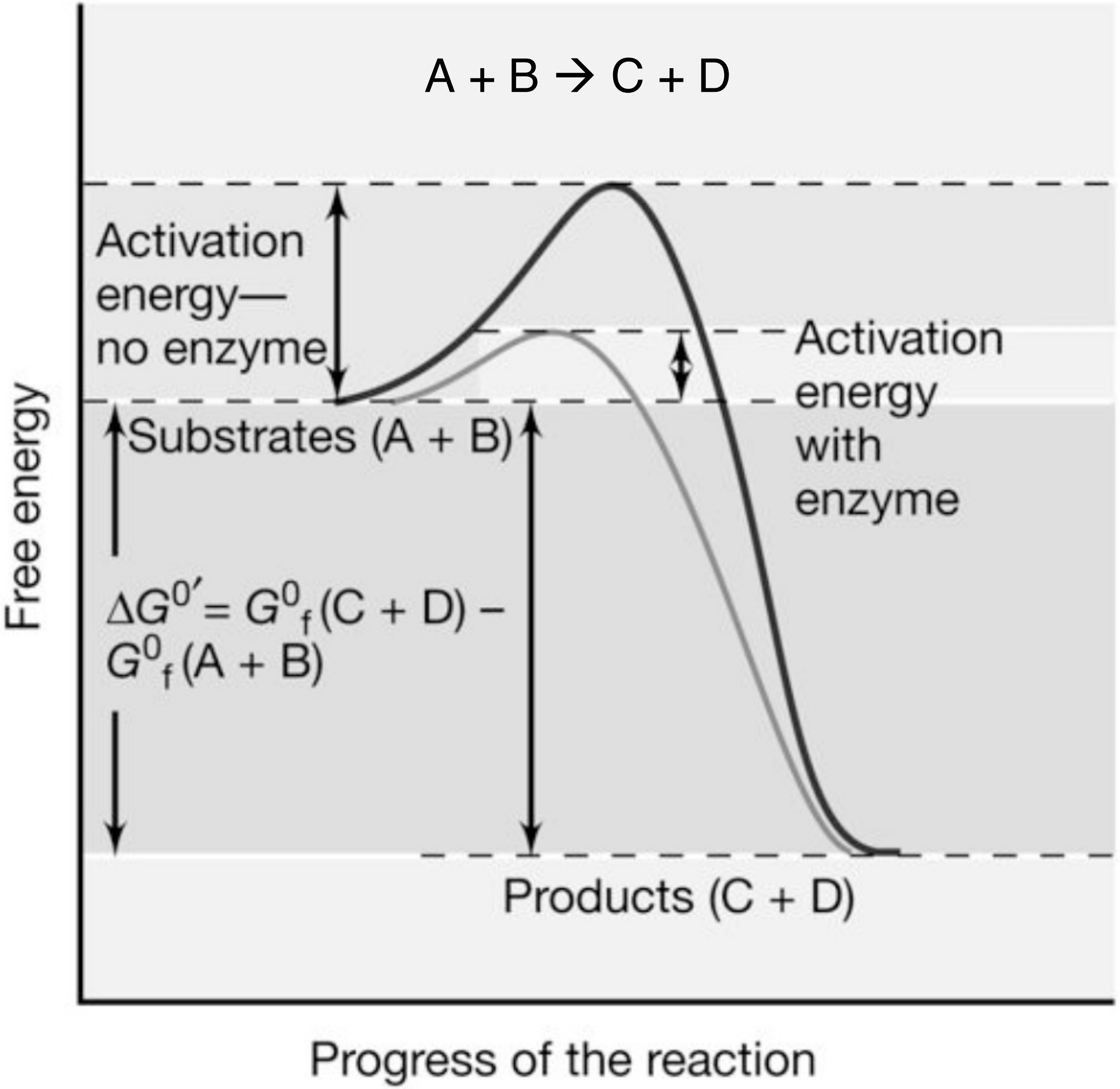
Organizing principles of microbial life

What determines the distribution, abundance and activity of microbes in the environment?

1. Bioenergetics
2. Division of labor (metabolic trade-offs)
3. Eco-physiology

Bioenergetics

Life is fueled by reduction-oxidation reactions



$\Delta G^{0'}$= free energy in standard conditions. It tells you whether a reaction is likely to happen and whether it consumes or releases energy

$\Delta G^{0'} < 0$ means that the reaction is exergonic, i.e. it yields energy

The energy liberated by the reaction is conserved as ATP, or other high energy bonds

Redox potential is a measure of the **tendency** of the solution to either **gain or lose electrons** when it is subjected to change by introduction of a new species.

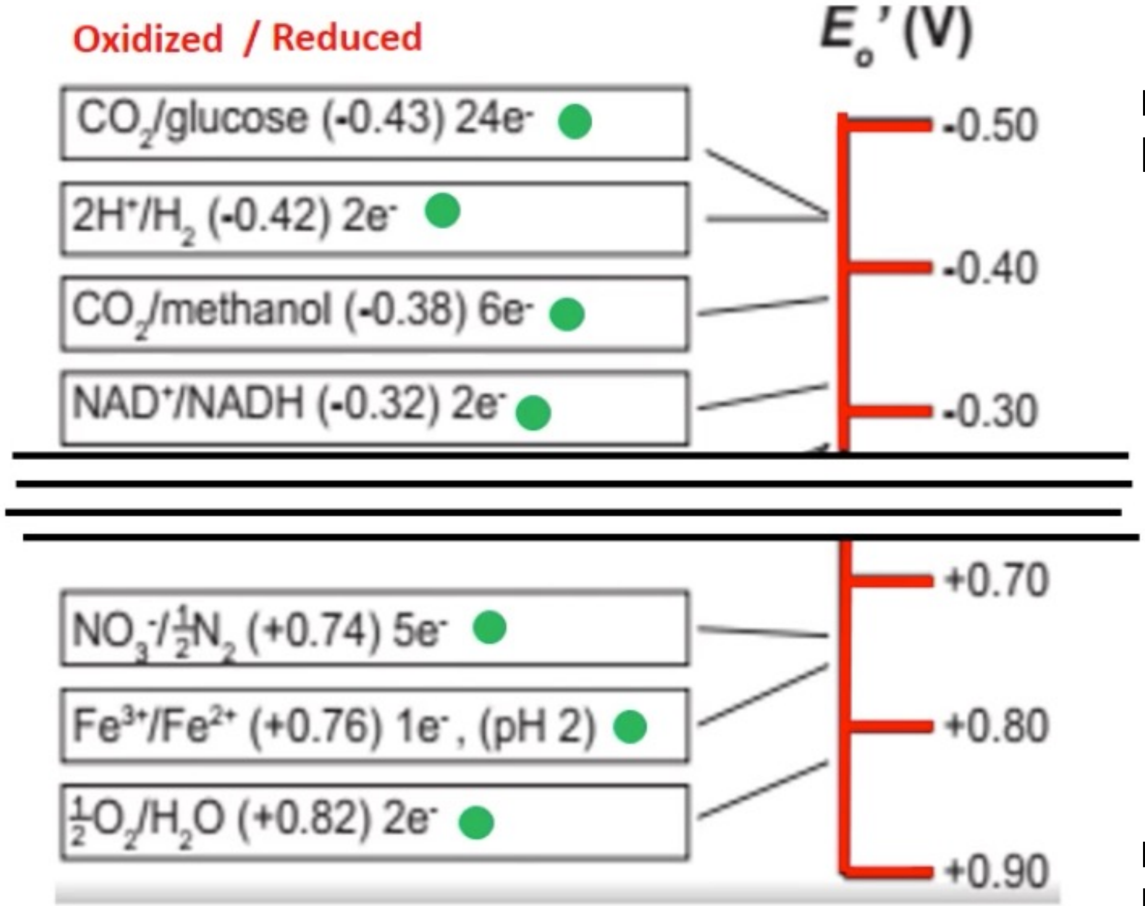
$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O$$

Glucose is being oxidized to CO_2, i.e. it donates electrons

Oxygen is being reduced to water, i.e. it accepts electrons

$\Delta G°' = -2870$ kJ/mol
Strongly exergonic

REDOX TOWER



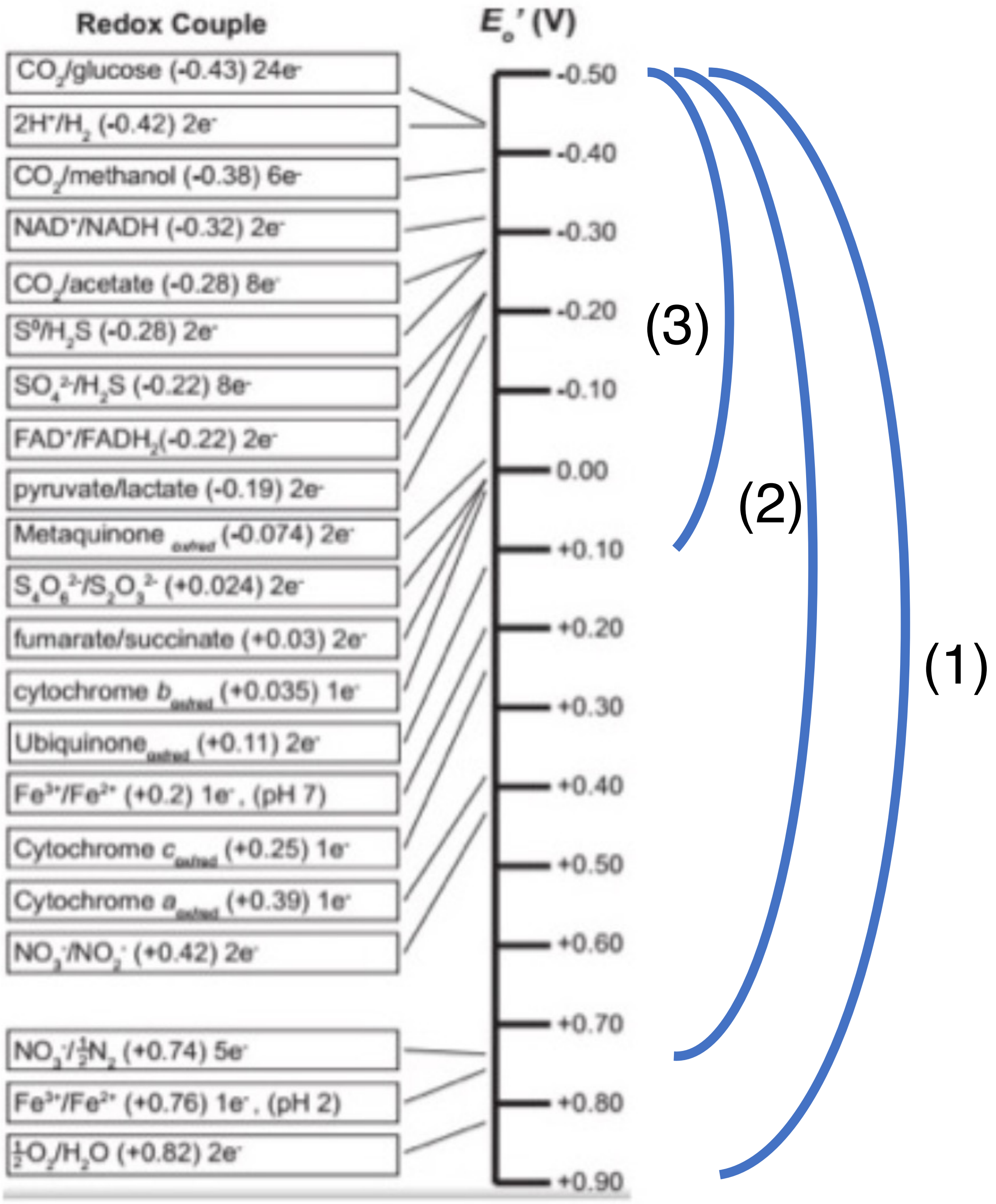
more negative reduction potential: will have a tendency to **lose electrons**

$\Delta E_0'$

more positive reduction potential: will have a tendency to **gain electrons**

$$\Delta G^{0'} = -nF\,\Delta E_0'$$

-2870 kJ/mol glucose
Aerobic respiration



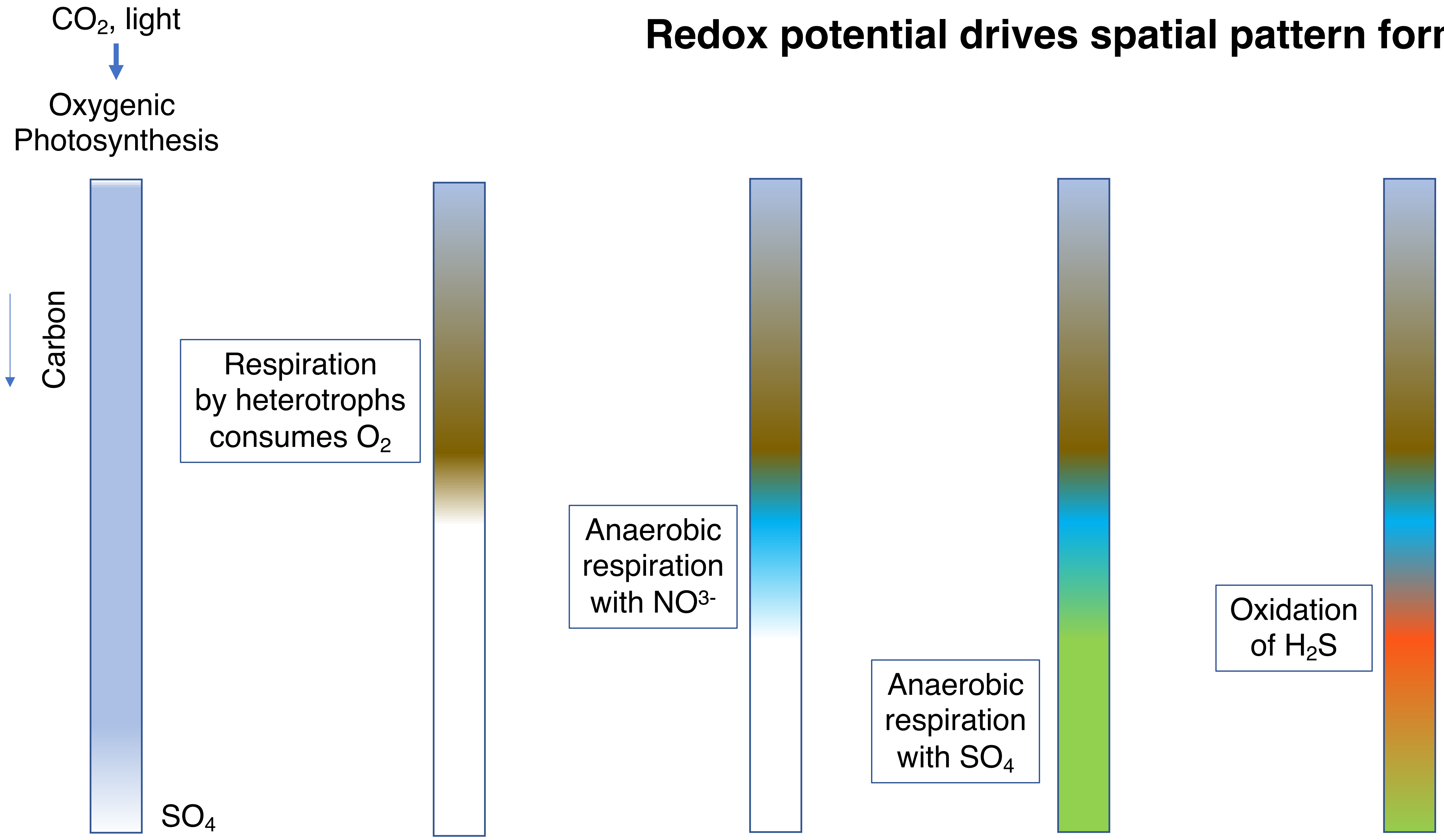
An organism that performs (1) has more energy for growth than one that performs (2) or (3)

