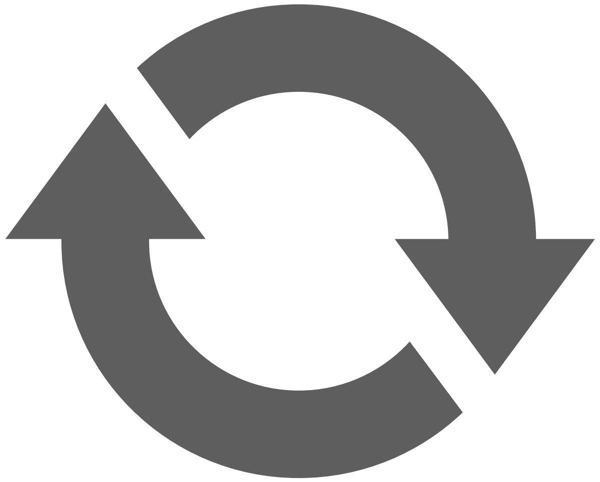
L08b

Symbiosis

- **Mutualism**
- **Parasitism**
- **Commensalism**

Dysbiosis



Holobiont

Symbiosis

- **Symbiosis:** An association between two dissimilar (or similar) (micro or macro-) organisms that have some degree of physical association, which is potentially long lasting, regardless of the implications for the fitness of either organism —> **living together**

Symbiosis

- **Parasitism:** An antagonistic symbiotic relationship in which one species is harmed, while the other benefits
- **Mutualism:** A symbiotic relationship in which both interacting species benefit, or are perceived to benefit. Benefit is often only confirmed empirically for the host symbiosis, in which the organisms are involved in a normal metabolic and immune signaling interactions
- **Commensalism**: A symbiotic relationship in which only one of interacting species benefit, or is perceived to benefit.

Dysbiosis

- ***Dysbiosis:*** *A status in which the relationship or interactions are heavily altered, possibly related to a major stress or infection event, are reversible (unhealthy state of the organisms), antonym is* ***Eubiosis***

- ***Dysbiosis*** *can cause/worsen a* ***disease***

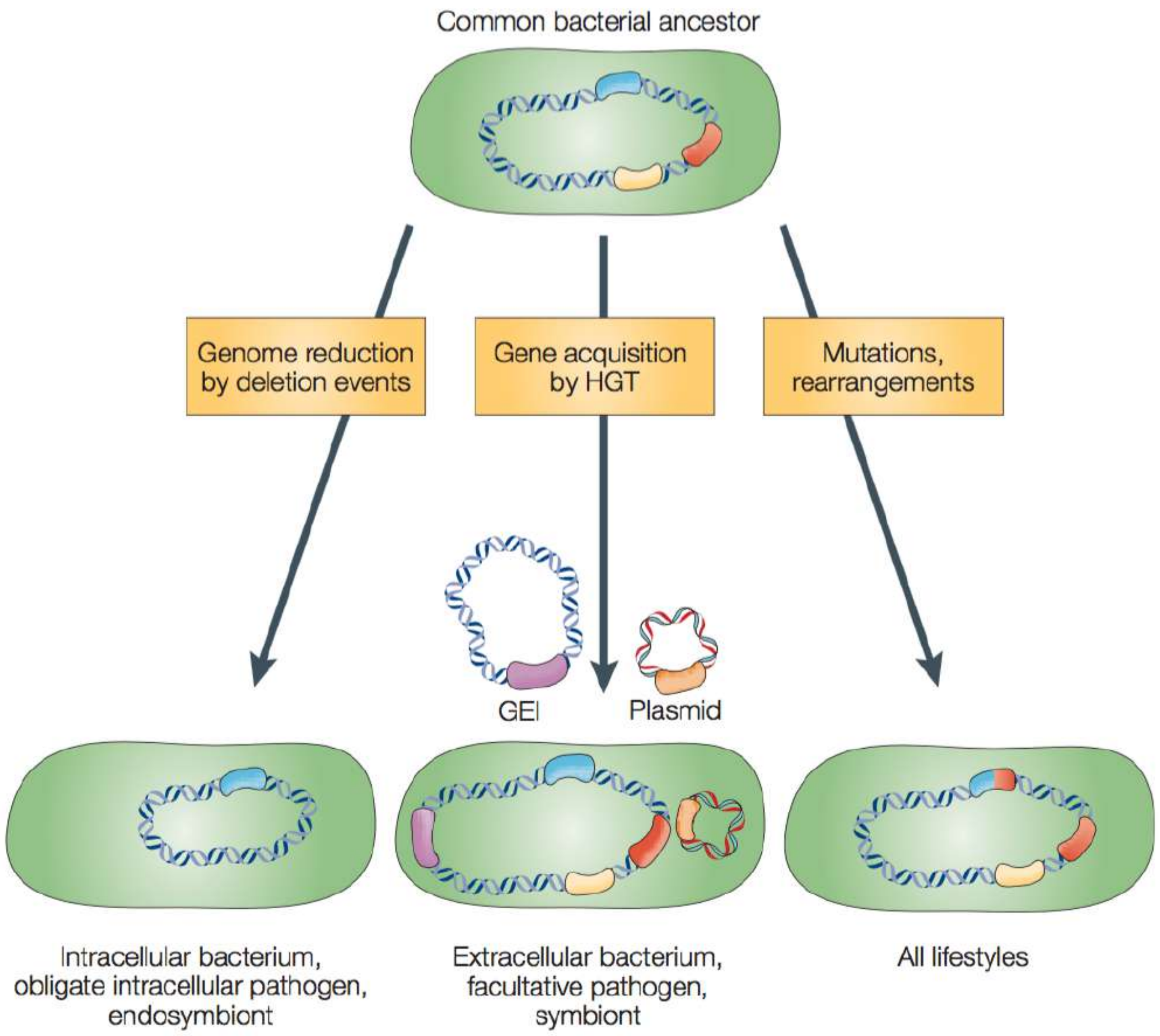
Holobiont

- From a non-biologist perspective, a holobiont can be thought of as a complex and interconnected system of organisms living in close association with each other
- *A **holobiont** is not a single organism but rather a collection of different species of organisms, including the host organism and various microorganisms (bacteria, archaea, viruses, fungi) that live within and on the host organism*
- *These microorganisms are not just passive inhabitants but are **actively** involved in various aspects of the **host biology**, including their digestion, immune responses, and even behaviour*

Symbiosis in the light of evolution

Origins many millions of years ago and have evolved to benefit the physiology of both partners, a process called **coevolution** —> **obligate symbiosis**

Obligate symbiosis: Streamlined genomes: retain only genes required for host fitness and essential molecular processes, such as translation, replication, and transcription



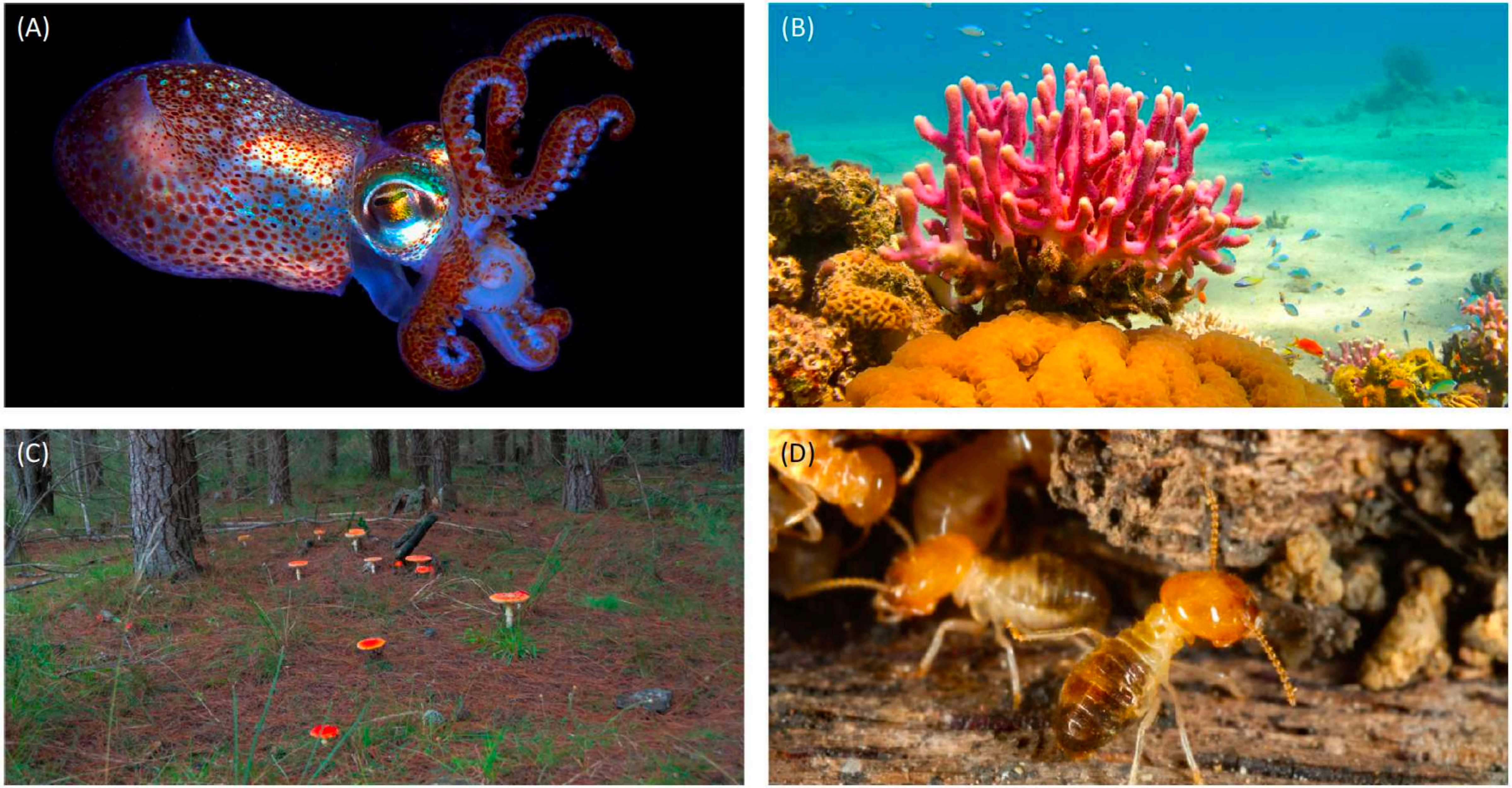
Dobrindt et al., 2004

Symbiosis lexicon

- **Parasites** are microorganisms that benefit **at some expense to the host**
- **Pathogens** actually cause a **disease** in the host
- **Commensals** have **no discernible effect** on the host
- **Mutualists are beneficial to the host**
- **Mutualistic microorganisms** as intimate **evolutionary partners** that influence both the evolution and physiology of their hosts
- **Pluricellular organisms have developed specialised structure to garden the symbiotic microbes**

Symbiosis, II

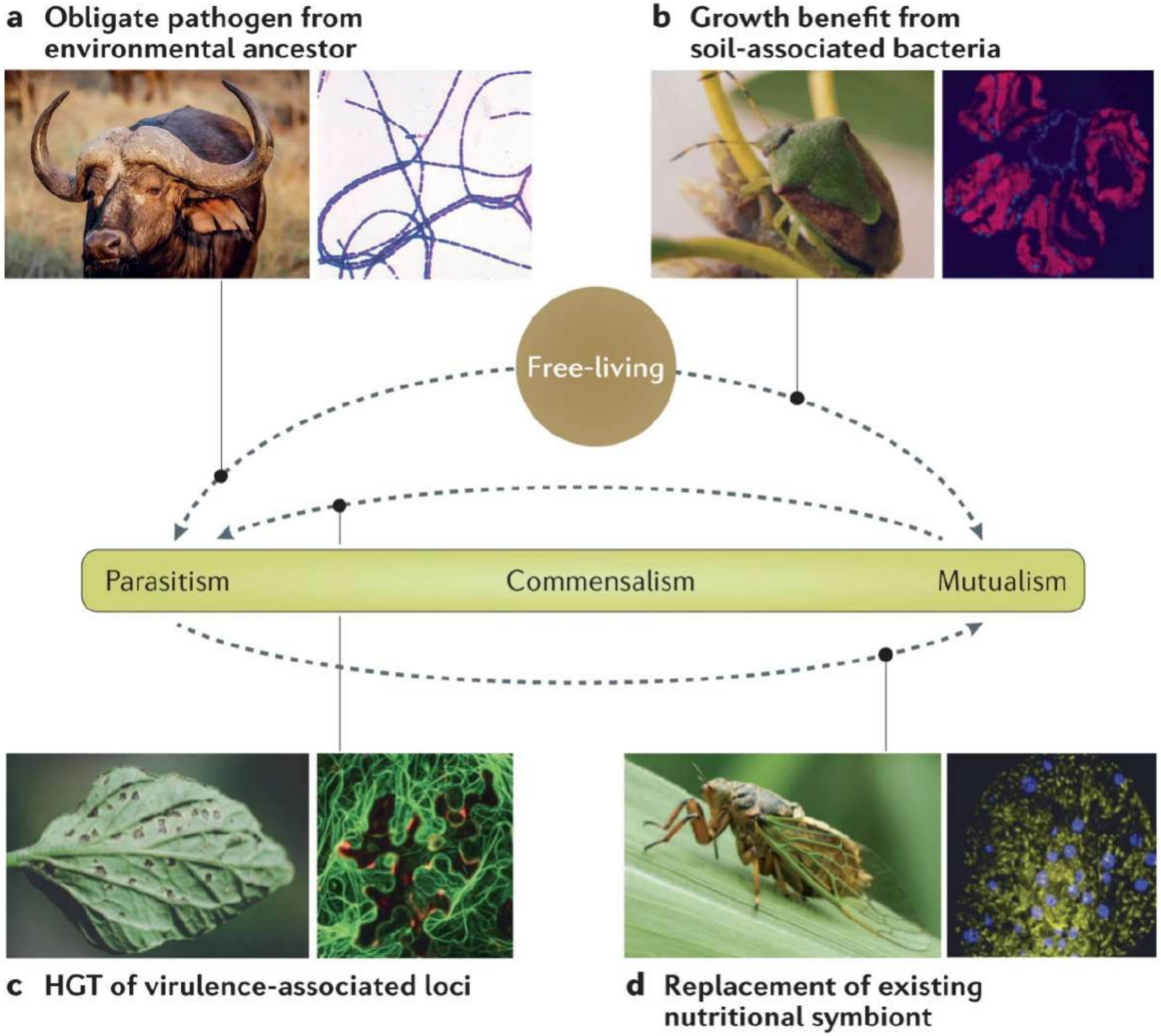
Stephens, 2022



Trends in Ecology & Evolution

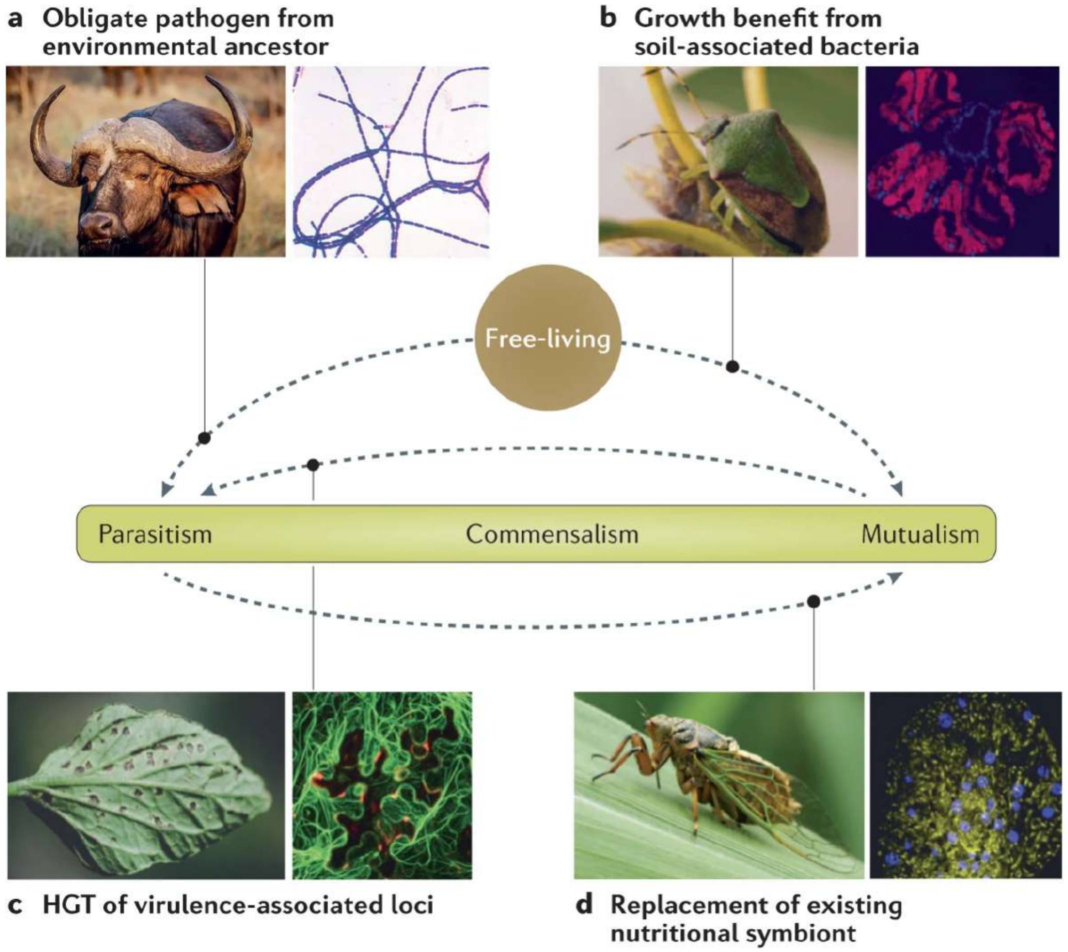
- Many hosts, both plants and animals, have **evolved specialized structures to filter and house beneficial microbes**
- Symbiotic organs share some core features linked to the **evolutionary maintenance of beneficial symbiosis**
- ‘Joint phenotypes’ have developed given the various selection pressures on symbiotic organs, including fitness feedbacks and conflicts between interacting genomes