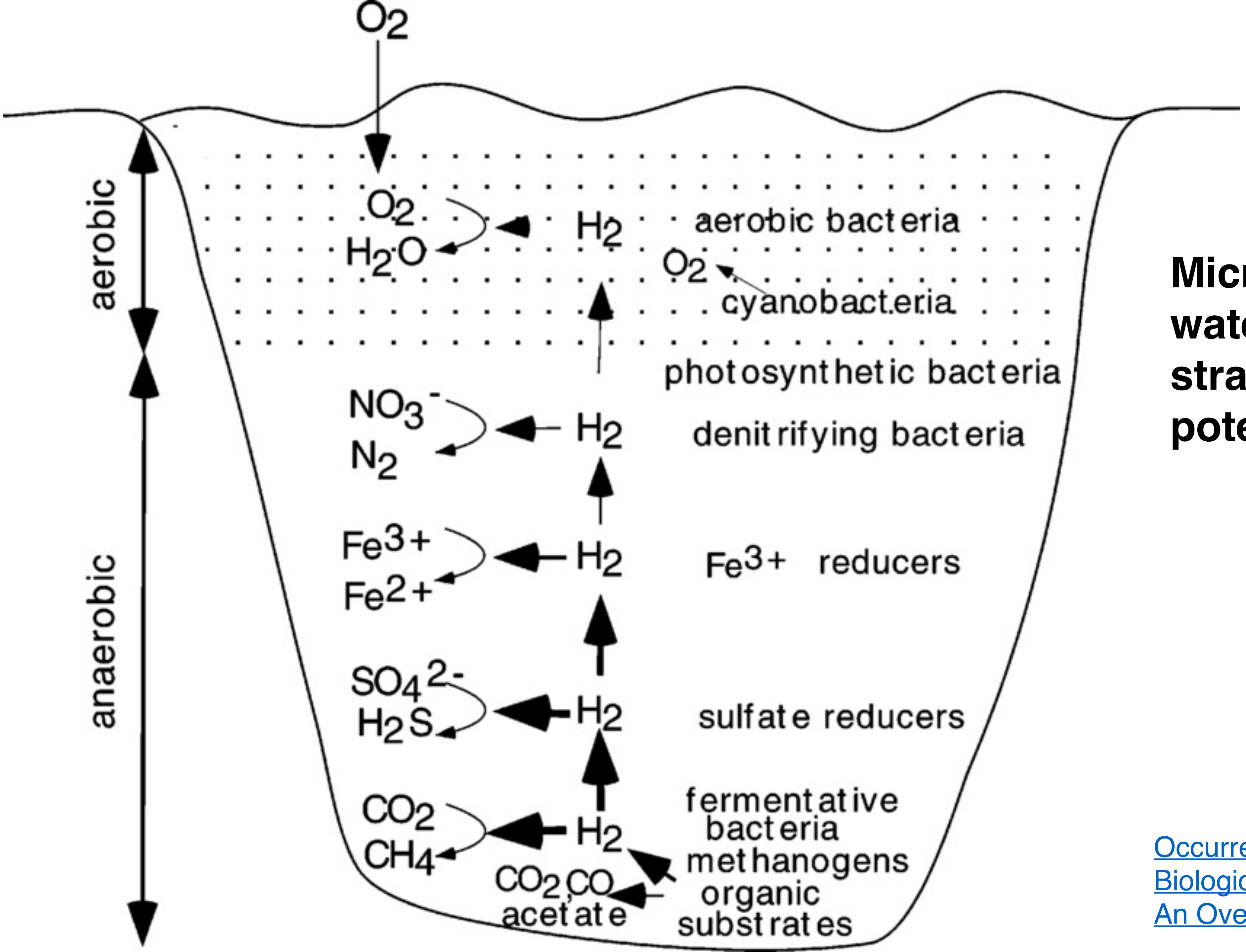
e.g. Aerobic respiration is more favorable than anaerobic respiration with nitrate or …

anaerobic respiration with nitrate is more favorable than with sulfate, etc.

Libretext.org

Redox potential drives spatial pattern formation



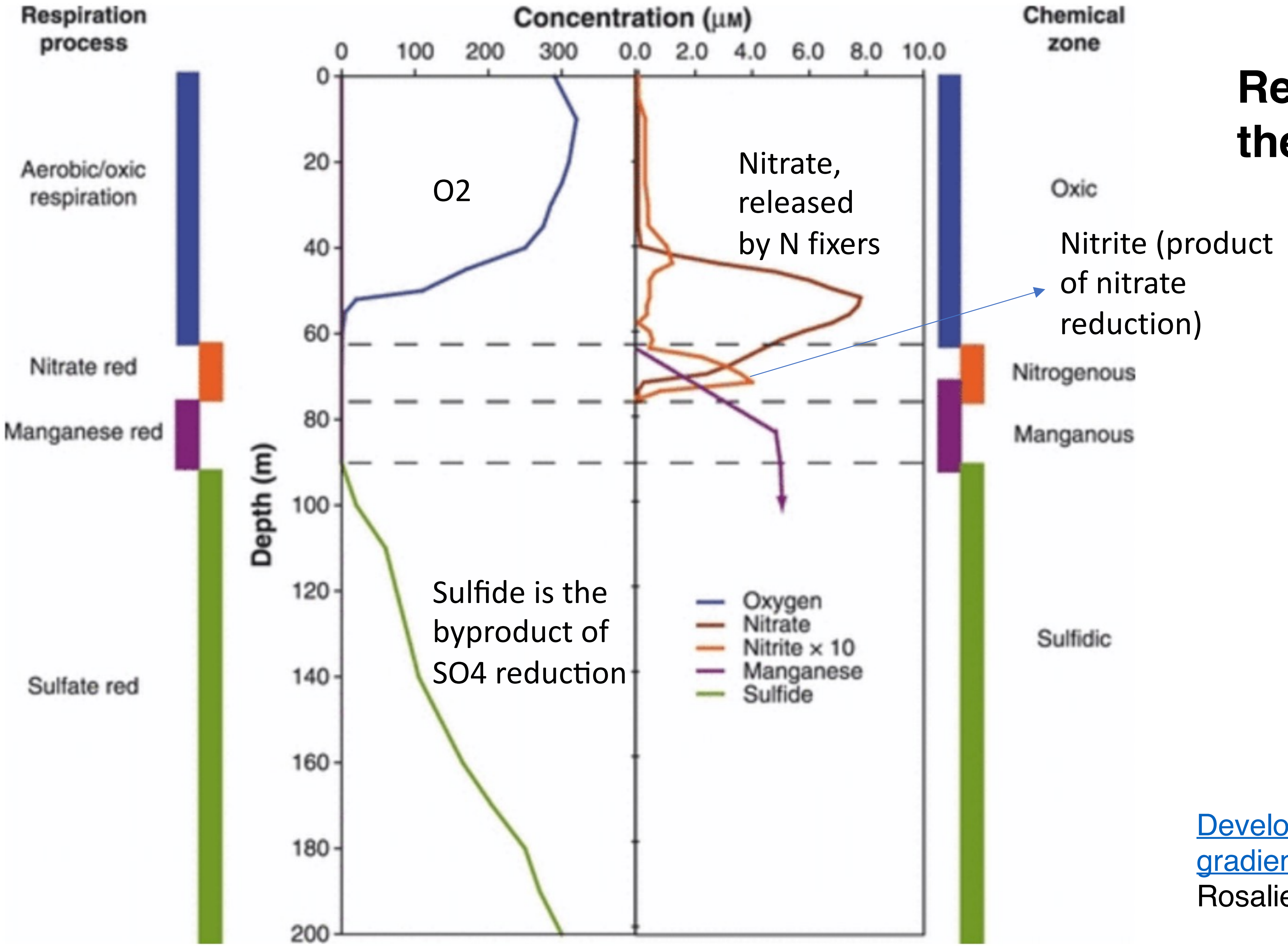


Microbial life in a water column can be stratified by redox potential

[Occurrence, Classification, and Biological Function of Hydrogenases: An Overview]. Vignais and Billoud

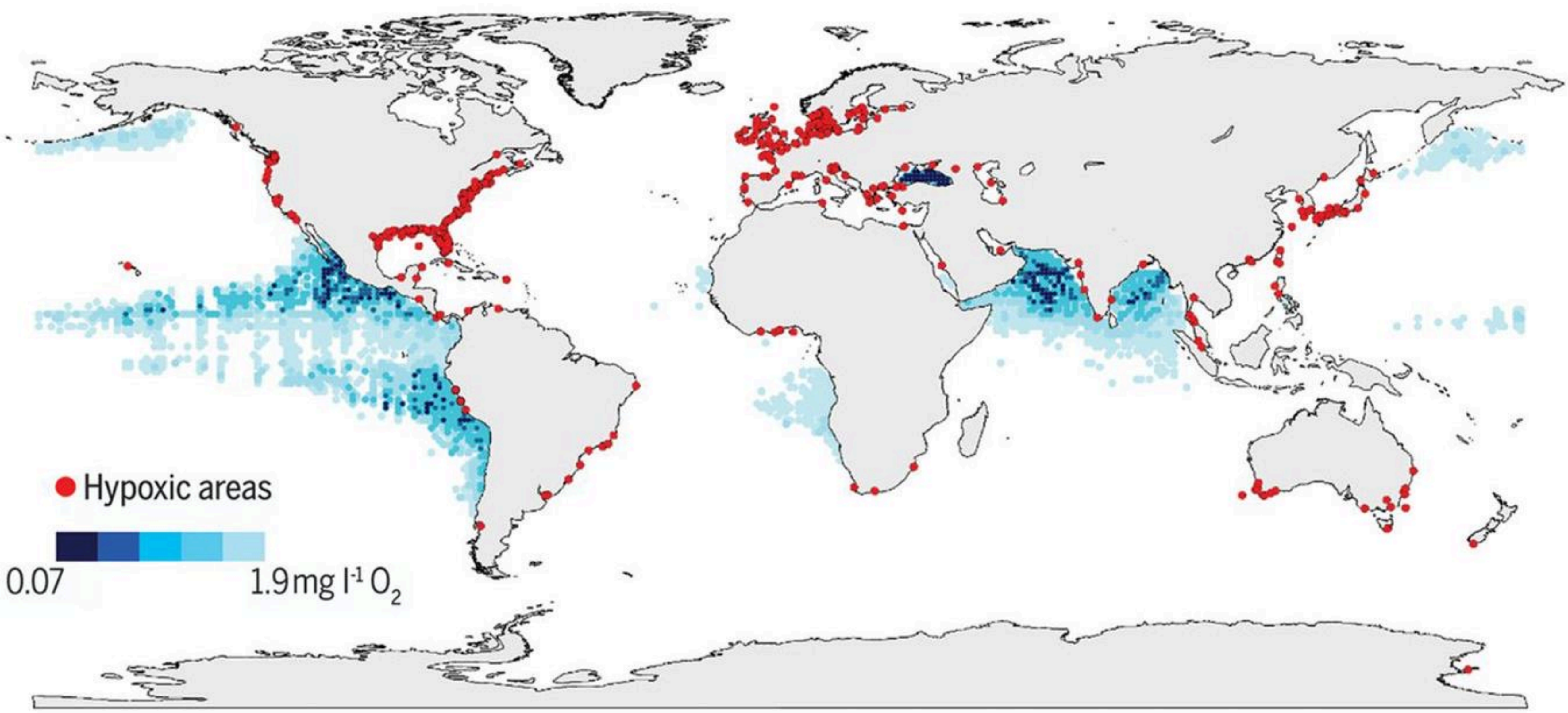
geologycafe.com

Redox stratification in the black sea

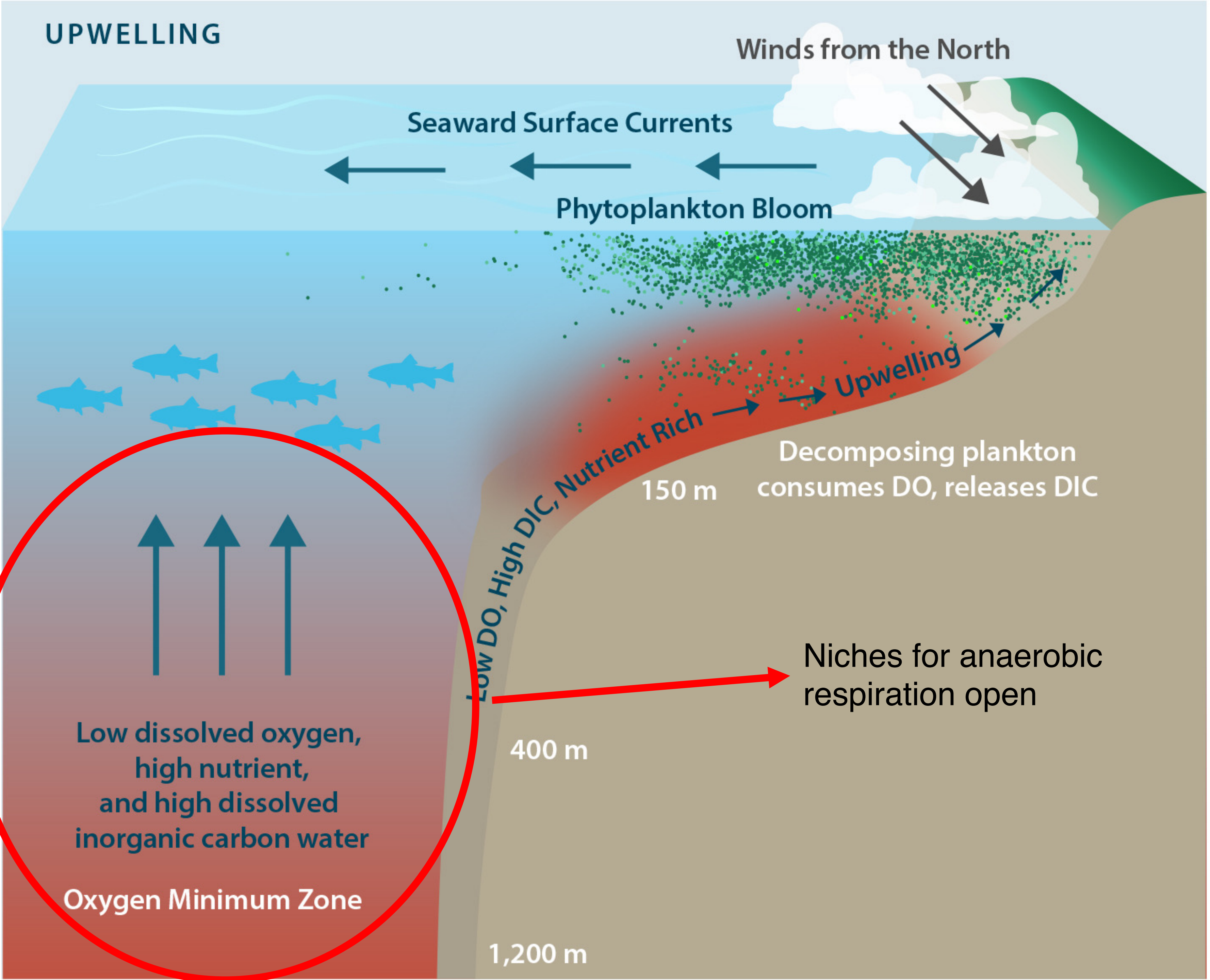


[Developing proxies to constrain redox gradients in terminal Ediacaran oceans](). Rosalie Tostevin

Source: Wikipedia (data from R. Diaz)



Global map of low and declining oxygen levels in the open ocean and coastal waters. The map indicates coastal sites where anthropogenic nutrients have resulted in oxygen declines to less than 2 mg L^{-1} (red dots), as well as ocean oxygen minimum zones at 300 metres (blue shaded regions).[1]



Source: Wikipedia. Francis Chan, John A. Barth, Kristy J. Kroeker, Jane Lubchenco and Bruce A. Menge. Modified from Gewin (2010) by Moni Kovacs.