Evolutionary transitions onto and along the parasite–mutualist continuum



Drew et al., 2021

Legend



a. Evolution of parasitic species in the *Bacillus cereus* group (for example, the causative agent of anthrax) from soil-dwelling ancestors

b. Environmental *Pantoea* bacteria evolving obligate mutualistic roles in stink bug growth and development

c. The widespread plant parasite *Pseudomonas syringae* likely evolving from mutualistic ancestors, driven by horizontal gene transfer (HGT) of type III secretion systems

d. Entomopathogens taking over the metabolic role of an ancient and degraded endosymbiont in cicadas

Drew et al., 2021

Holobiont

Coral
Sponge
Seagrass

Human
Mycorrhizae
Seagrass and plants
& Trees

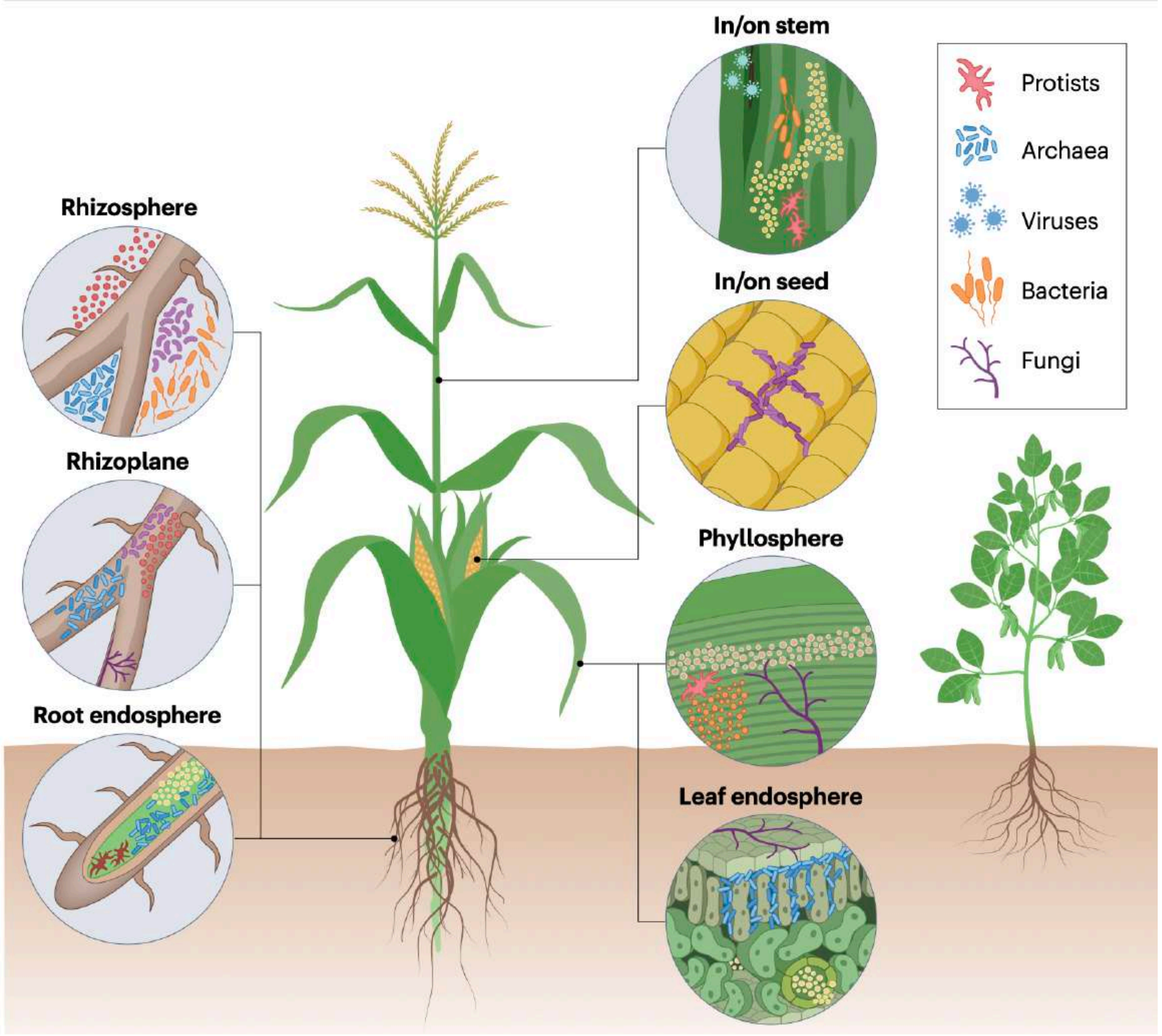
Case studies:

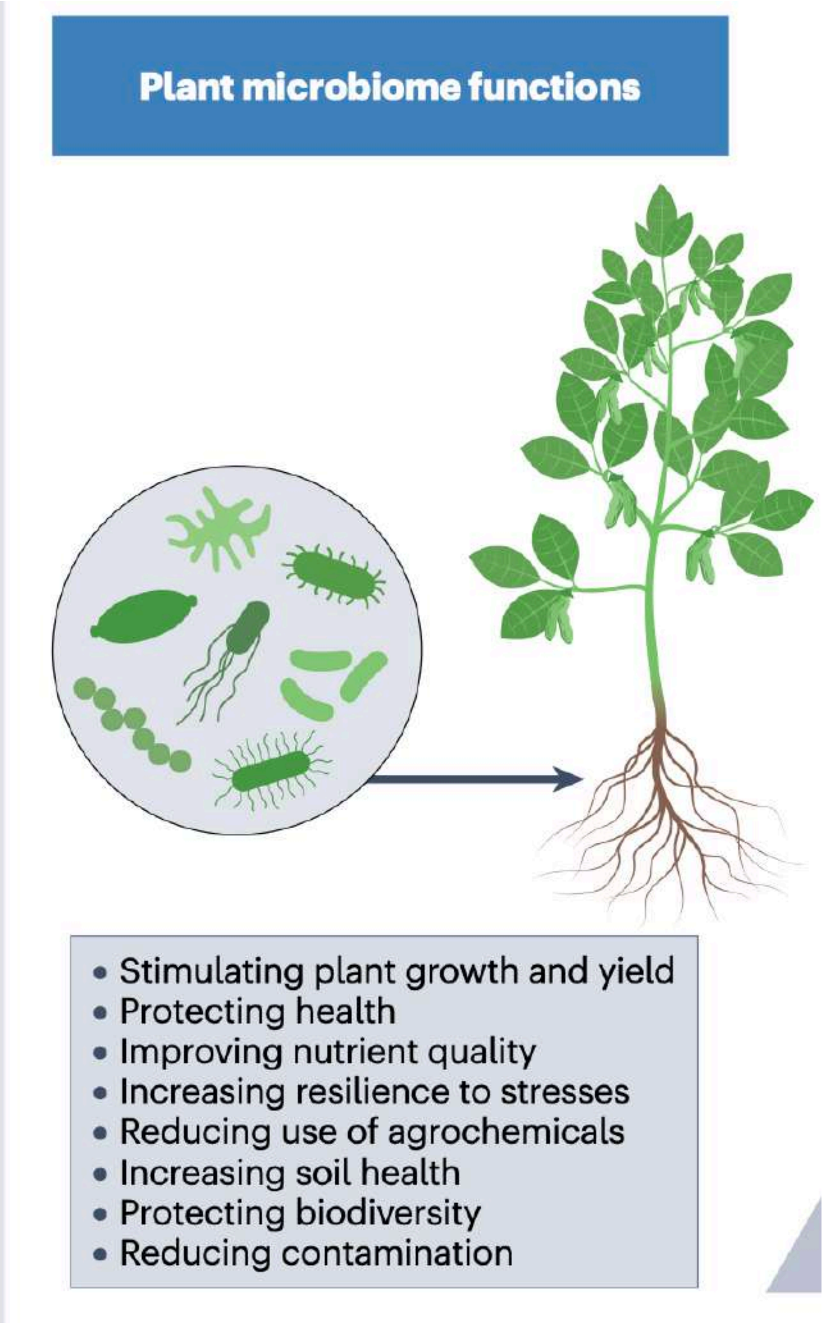
0. Plants and Trees
1. Legume-Root Nodule
2. Lichen
3. Mycorrhizae
4. Hydrothermal vent chemolithotrophs and their animal hosts
5. Bobtail squid and *Aliivibrio fischeri*
6. Gut microbiota - Thermites and Mammals
7. Humans