A microbial mat
In Sippewissett Marsh

[Millimeter-Scale Patterns of Phylogenetic and Trait Diversity in a Salt Marsh Microbial Mat](#). **Armitage, Ghallager, Youngblut .. Zinder.**

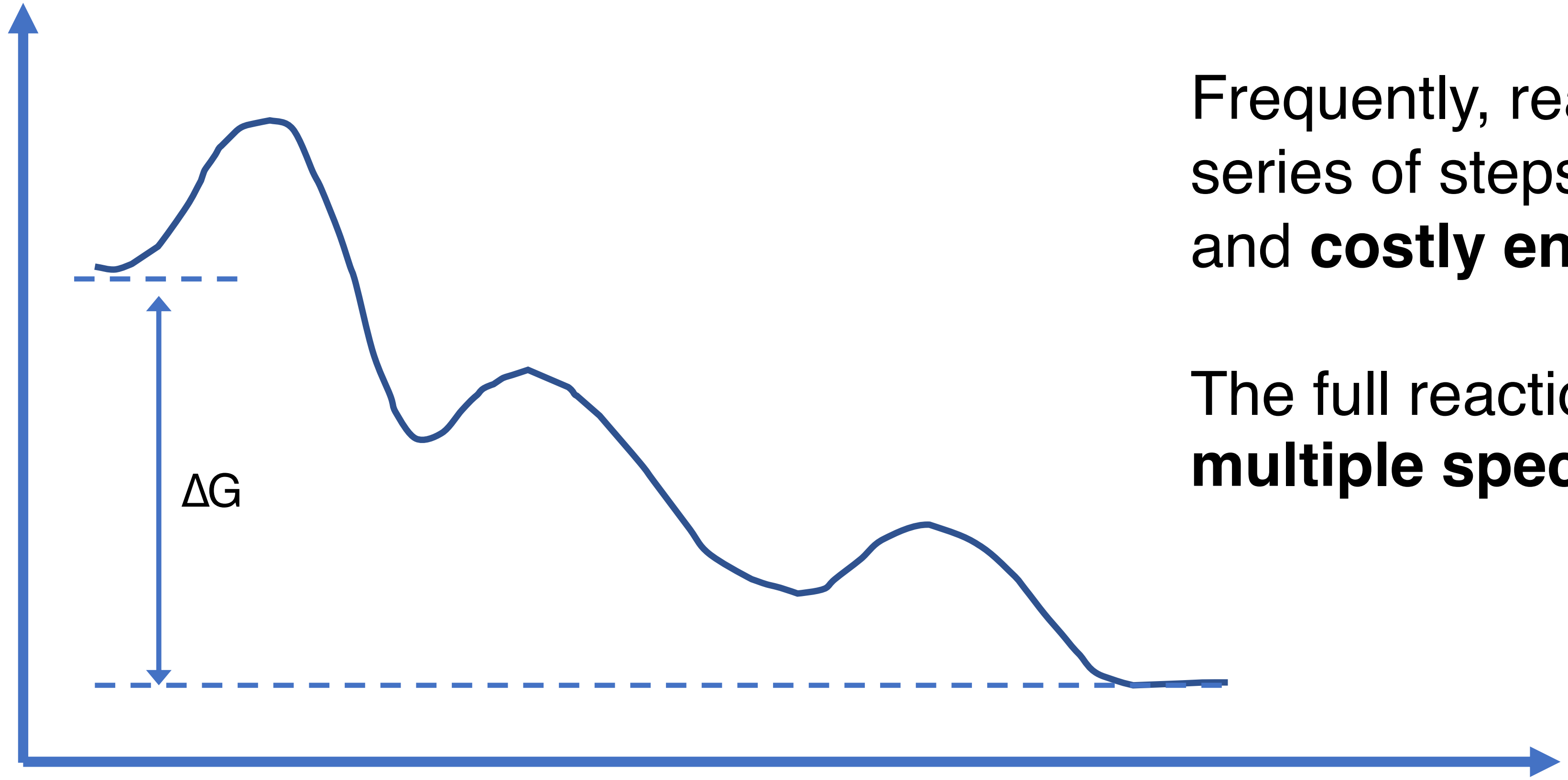
Similar patterns to those that appear in a meromictic lake or oxygen minimum zones can appear at mm-scales in microbial mats (or Winogradsky columns)

Organizing principles of microbial life

Life is fueled by reduction-oxidation reactions

So, it’s that it?

Thermodynamics tells you whether a reaction can happen, but not how

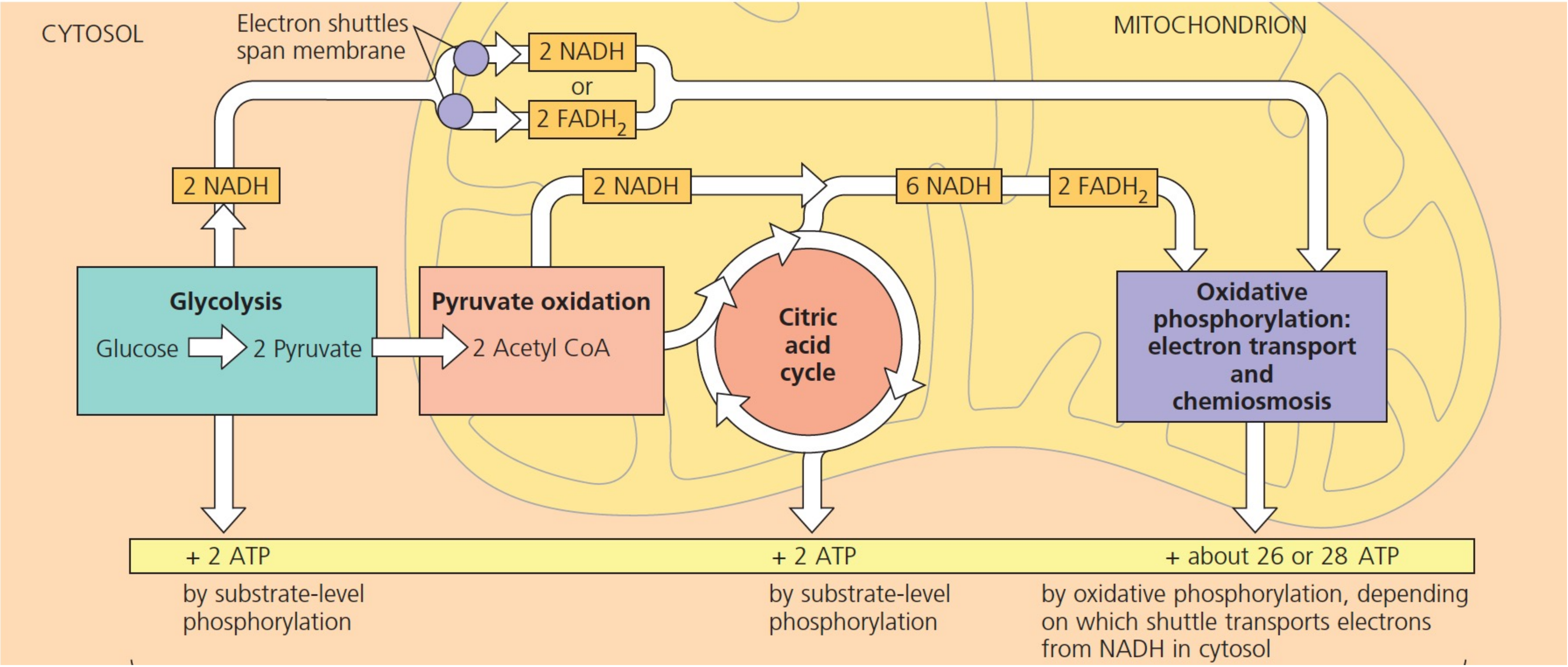


Free energy calculations tell you nothing about the pathway of the reaction or the kinetics

Frequently, reactions take place in a series of steps and involve **complex** and **costly enzymatic machineries**

The full reaction can also involve **multiple species** of microorganisms

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O$$



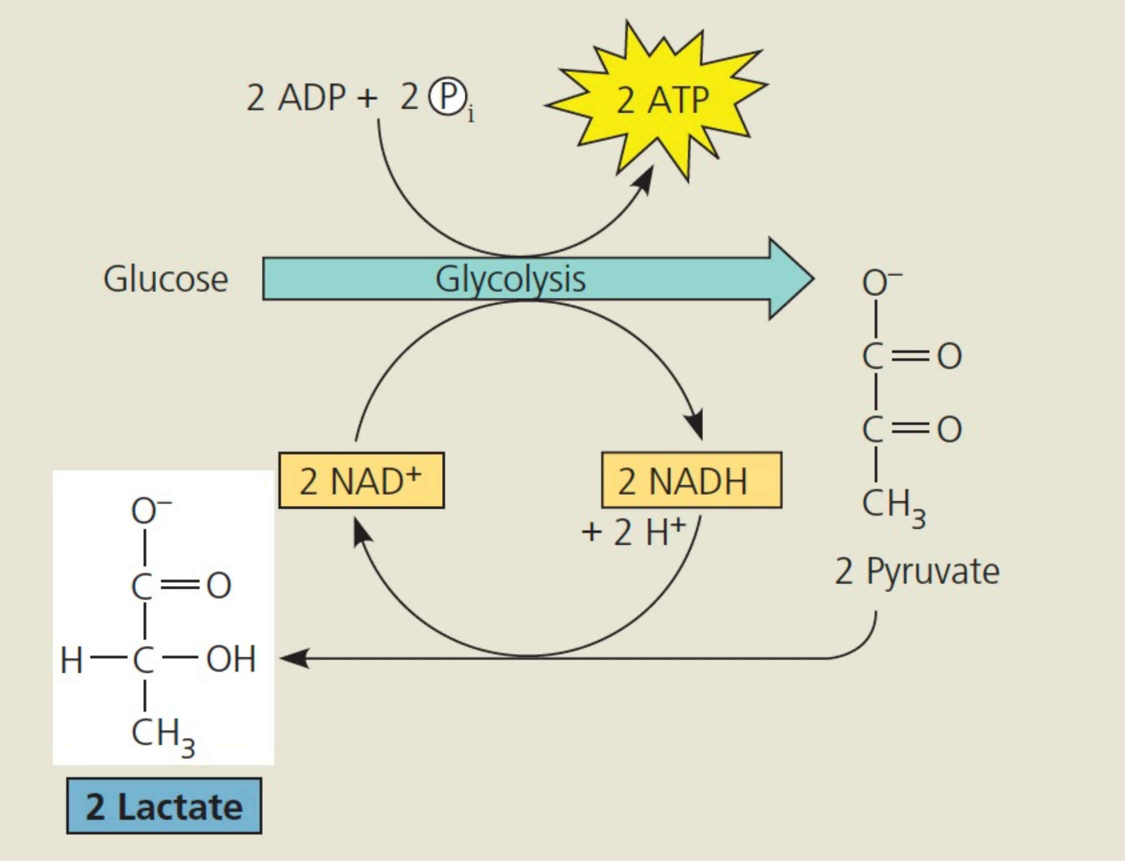
An eukaryotic cell
Source: masteringbiology.com

Fermentation

Respiration is not the only way to generate energy. Fermentation is highly favorable in the absence of oxygen

In fermentation NAD+ is the electron acceptor inside the cell.

“ Fermentation consists of glycolysis plus reactions that regenerate NAD+ by transferring electrons from NADH to pyruvate or derivatives of pyruvate.”



(b) Lactic acid fermentation

mastering biology.com

Fermentation

To start, respiration is not the only way to generate energy. Fermentation is highly favorable in the absence of oxygen

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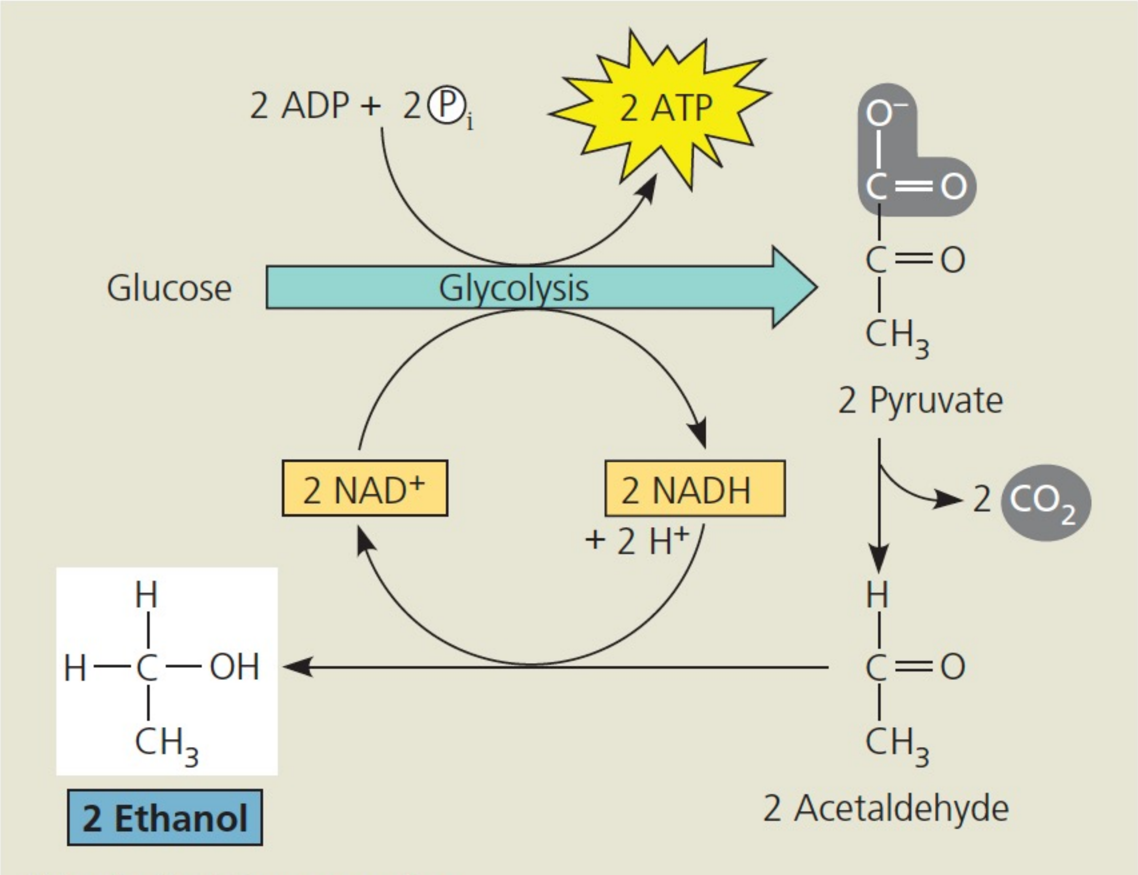

(a) Alcohol fermentation

ΔG0 ‘ = -234.28 kJ/mol

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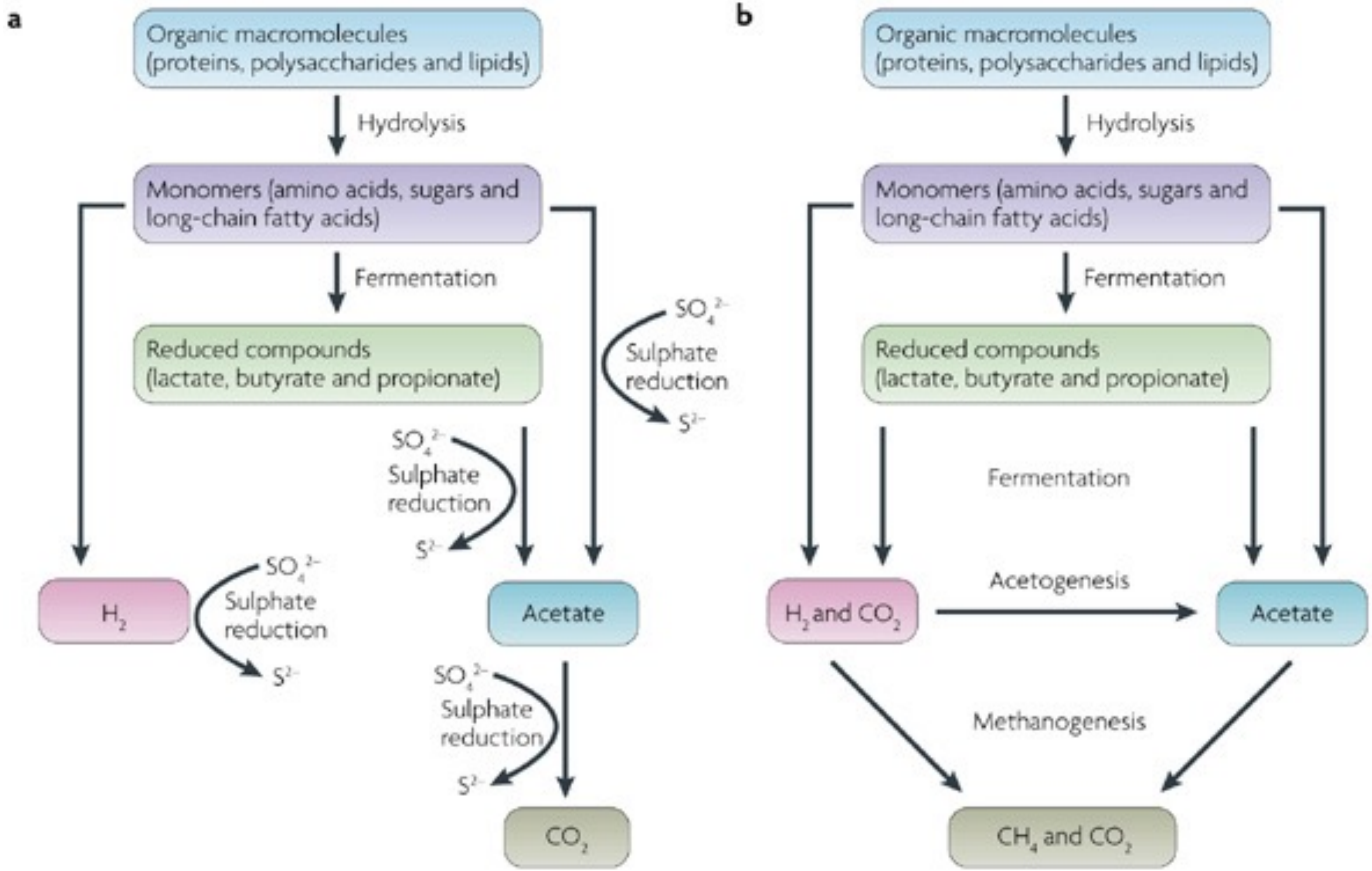
Trophic organization of anaerobic microbial ecosystems

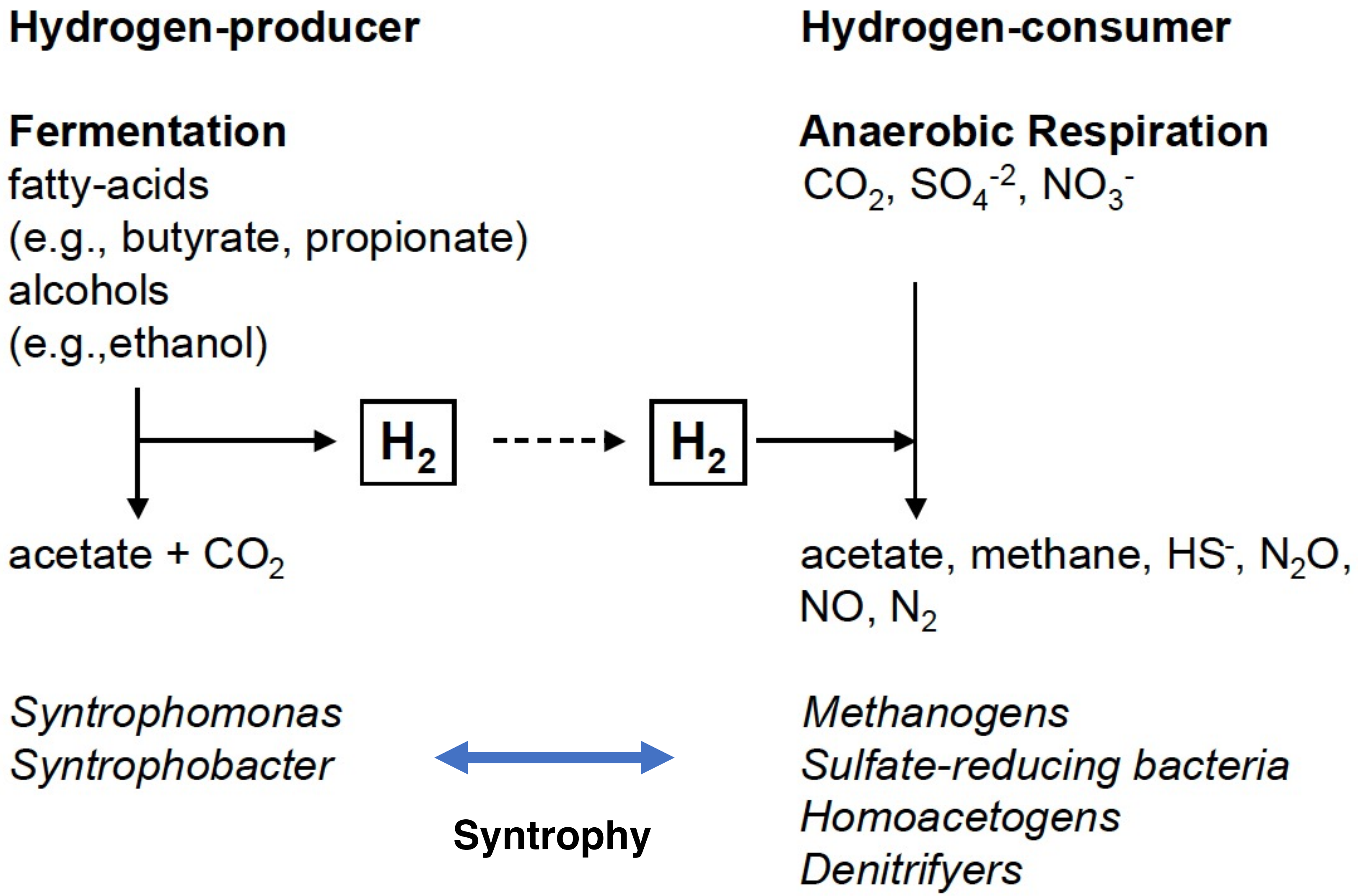


Why is there one organism that can do all of this work?

Nature Reviews | Microbiology

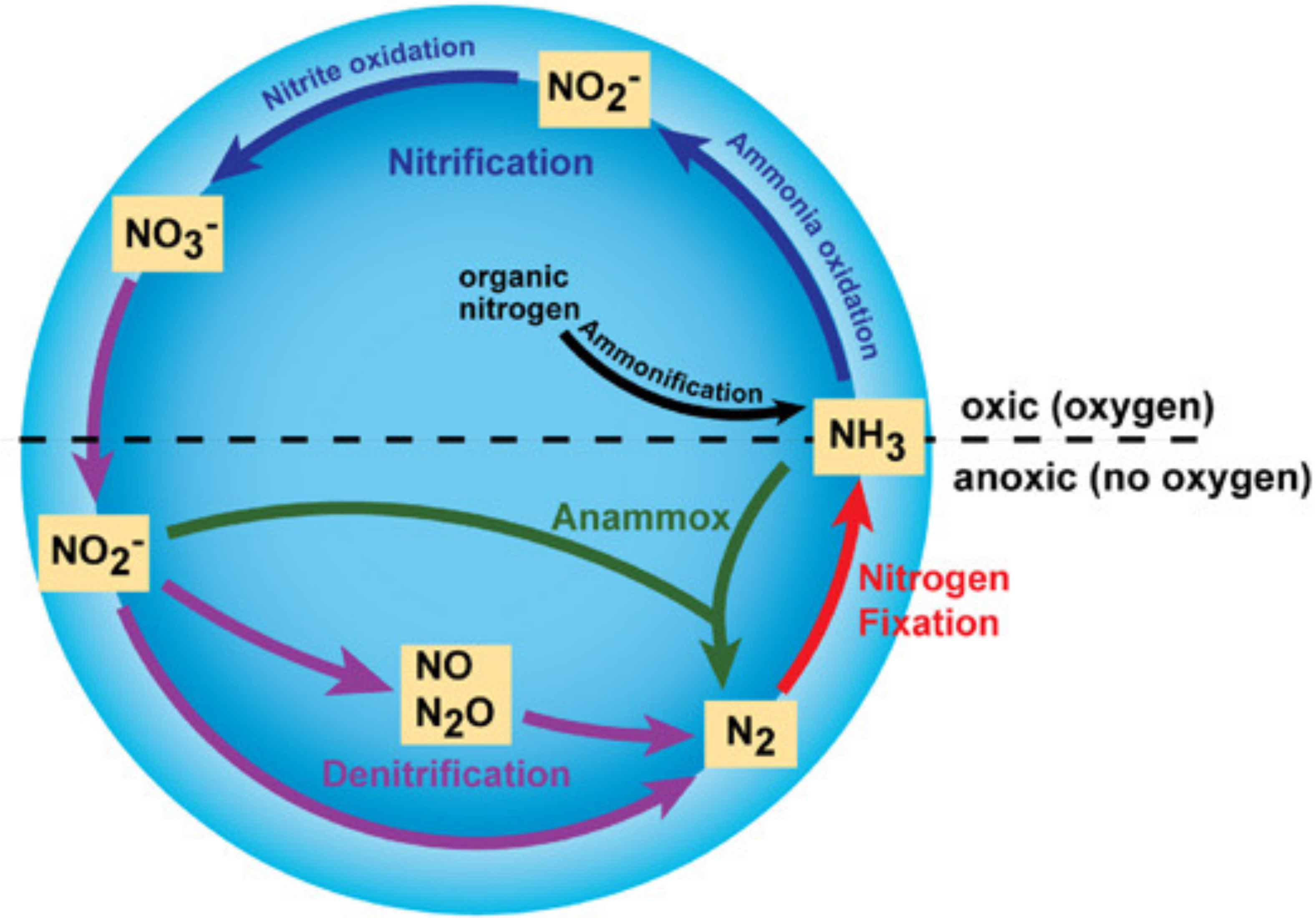
Why is labor divided in anaerobic environments?

The question of why is labor divided is a central problem in microbiology



Source: Martin Koenneke

Why is labor divided?



Denitrification (NO_{3-} –> N_2) can be performed by a single organism

However, often organisms divide labor (perform partial reactions)

For more, talk to Seppe

Nature Education: Knowledge project

Organizing principles of microbial life

What determines the distribution, abundance and activity of microbes in the environment?