U= nutritional
B= behaviour
Strawberry= gutless
Orange= light energy

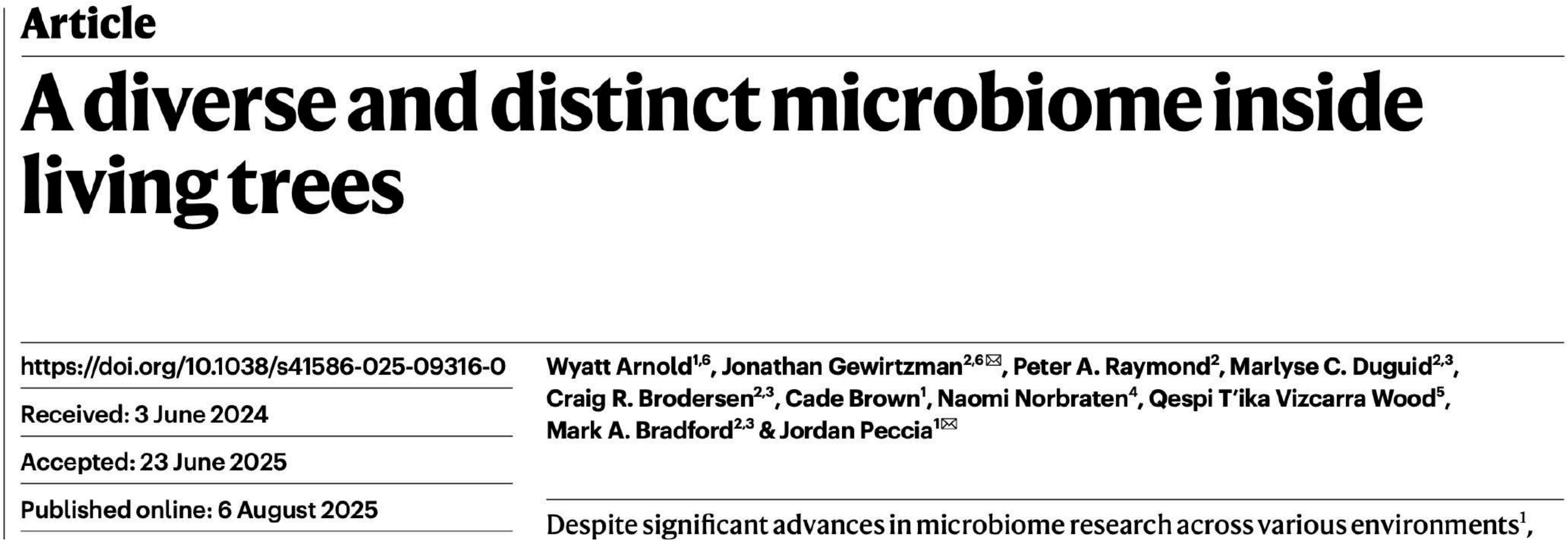
Plants

Compant et al., 2024





- Stimulating plant growth and yield
- Protecting health
- Improving nutrient quality
- Increasing resilience to stresses
- Reducing use of agrochemicals
- Increasing soil health
- Protecting biodiversity
- Reducing contamination



Article

A diverse and distinct microbiome inside living trees

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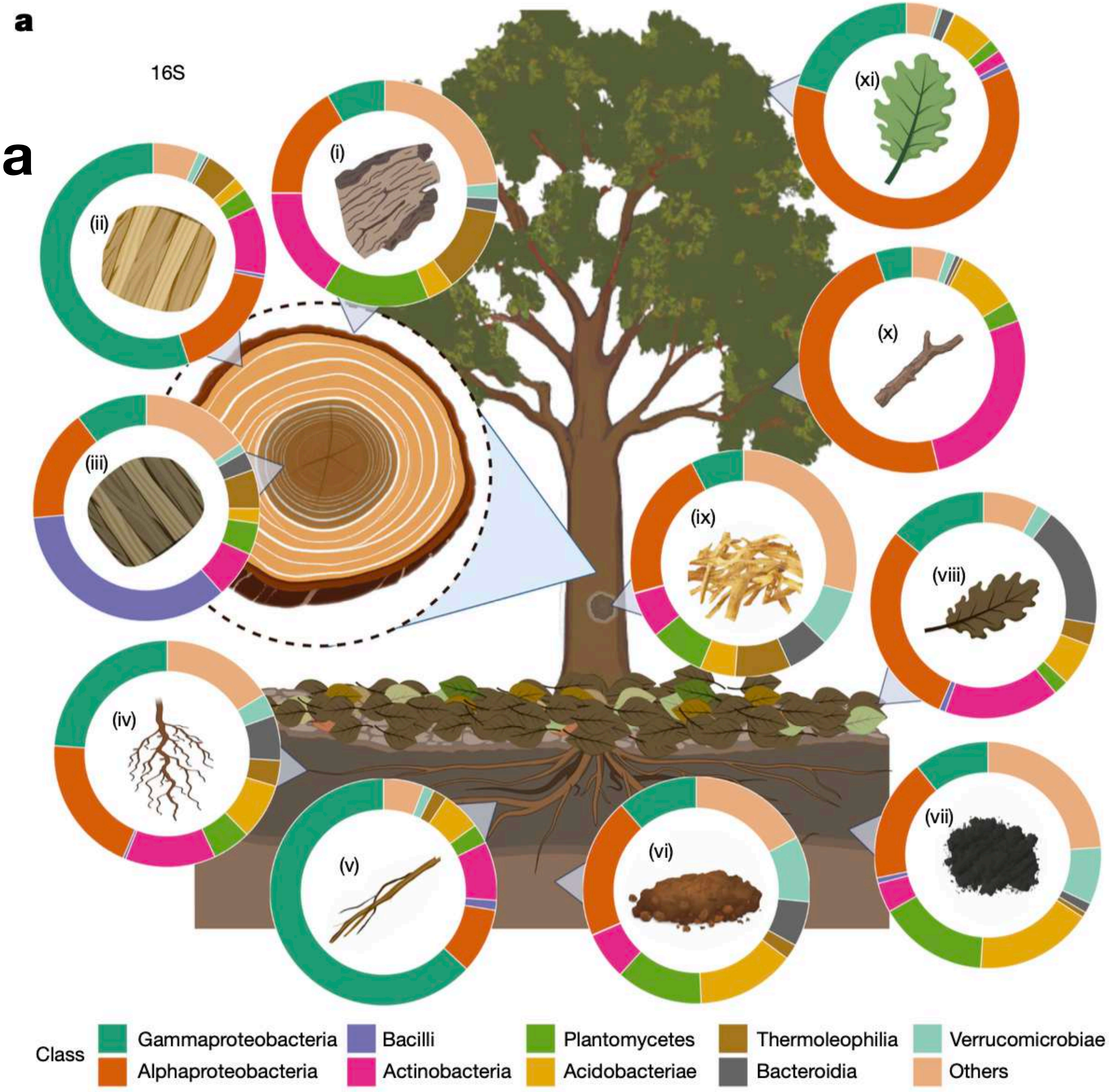
Wyatt Arnold[1,6], Jonathan Gewirtzman[2,6]✉, Peter A. Raymond[2], Marlyse C. Duguid[2,3], Craig R. Brodersen[2,3], Cade Brown[1], Naomi Norbraten[4], Qespi T'ika Vizcarra Wood[5], Mark A. Bradford[2,3] & Jordan Peccia[1]✉

Despite significant advances in microbiome research across various environments[1],

As we examined a range of species with variable patterns of heartwood formation, we operationally defined ‘heartwood’ as the innermost 5 cm of wood tissue and ‘sapwood’ as the outermost 5 cm of wood tissue

Despite a general lack of difference between tissues, two species, Acer saccharum (red maple) and *Betula lenta* (black birch), showed significantly higher prokaryotic abundances in their heartwood, whereas three species, *Fraxinus americana* (white ash), *Pinus strobus* (Eastern white pine) and *Quercus rubra* (red oak), showed significantly higher prokaryotic abundances in their sapwood (Wilcoxon signed-rank, $P < 0.05$, two-sided)

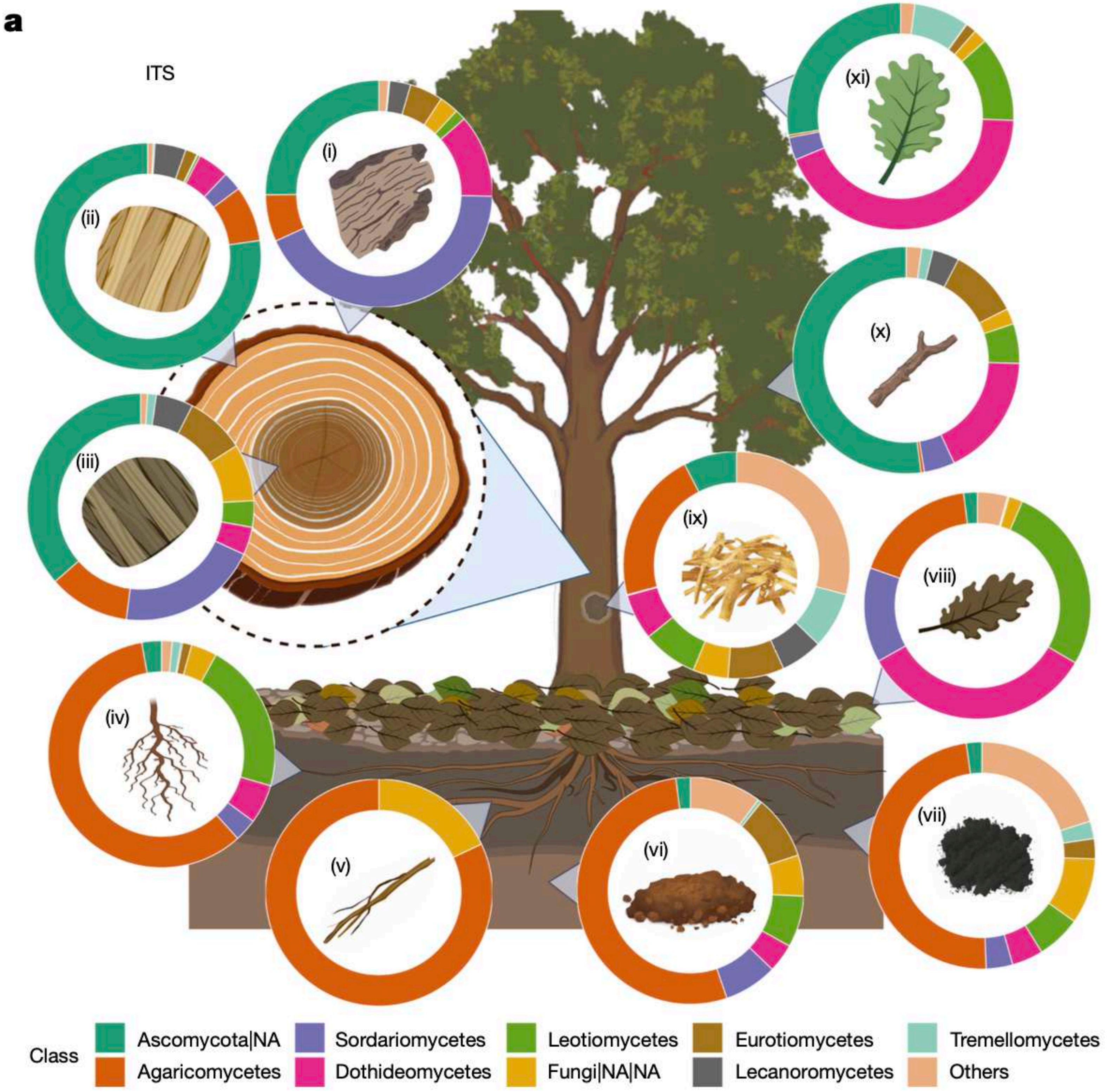
Bacteria + Archaea



Arnold et al., 2025

In the bark (i), sapwood (ii), heartwood (iii), fine roots (iv), coarse roots (v), mineral soil (vi), organic soil (vii), leaf litter (viii), heart rot (ix), branches (x) and leaves (xi).

Fungi



Arnold et al., 2025

in the bark (i), sapwood (ii), heartwood (iii), fine roots (iv), coarse roots (v), mineral soil (vi), organic soil (vii), leaf litter (viii), heart rot (ix), branches (x) and leaves (xi)

Legume-Root Nodule Symbiosis
Lichen
Mycorrhizae

Legume-Root Nodule Symbiosis

- Partners in a symbiosis are called **symbionts, and most nitrogen-fixing bacterial symbionts of plants are collectively called rhizobia**, derived from the name of a major genus, *Rhizobium*
- Species of rhizobia are *Alpha*- or *Betaproteobacteria* that can grow freely in soil or infect leguminous plants and establish a symbiotic relationship
- The same genus (or even species) of legume can contain both rhizobial and non-rhizobial strains
- **Infection of legume roots by rhizobia** leads to the **formation of root nodules** in which the bacteria **fix gaseous nitrogen (N_2)**
- Nitrogen fixation in root nodules accounts for **a fourth of the N_2 fixed annually on Earth** and is of enormous agricultural importance, as it increases the fixed nitrogen content of soil
- Rhizobia can fix N_2 when grown in pure culture under microaerophilic conditions (a low-oxygen environment is necessary because the key nitrogen-fixing enzyme, called **nitrogenase**, is inactivated by high levels of O_2)
- In nodule, **O_2 levels** are precisely controlled by the **O_2-binding protein leghemoglobin** (Fe-containing protein induced through the interaction of the plant and bacterial partners)
- **Specificity in association**

Root Nodule Formation

1. **Recognition** of the correct partner by both plant and bacterium and attachment of the bacterium to the root hairs
2. **Secretion of oligosaccharide signalling molecules (Nod factors) by the bacterium**
3. **Bacterial invasion** of the root hair
4. **Movement of bacteria** to the main **root** by way of the **infection thread**
5. **Formation of modified bacterial cells (bacteroids) within the plant cells**, development of the **N_2-fixing state**, and continued plant and bacterial cell division forming the mature **root nodule**