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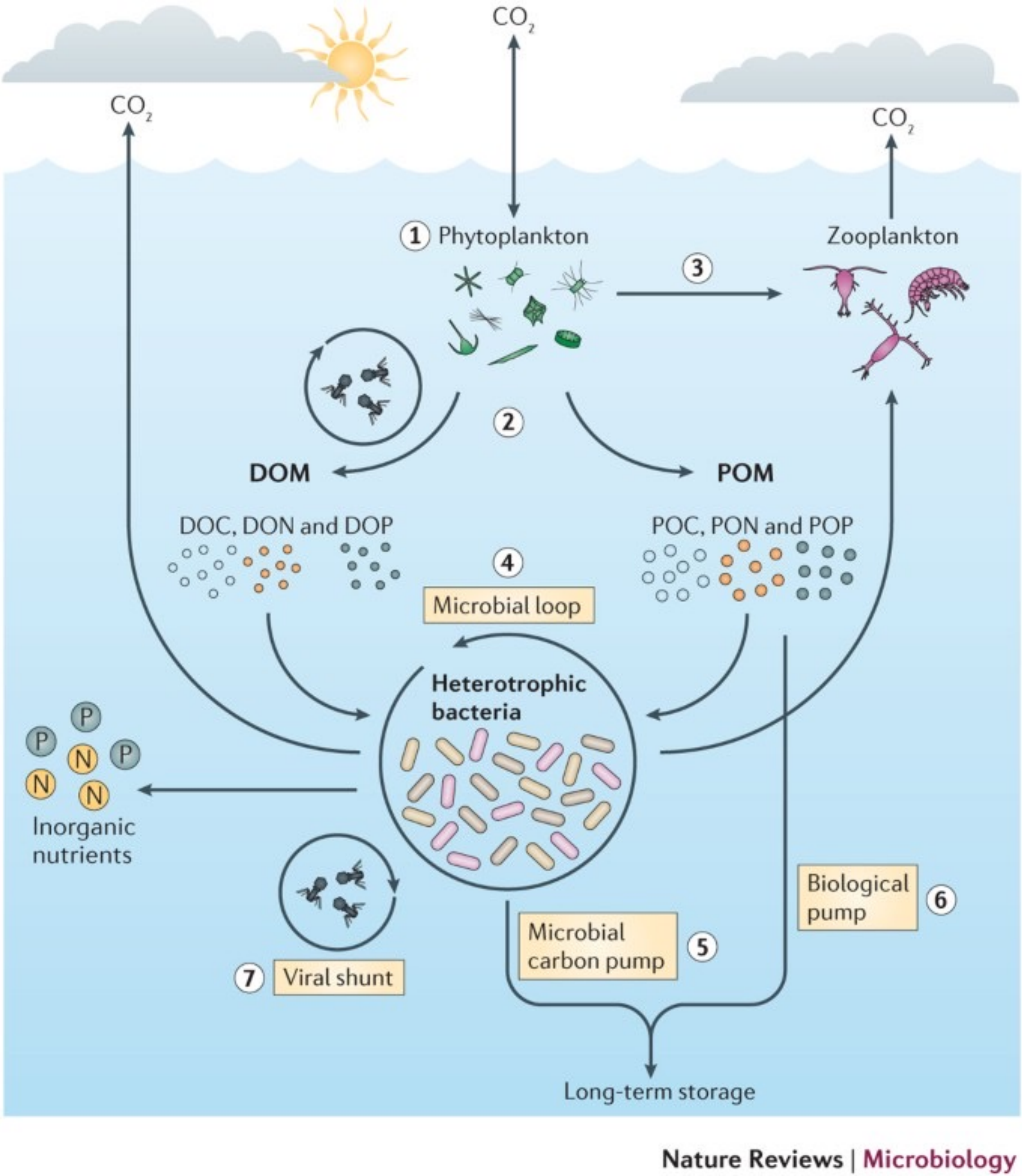
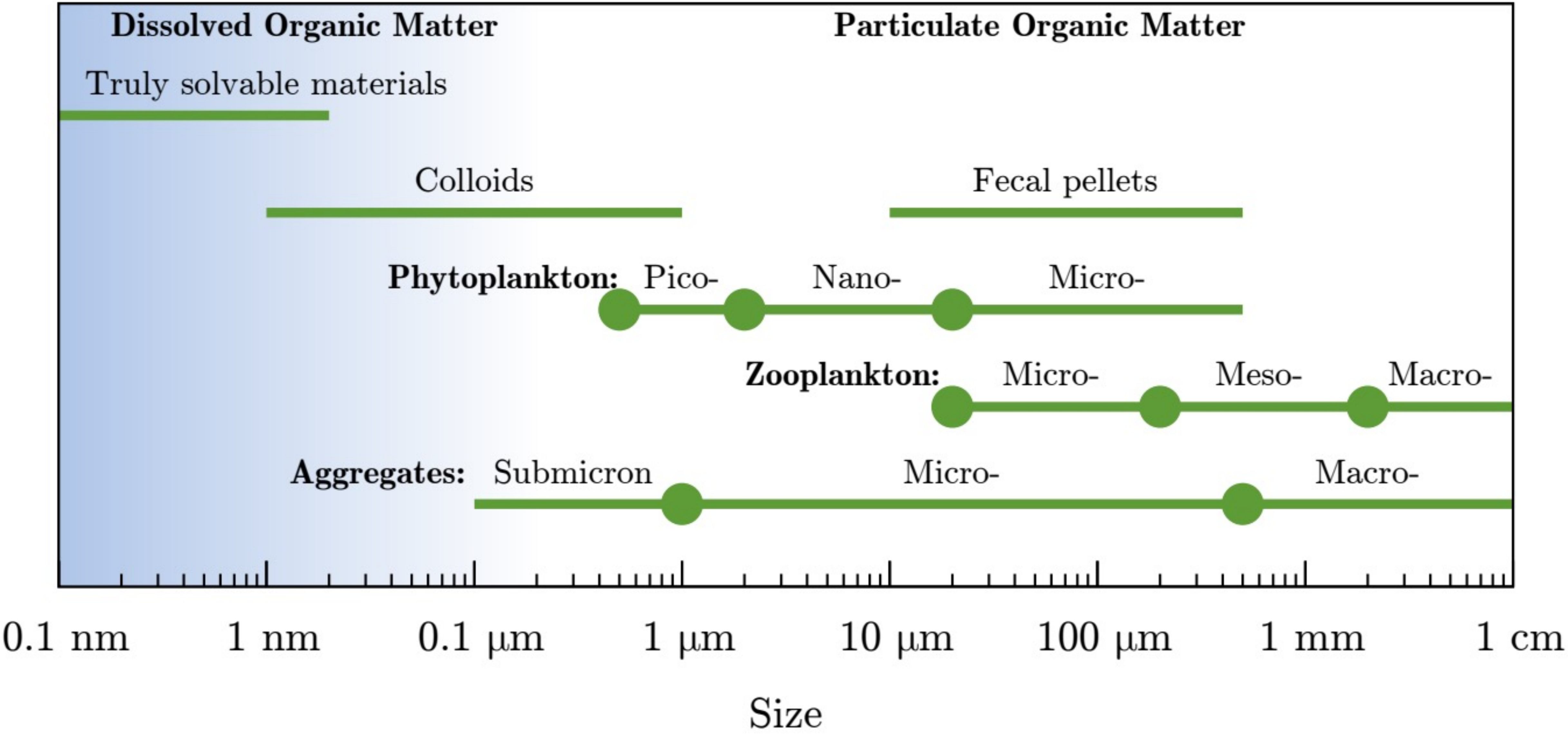
2. Division of labor (metabolic trade-offs)
3. Eco-physiology

Aerobic carbon respiration in the ocean

$$C_6H_{12}O_6 + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O$$



Master recyclers: features and functions of bacteria associated with phytoplankton blooms. Buchan et al. 2014



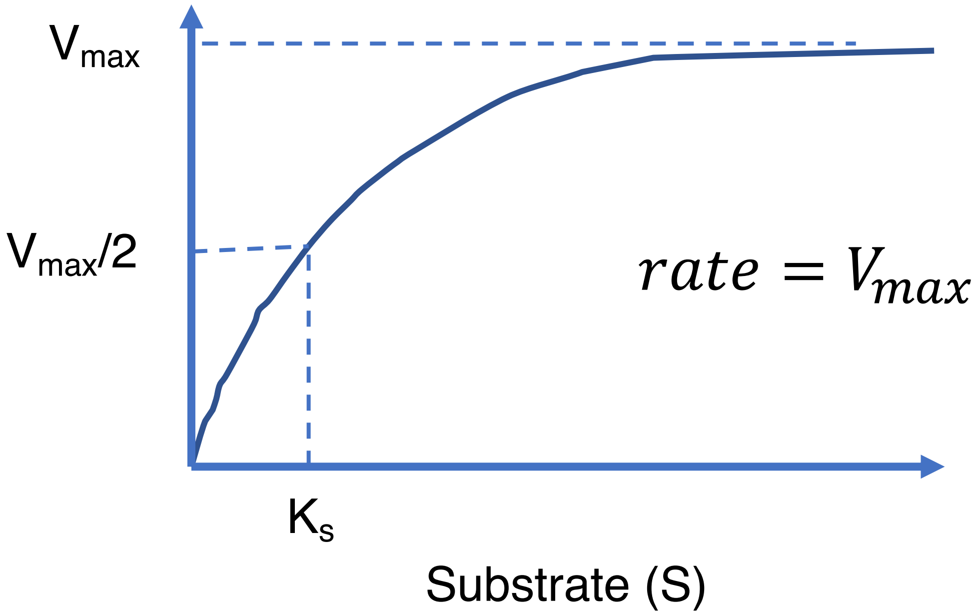
Adapted from Simon et al., 2002.

DOM

Many different small molecules, each may be at very low concentrations
e.g. the concentration of glucose in seawater ranges from 2 to 15 nM

Bacterial utilization of dissolved glucose in the upper water column of the Gulf of Mexico. Askoog et al, 1999

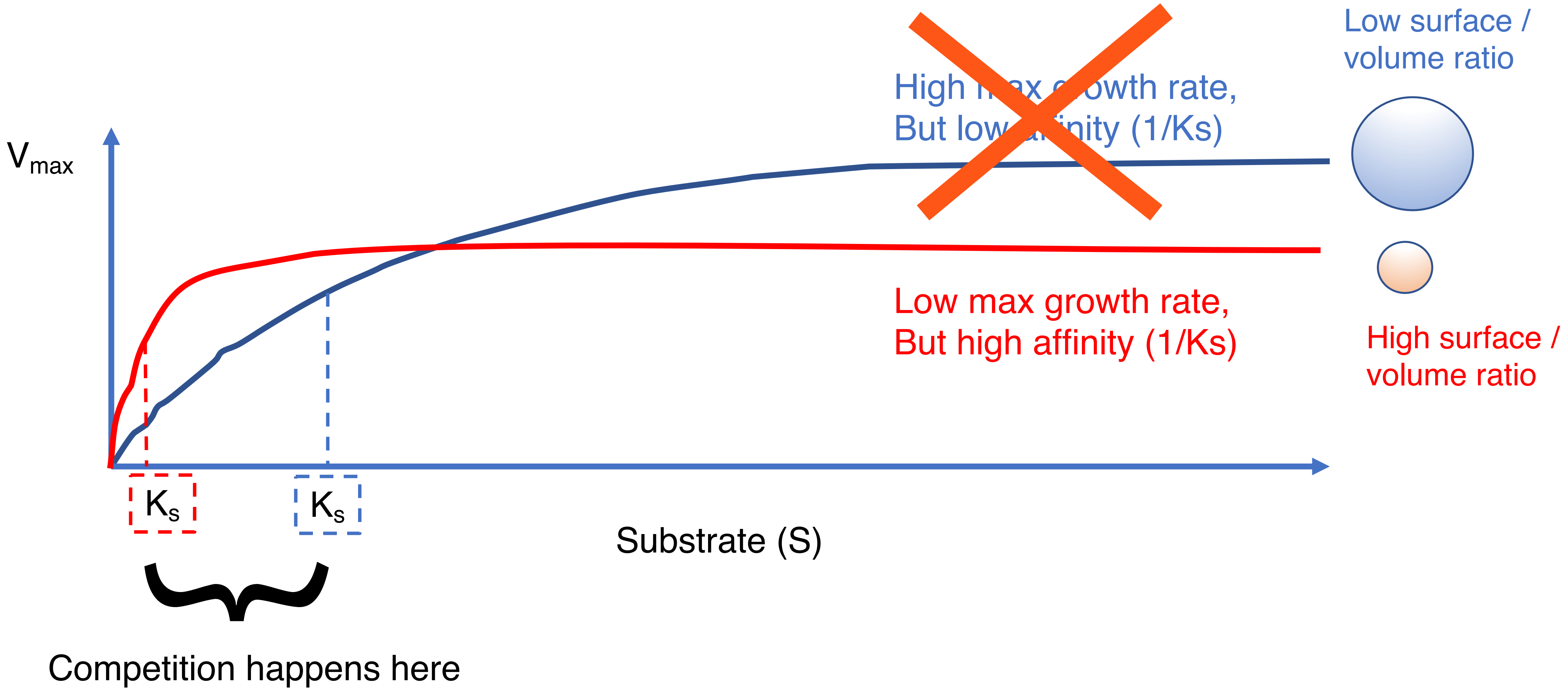
(for reference, E. coli half saturation Monod constant (K_s) is in the μM range)



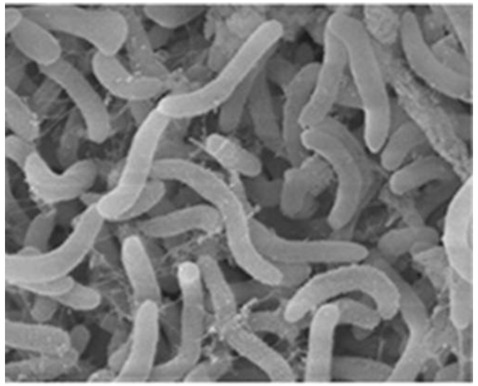
$$rate = V_{max} \frac{S}{K_s + S}$$

DOM

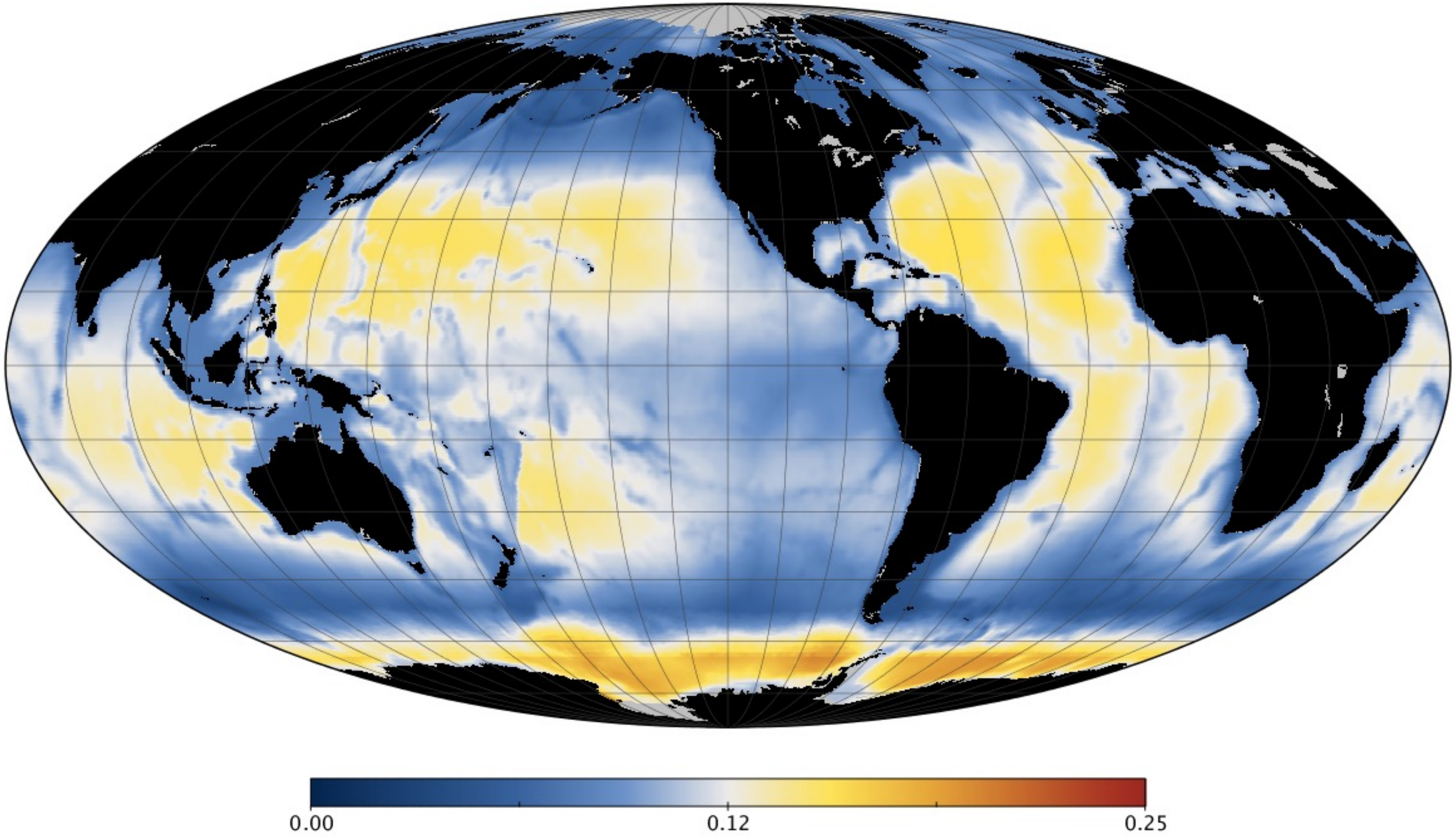
Competitive outcomes are defined at **low** substrate concentrations. The species that can survive at the lowest [S] wins (can be shown in a chemostat model)



Pelagibacter ubique, the most numerically dominant organism (heteroptrophic bacterium)



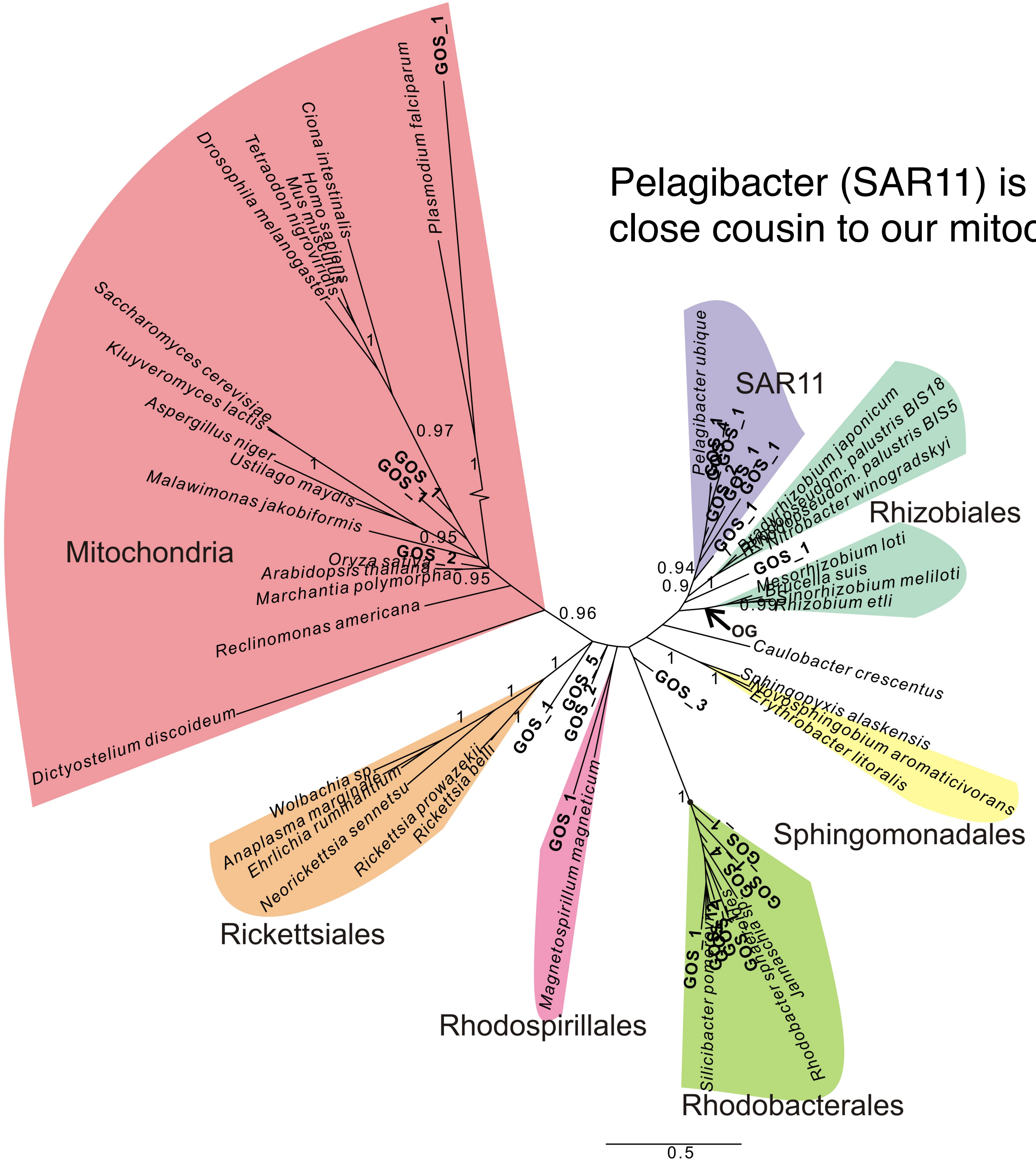
< 1μM, total abundance 10^{28}



http://docpollard.org/marine_diversity/

And by the way …

Pelagibacter (SAR11) is a relatively close cousin to our mitochondria



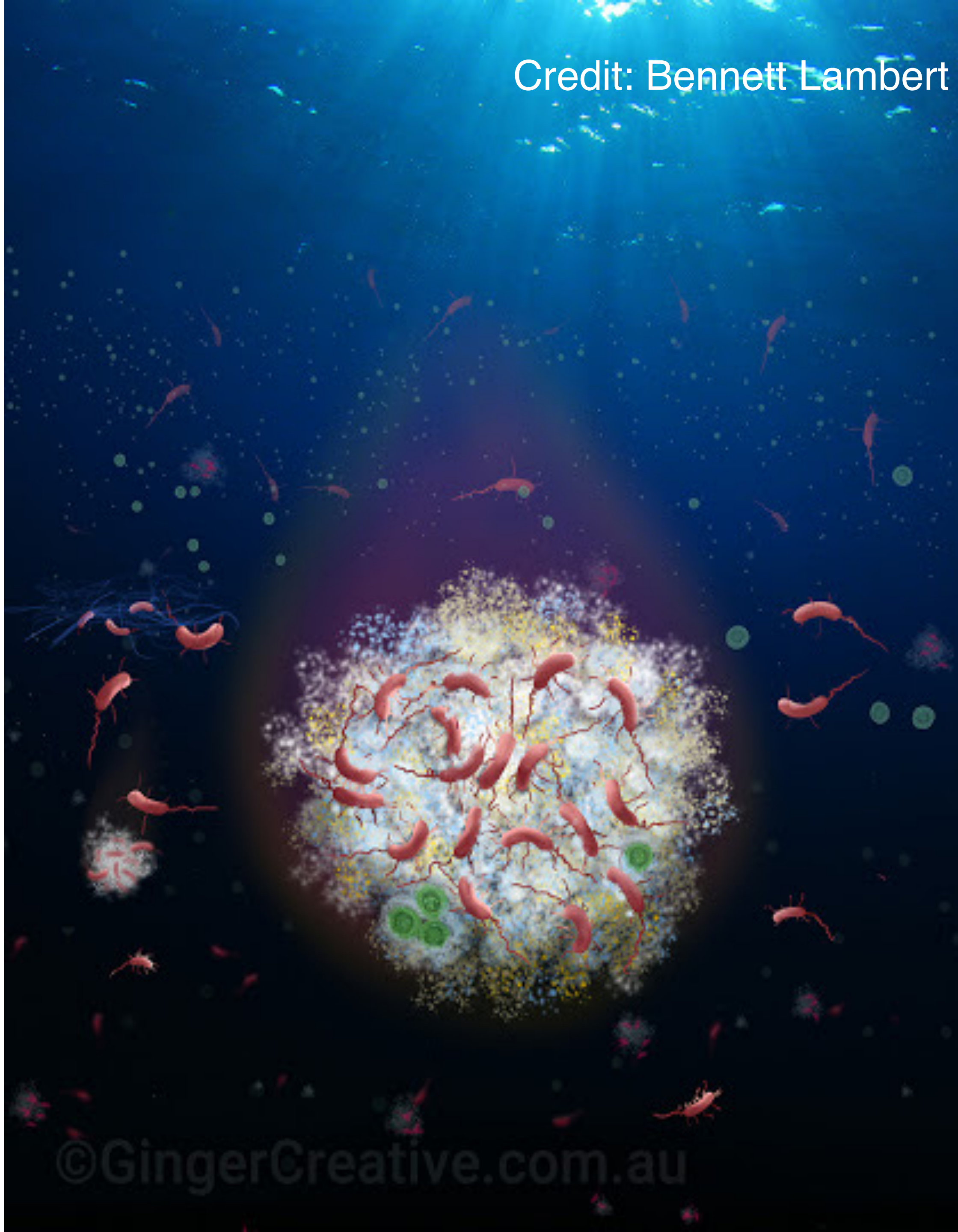
A Phylometagenomic Exploration of Oceanic Alphaproteobacteria Reveals Mitochondrial Relatives Unrelated to the SAR11 Clade.
Brindefalk et al. 2011

POM

High concentration of organic matter, many macromolecules (complex carbohydrates, proteins)

Gradients attract chemotactic microbes

Dense microbial communities can assemble on phycospheres and other marine particles



POM

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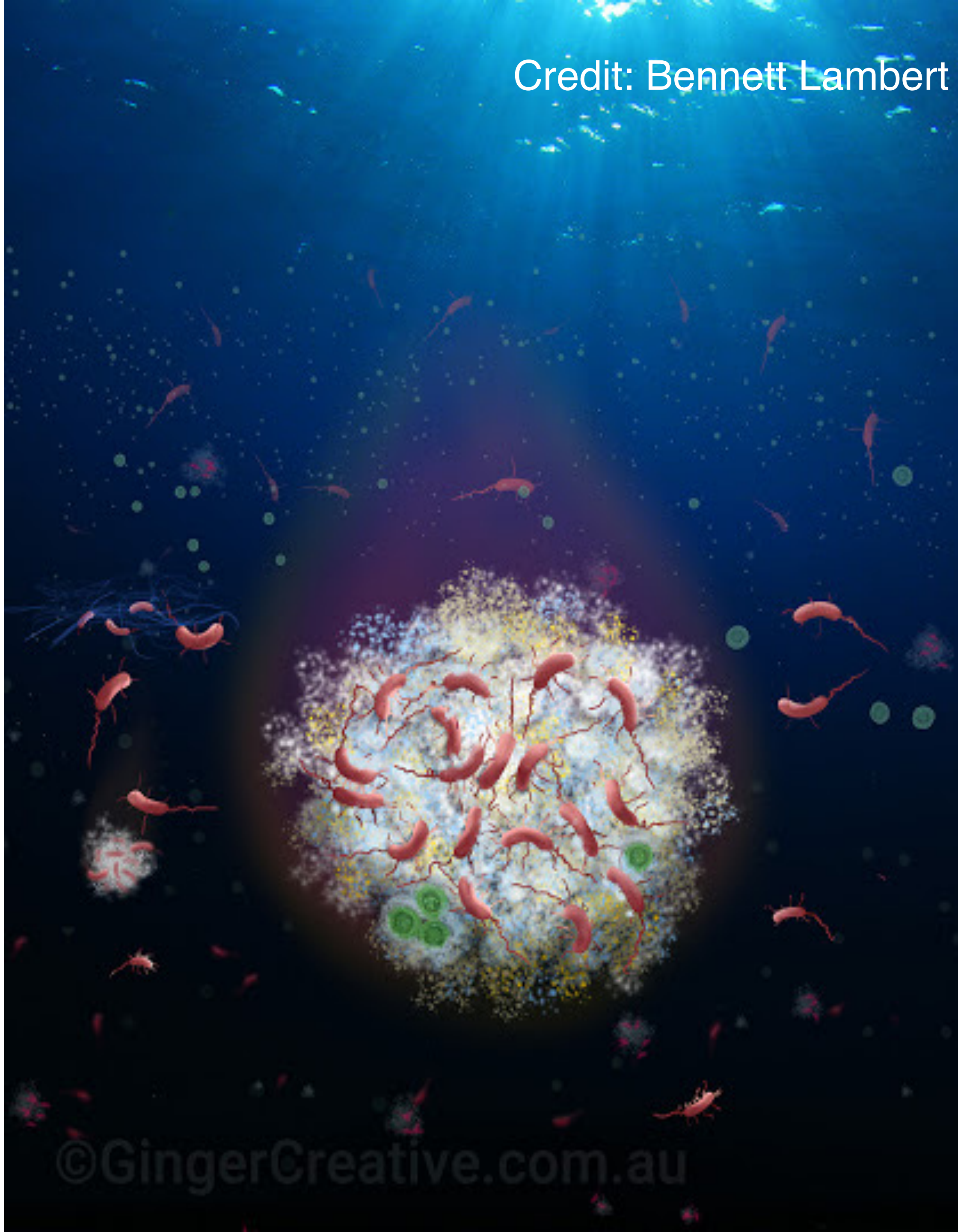
Gradients attract chemotactic microbes

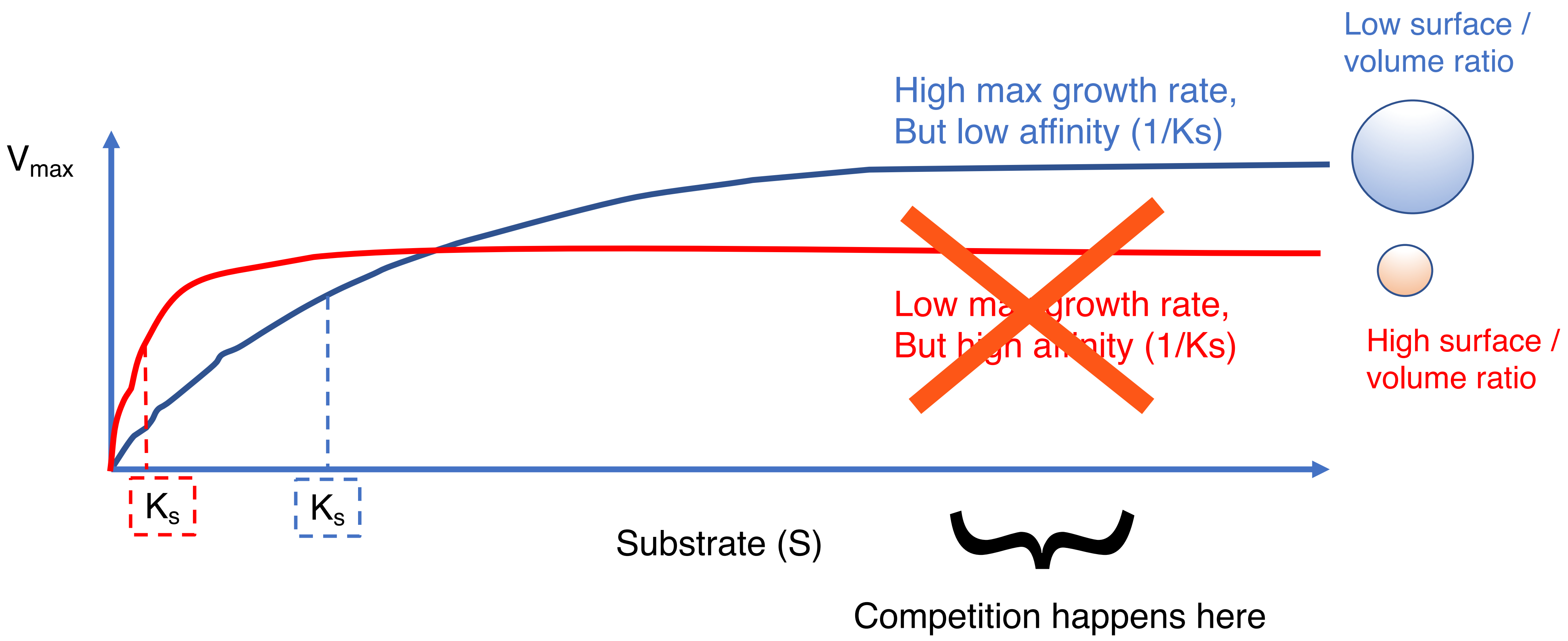
Dense microbial communities can assemble on phycospheres and other marine particles

Particle associated bacteria can produce a large number of antimicrobial compounds, signalling molecules, public goods, etc. Interactions are key on particles



POM

Competitive outcomes are defined at **high** substrate concentrations. Interactions can also determine what organism becomes more abundant on a particle