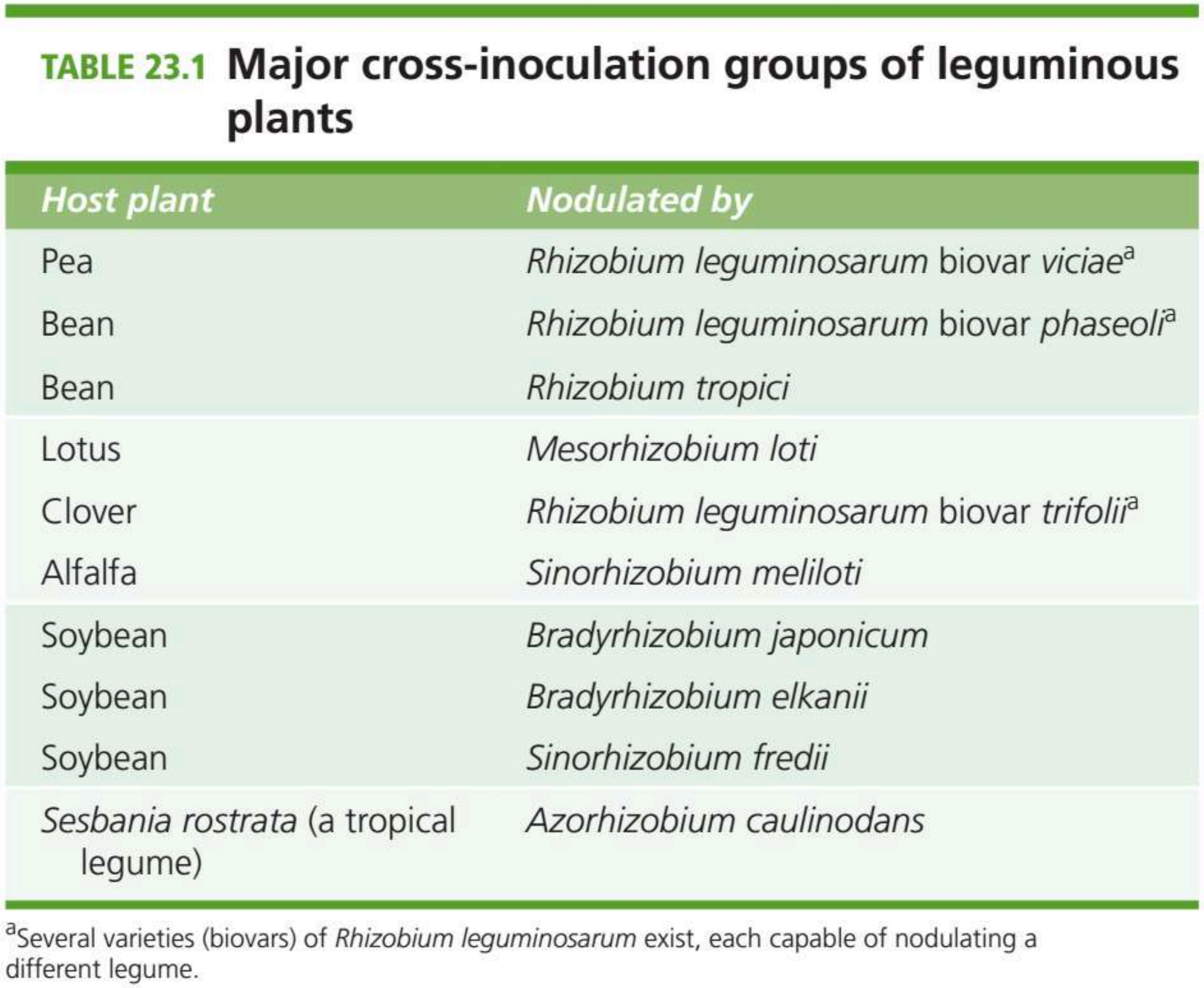


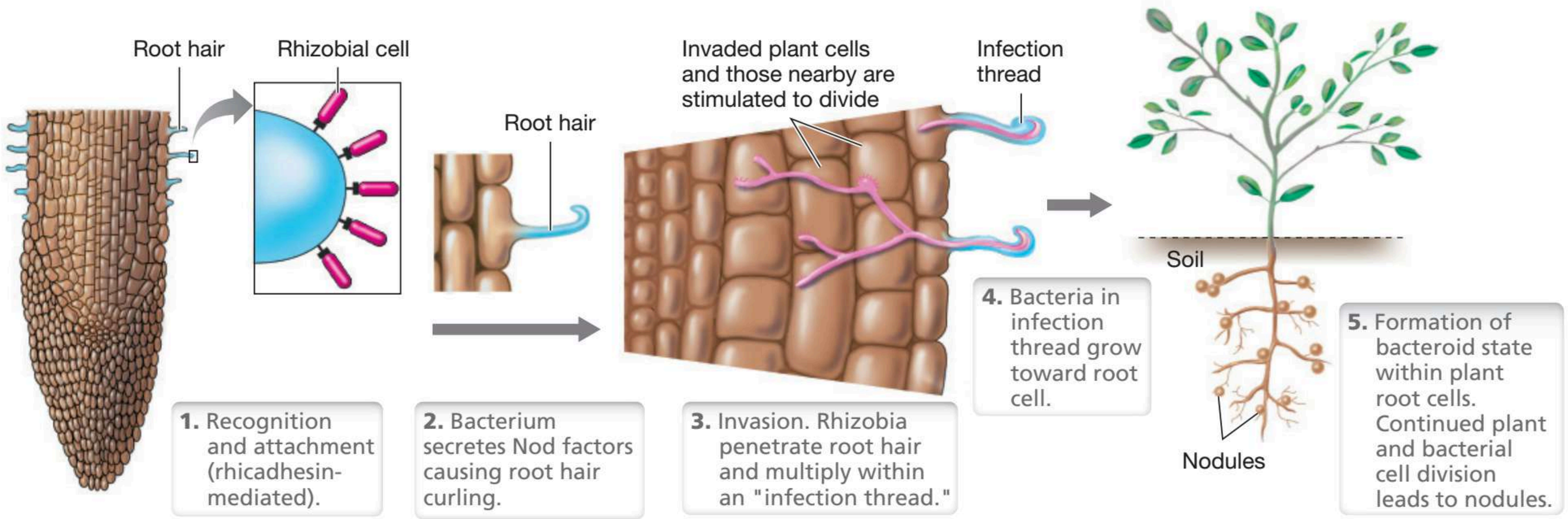
TABLE 23.1 Major cross-inoculation groups of leguminous plants

Host plant	*Nodulated by*
Pea	*Rhizobium leguminosarum* biovar *viciae*[a]
Bean	*Rhizobium leguminosarum* biovar *phaseoli*[a]
Bean	*Rhizobium tropici*
Lotus	*Mesorhizobium loti*
Clover	*Rhizobium leguminosarum* biovar *trifolii*[a]
Alfalfa	*Sinorhizobium meliloti*
Soybean	*Bradyrhizobium japonicum*
Soybean	*Bradyrhizobium elkanii*
Soybean	*Sinorhizobium fredii*
Sesbania rostrata (a tropical legume)	*Azorhizobium caulinodans*

[a] Several varieties (biovars) of *Rhizobium leguminosarum* exist, each capable of nodulating a different legume.

Madigan et al. 2018

Root Nodule Formation



1. Recognition and attachment (rhicadhesin-mediated).

2. Bacterium secretes Nod factors causing root hair curling.

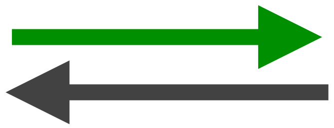
3. Invasion. Rhizobia penetrate root hair and multiply within an "infection thread."