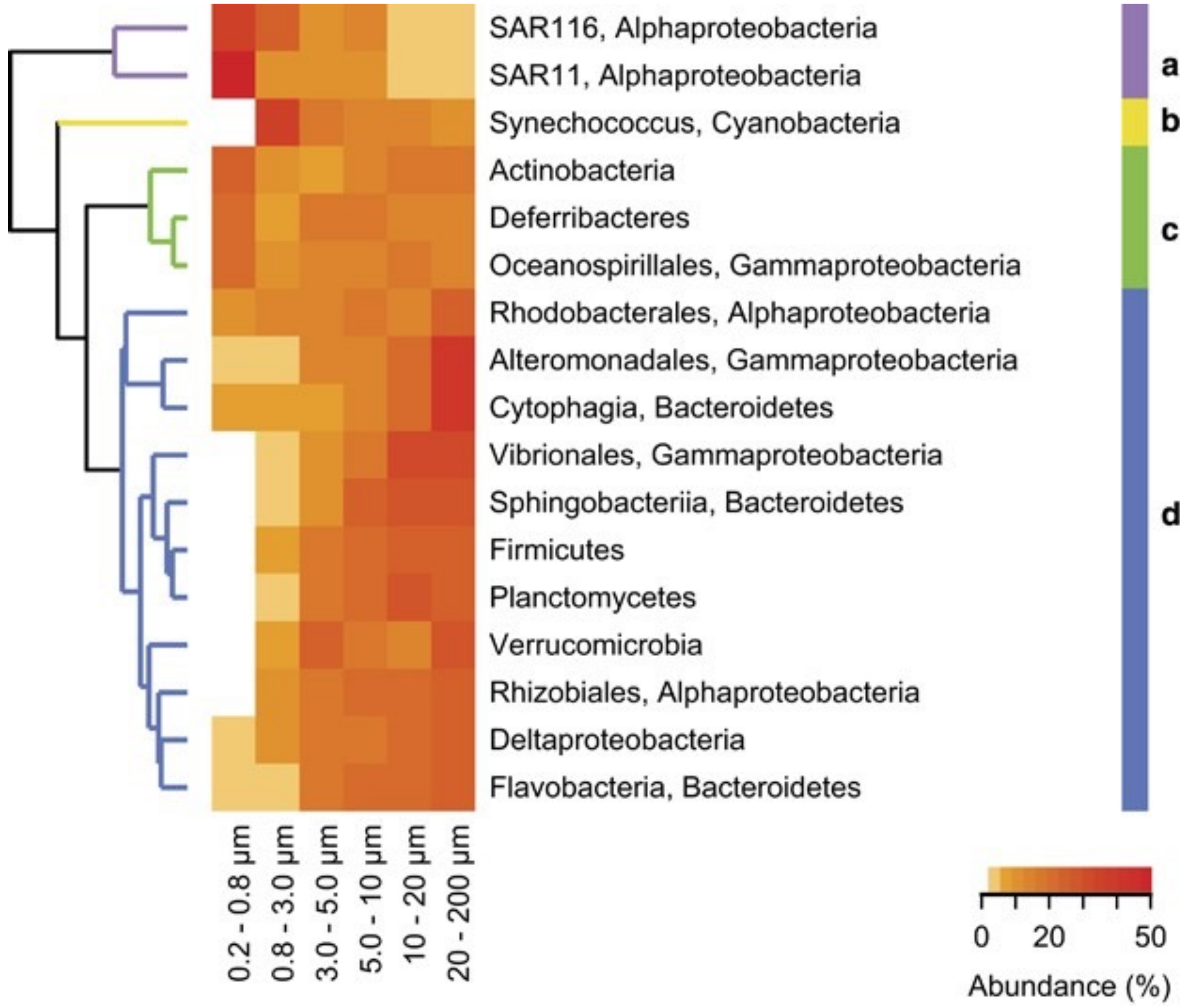


POM vs. DOM

In the ocean, heterotrophic, aerobic microbes can be split in at least two groups based on their “habitat” preference.

Organisms like SAR11 dominate the planktonic phase (< 1μm)

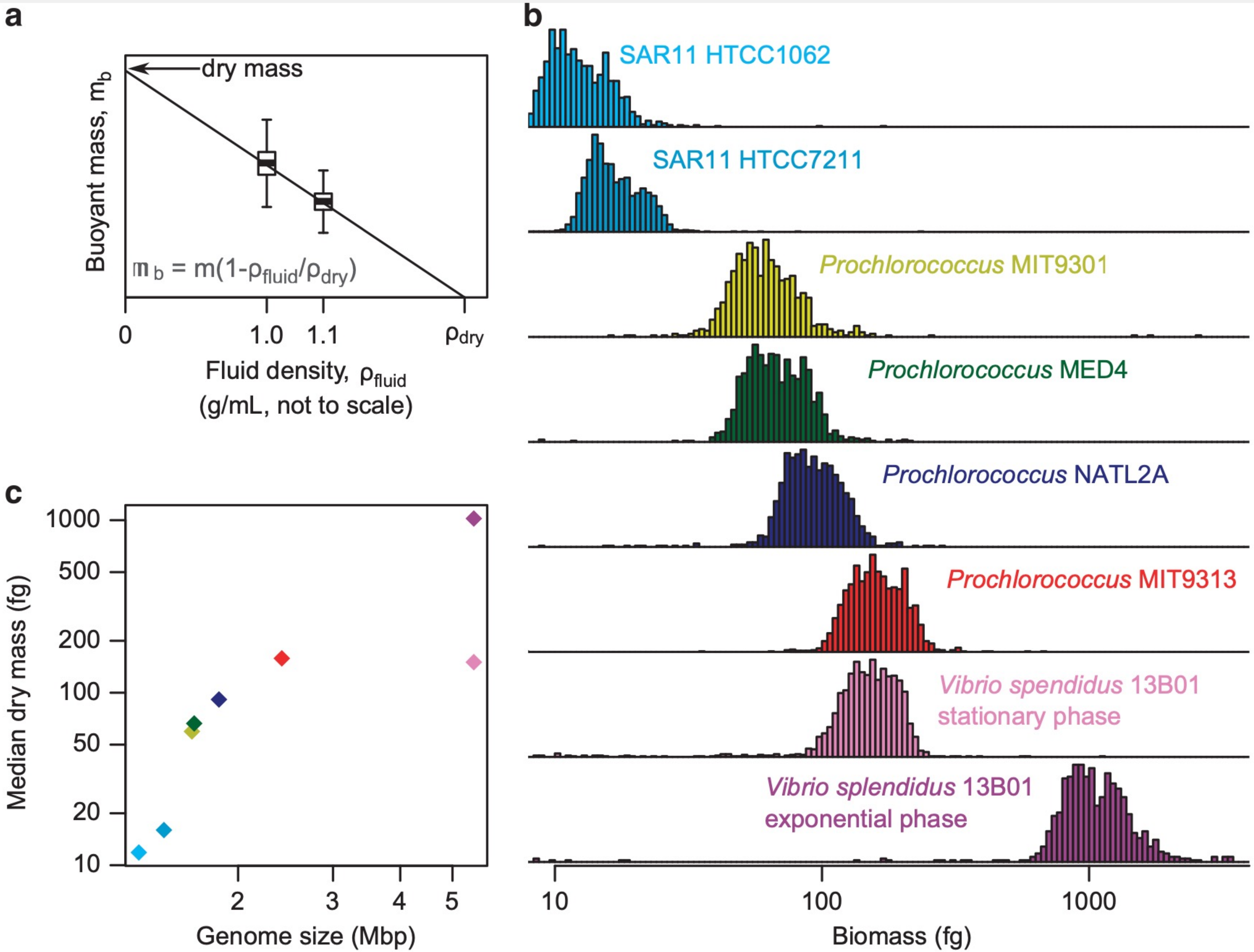
On particles (e.g. > 5μm), there are many more ‘species’, some of which have sophisticated mechanisms to break down complex organic matter



Patterns of bacterial diversity in the marine planktonic particulate matter continuum. Mestre et al. 2017

Direct single-cell biomass estimates for marine bacteria via Archimedes' principle

Cermak et al. 2017



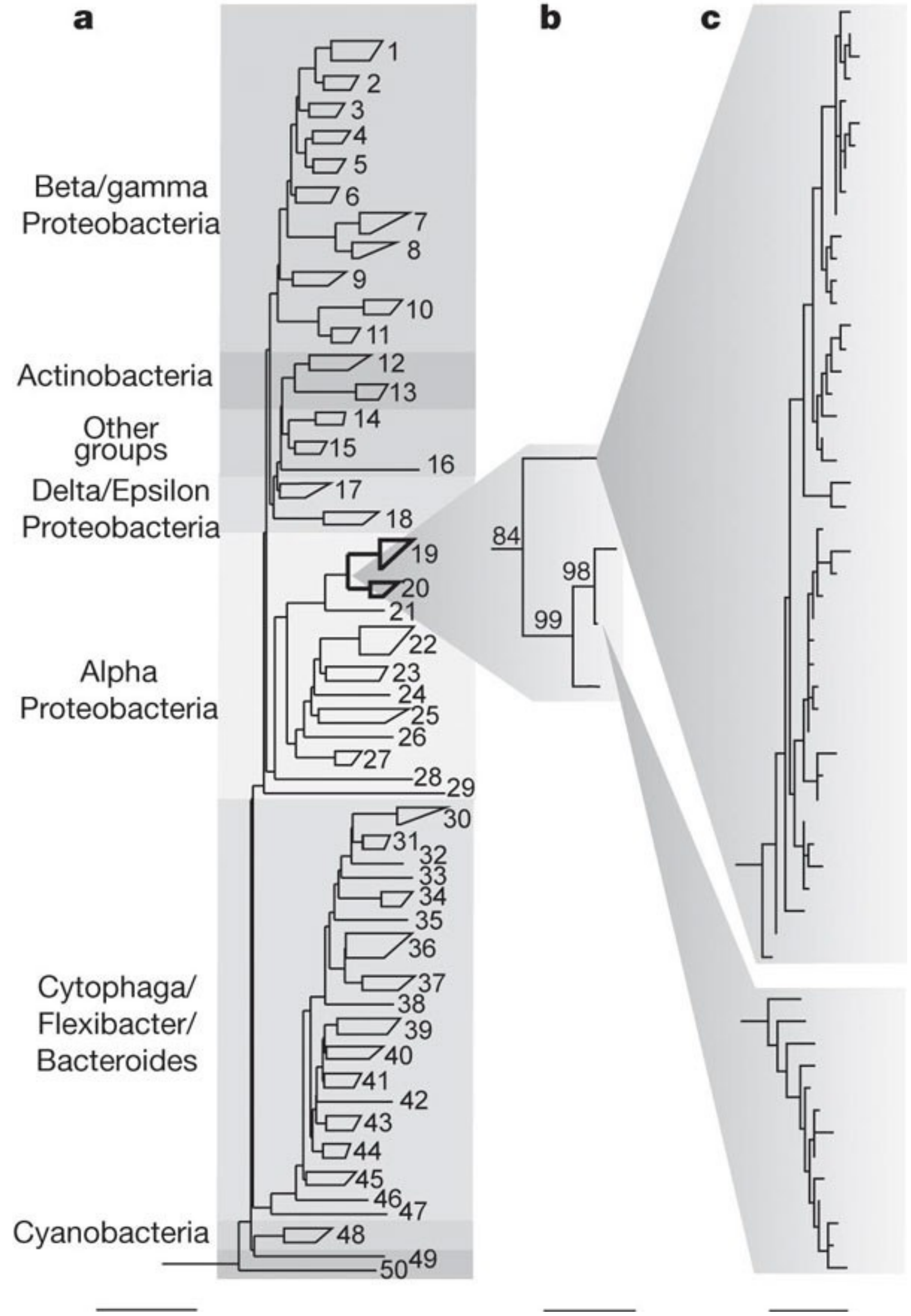
Organizing principles of microbial life

What deter[...] e
environmen[...]

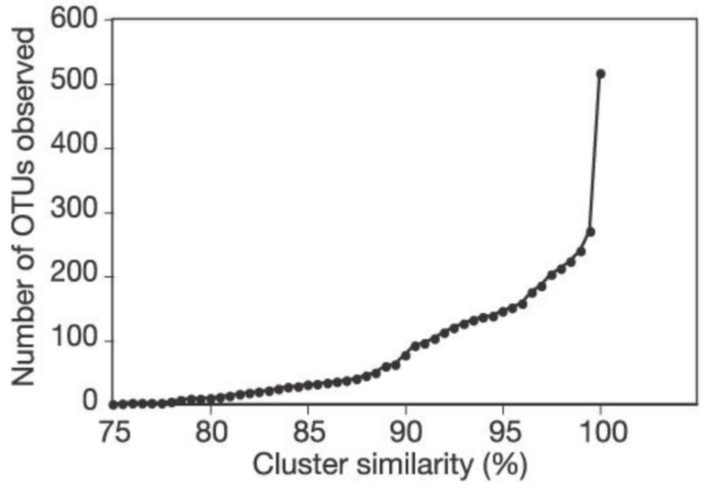
1. Bioener[...]
2. Division[...]
3. Eco-phy[...]

That's all great, but what about the extraordinary genotypic (genes, strains, species) diversity of microbes?

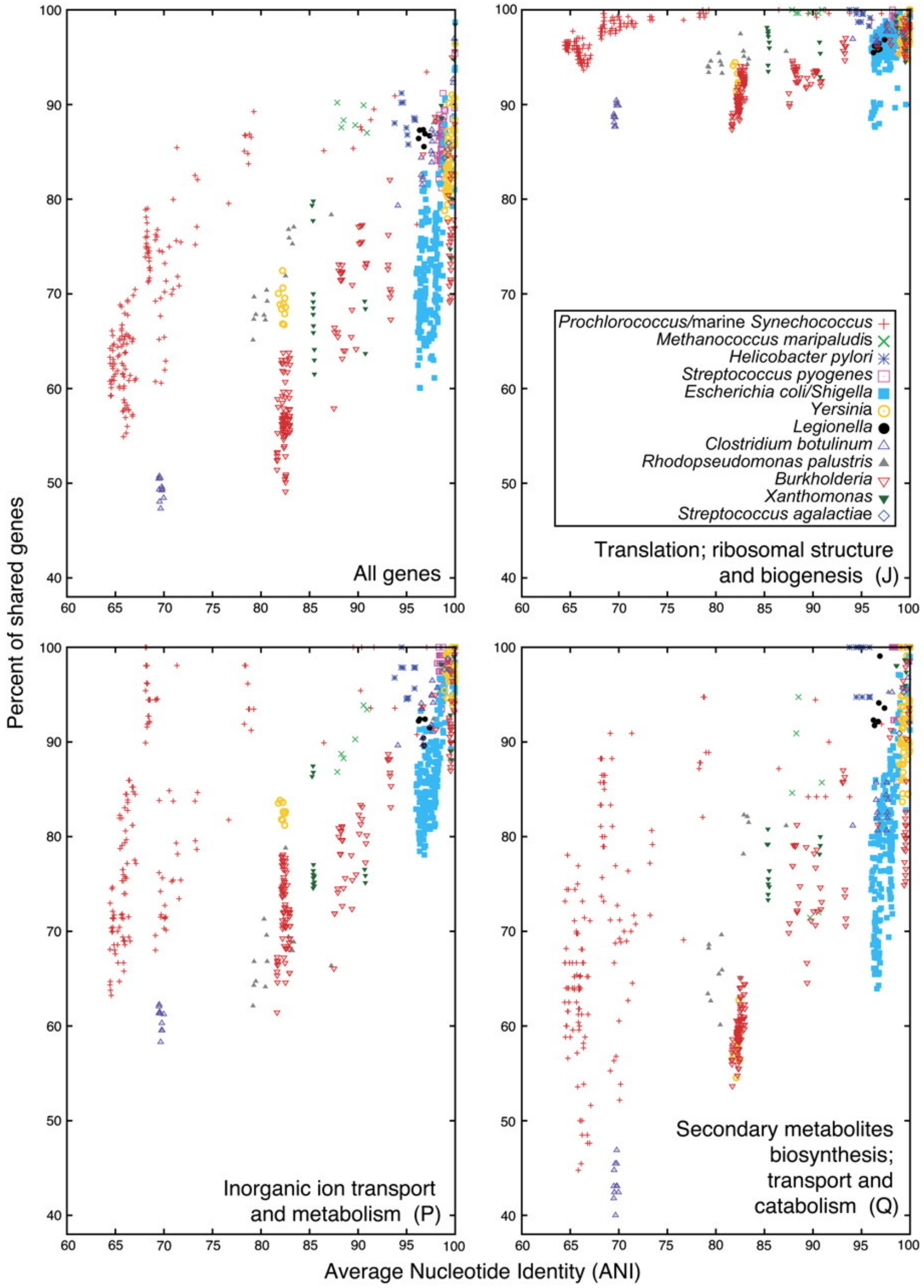
Phylogenetic distance relationships between the coastal bacterioplankton based on partial 16S rRNA sequencingm
Acinas et al. 2004