4. Bacteria in infection thread grow toward root cell.

5. Formation of bacteroid state within plant root cells. Continued plant and bacterial cell division leads to nodules.

Madigan et al. 2018

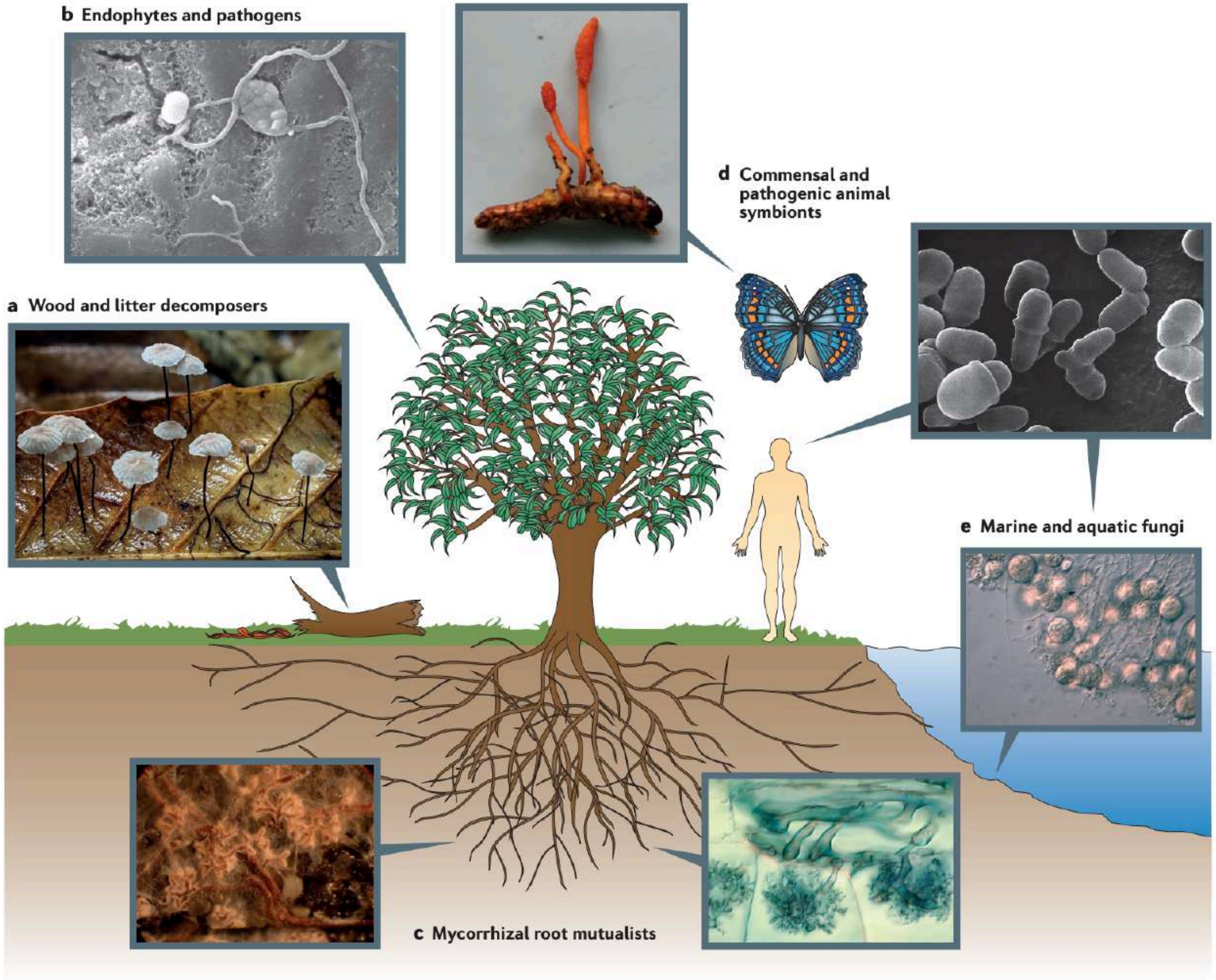
Sugar from photosynthesis



Glutamine & Asparagine from N_2 fixation

Mycobiome

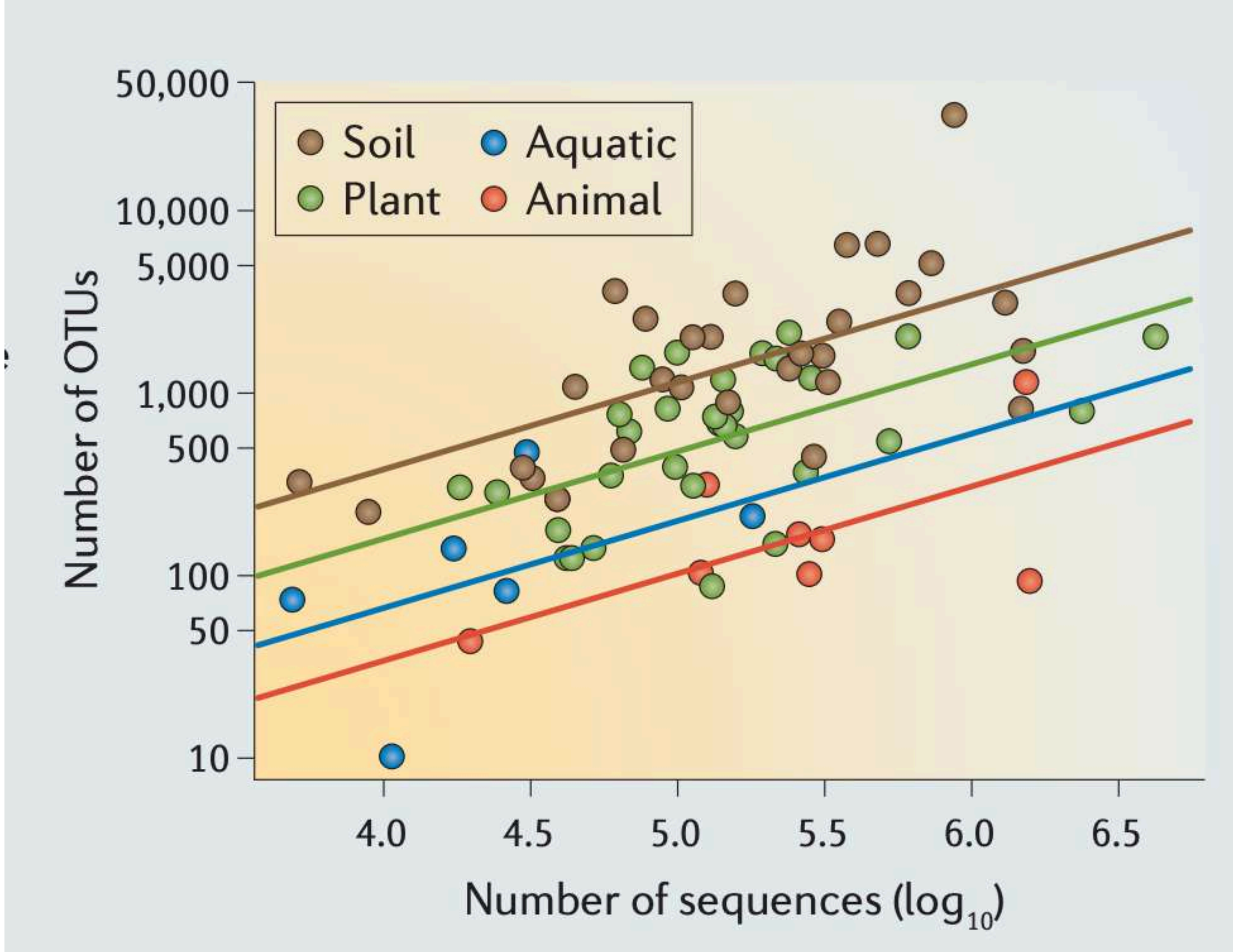
Peay et al., 2016



- **Fungi** are most **commonly associated** with terrestrial ecosystems, but can also be found growing on nearly any substrate on Earth, from deep ocean sediments to the human scalp

Mycobiome

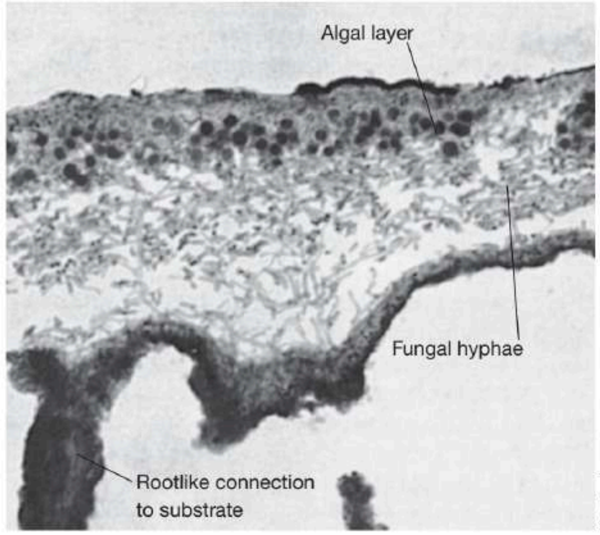
- Majority of fungal species are **saprotrophs that are capable of decomposing complex polymers**, such as cellulose and chitin, although individual species can **vary** considerably in both the **substrates** that they decompose and the **enzymatic pathways** that they use
- In terrestrial and freshwater systems, fungi can dominate the decomposition of plant **necromass**