The number of variants increase nonlinearly with level of genetic resolution

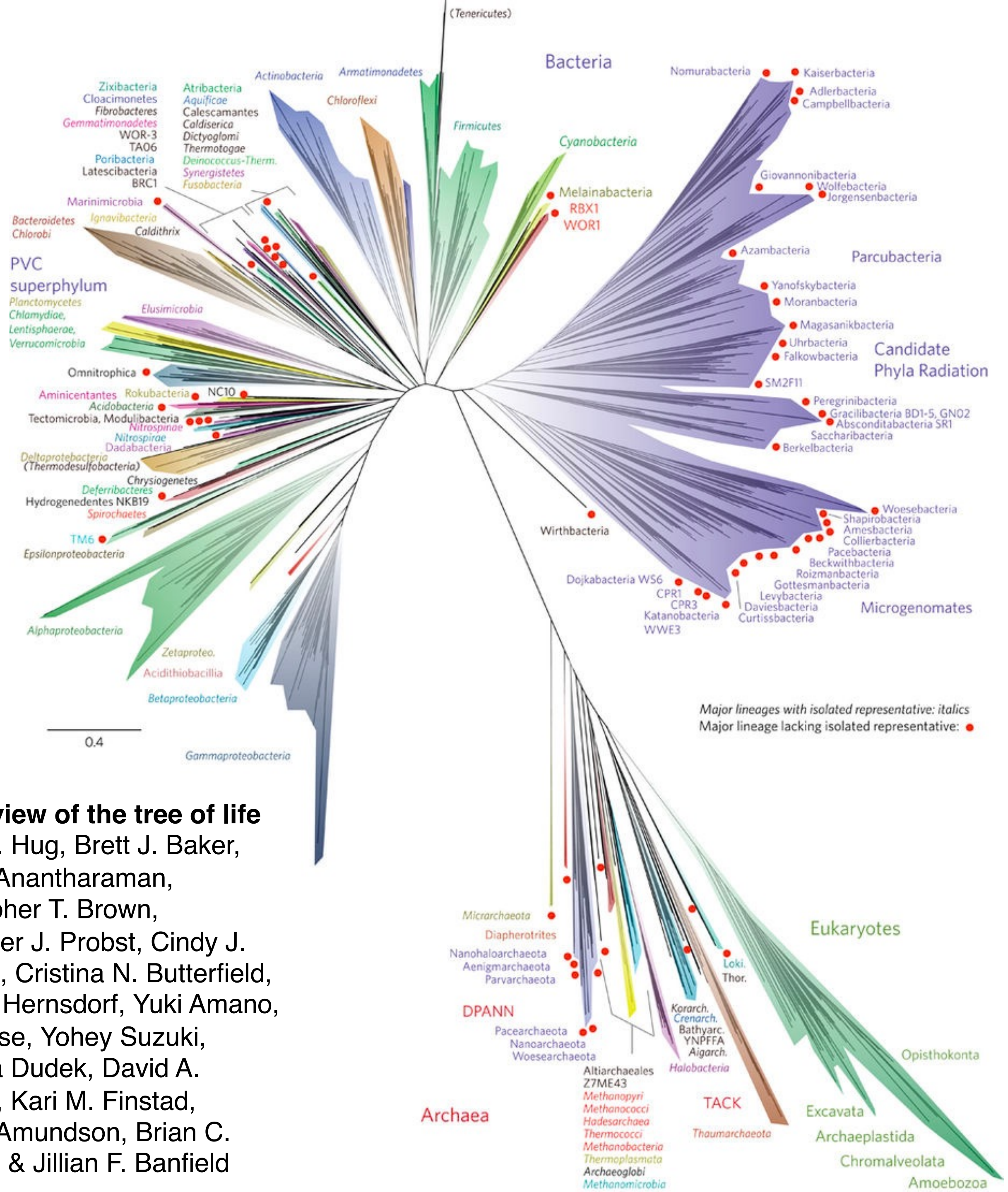


How do we explain this diversity?



Comparison of average nucleotide identities (ANI) with gene content. 773 genomes available in NCBI's RefSeq database were initially clustered using 16S rRNA identity of at least 97% as a guide to form groups.

W. Ford Doolittle, and Olga Zhaxybayeva
Genome Res. 2009;19:744-756

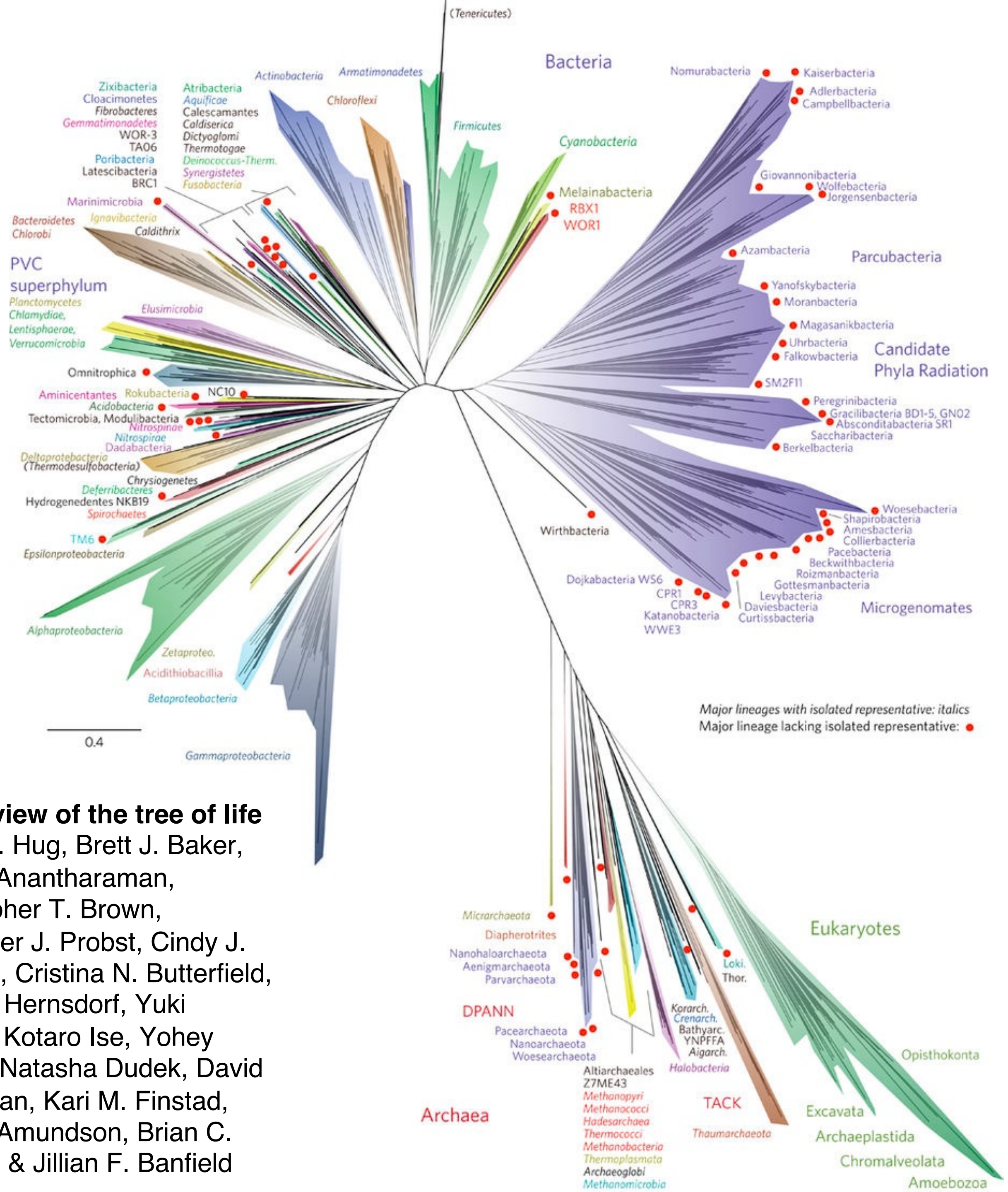


A new view of the tree of life
Laura A. Hug, Brett J. Baker, Karthik Anantharaman, Christopher T. Brown, Alexander J. Probst, Cindy J. Castelle, Cristina N. Butterfield, Alex W. Hernsdorf, Yuki Amano, Kotaro Ise, Yohey Suzuki, Natasha Dudek, David A. Relman, Kari M. Finstad, Ronald Amundson, Brian C. Thomas & Jillian F. Banfield

"To render this tree of life, we aligned and concatenated a set of 16 ribosomal protein sequences from each organism. This approach yields a higher-resolution tree than is obtained from a single gene, such as the widely used 16S rRNA gene[16]."

This based on metagenomes and single cell sequencing

"Candidate Phyla Radiation (CPR)[7], highlighted in purple in Fig. 1. … all members have relatively small genomes and most have somewhat (if not highly) restricted metabolic capacities[7,13,24]. Many are inferred (and some have been shown) to be symbionts[7,25,26]. Thus far, all cells lack complete citric acid cycles and respiratory chains and most have limited or no ability to synthesize nucleotides and amino acids."



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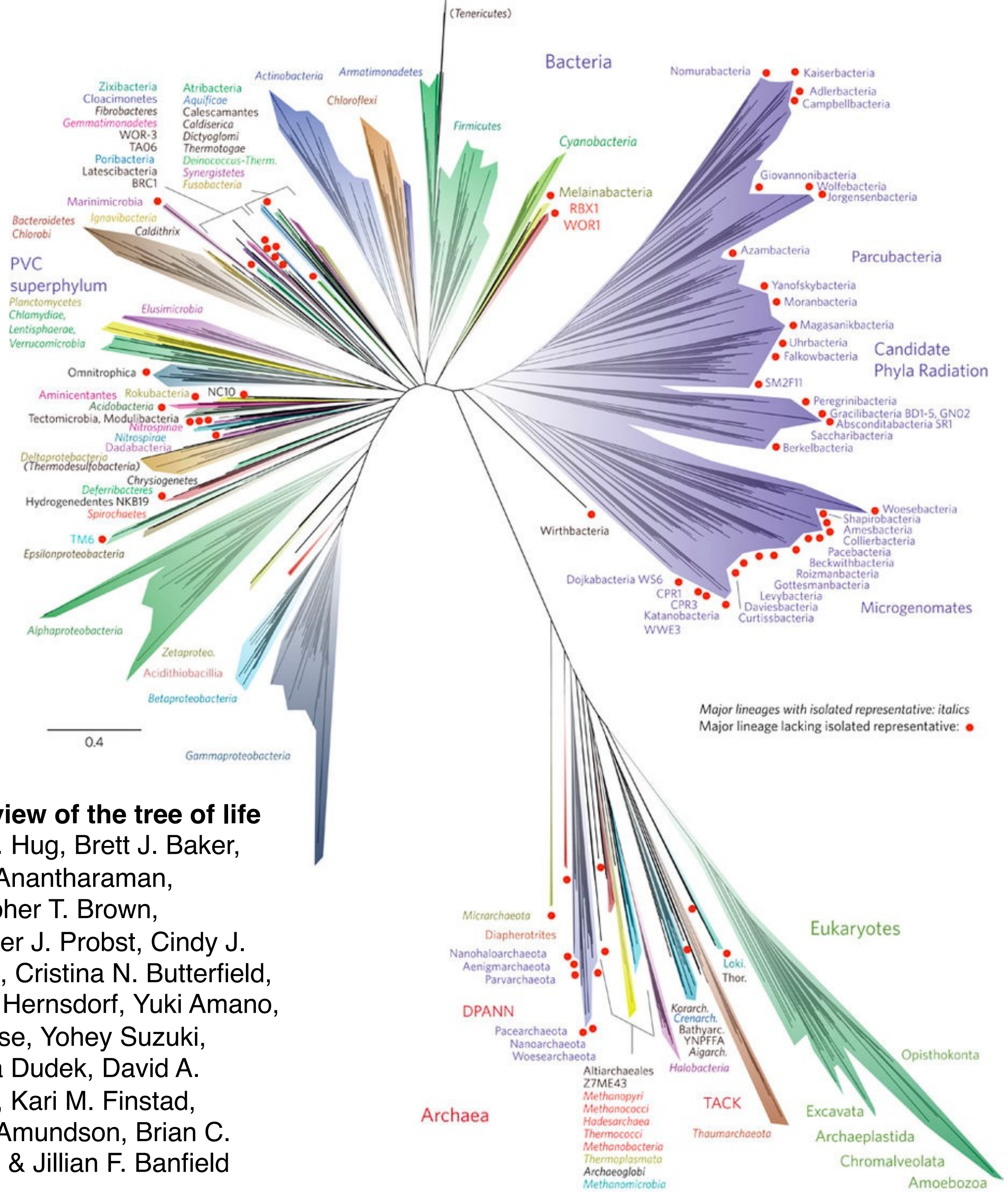
“Furthermore, CPR members have unique ribosomal features. While the members of CPR are generally uncultivable, and therefore missed in culture-dependent methods, they are also often missed in culture-independent studies that rely on 16S rRNA sequences. Their rRNA genes appear to encode proteins and have self-splicing introns,”

From Wikipedia



A new view of the tree of life
Laura A. Hug, Brett J. Baker, Karthik Anantharaman, Christopher T. Brown, Alexander J. Probst, Cindy J. Castelle, Cristina N. Butterfield, Alex W. Hernsdorf, Yuki Amano, Kotaro Ise, Yohey Suzuki, Natasha Dudek, David A. Relman, Kari M. Finstad, Ronald Amundson, Brian C. Thomas & Jillian F. Banfield

One of the hardest problems is to map this phylogenetic (i.e. evolutionary structure) to function.

Yes, the old structure – function problem

Only in very few cases we find a (close to) 1:1 mapping between clades and function

For example, oxygenic photosynthesis and cyanobacteria, methanogenesis and *archaea.*

It's generally unclear at what level of phylogenetic resolution one should describe communities

Outlook: peeling the onion

Wherever there is a source of energy that can sustain life, you will find a microbe (bacteria and archaea) using it.

Microbes have coevolved with the planet

Bioenergetics provides the first level explanation of the distribution, abundance and activity of microbial metabolisms

Outlook: peeling the onion

Metabolic constrains, physiological trade-offs, etc. explain (some) of the apparent division of metabolic labor among species of microbes

– this is an exciting research frontier and a great of arena for those interested in finding general principles that govern evolution.

Outlook: however, diversity and function

However, bioenergetics and division of metabolic labor are not sufficient to deal with the extraordinary diversity of microbes

What processes generate and maintain diversity? E.g. viral predation, spatial structure and behaviors, inter-species interactions, selfish genetic elements, etc., etc.

Is diversity irrelevant for function? How to interpret microbial community composition in terms of function?

Outlook: omics, a blessing and a curse

Focusing on microbes as a way to understand ecology and evolution, a challenge is to move from idiosyncratic descriptions of systems (e.g. how many species microbes live on my shower curtain, for example), to generalizable principles

Microbiology has been built on model organisms, disconnected from the environments where they once lived.

This has been great to learn molecular biology and physiology, but at the cost of learning how those molecular features play out in the environment.