Peay et al., 2016

https://courses.lumenlearning.com/microbiology/chapter/lichens/

Lichen

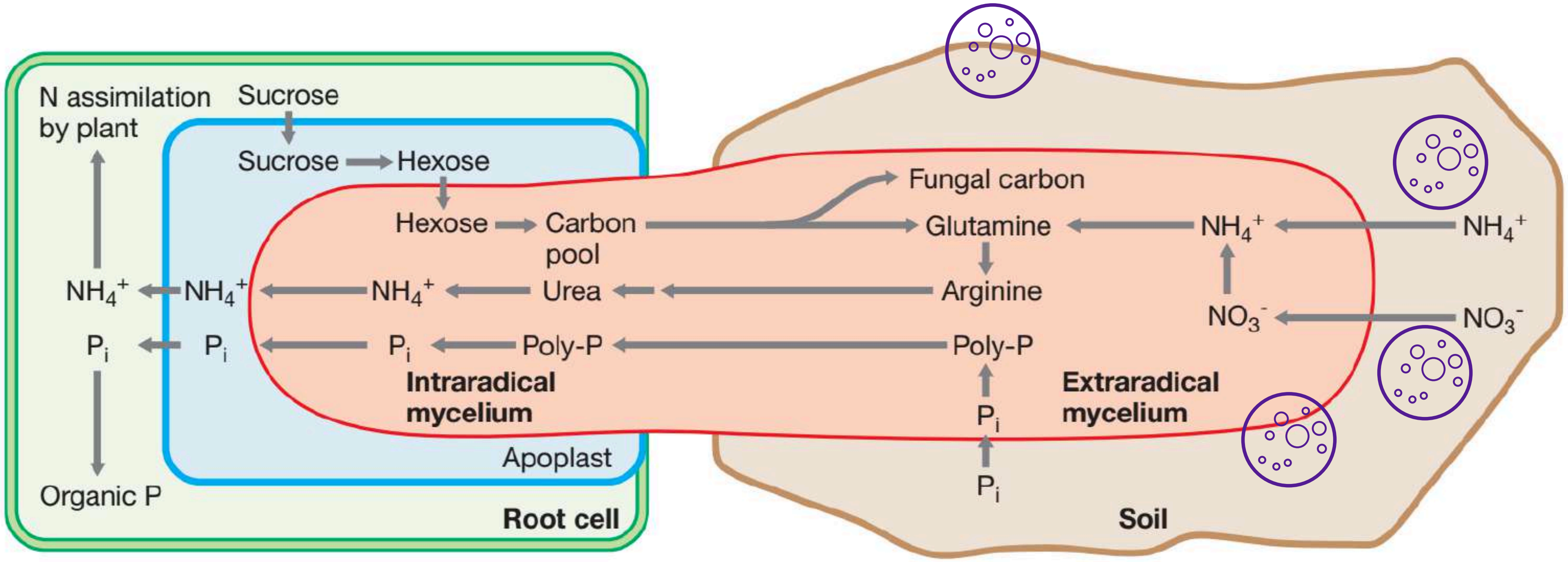


Madigan et al. 2018

- **A lichen** is a mutualistic association between two dominant microorganisms, a **fungus** (**constant humid environment, scavenging limiting elements by lichen complex organic acidic compounds**), usually an ascomycete **but many fungi** (**basidiomycete yeast**) and either an **alga or a cyanobacterium** (**photosynthesis**) but there are also **archaea** (**B12 and protection from toxic compounds**)
- **Morphology** of any given lichen is primarily **determined by the fungus**, and many fungi (more than 18,000 named species) are able to form lichen associations
- **Diversity among the phototrophs is much lower**, and thus many different kinds of lichens have the same phototrophic partner, some N_2 fixation
- **Lichen acids**, **complex organic compounds secreted by the fungus, promote the dissolution and chelation of inorganic nutrients from the rock or other surface** that are needed by the **phototroph**
- **Fungus protects** the phototroph from drying most of the habitats
- **Dry habitats**, fungi tolerate better than phototrophs
- The fungus actually **facilitates the uptake of water**
- Lichens typically **grow quite slowly**

Mycorrhizae

- **Mycorrhizae are symbiotic relationship between plant roots and fungi** in which nutrients are transferred in both directions, ~450 million years ago
- Over 80% of land plants (>250 000 plant species), from the Greek words for fungus and root
- Fungus and associated- microbes transfer inorganic nutrients—in particular, phosphorus and nitrogen—from soil to plant
- Plant transfers primarily carbohydrates to fungus and associated microbes
- Mycorrhizal fungi are crucial components of the plant microbiota and are key actors in terrestrial ecosystems, where they facilitate the exchange of carbon (C) and minerals
- Interacting with various plants mycorrhizal fungi provide multiple ecological services in natural and agricultural environments



Associated microbes

Madigan et al. 2018

Sugar from photosynthesis →

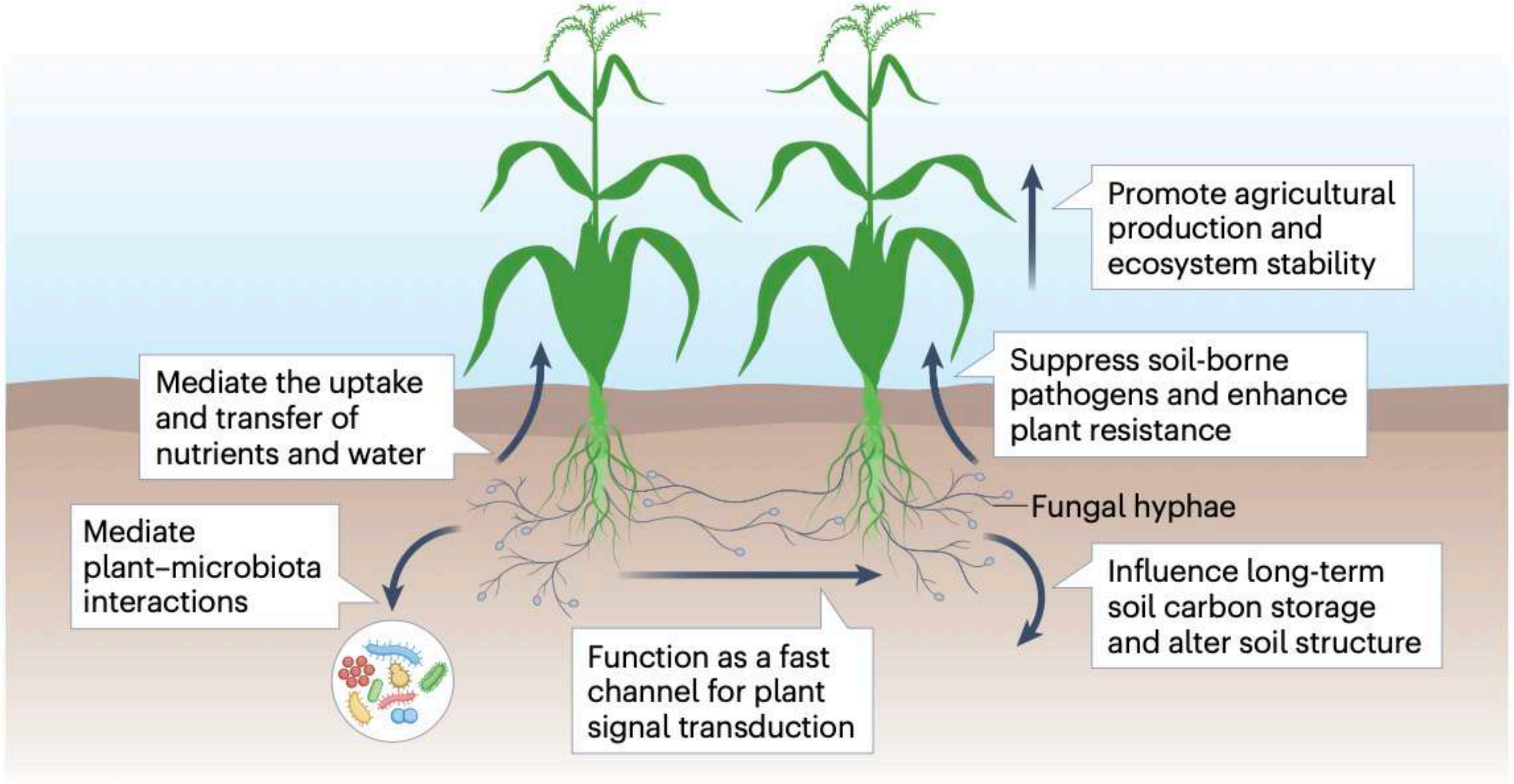
← **Nutrients from soil**

Mycorrhizae

- **Ectomycorrhizal fungi** engaged in a mycorrhizal symbiosis that is characterized anatomically by fungal hyphae that **wholly enclose the fine roots of the tree host**. Ectomycorrhizal fungi include diverse species from the Basidiomycota and Ascomycota phyla. **Some ectomycorrhizal fungi are involved in organic matter decomposition**.
- **Ectomycorrhizae, fungal cells form an extensive sheath (fungal mantle) around the outside of the root** with only a slight penetration into the root cellular structure (**roots of forest trees, especially conifers, beeches, and oaks, and are most highly developed in boreal and temperate forests**)—> **single species of tree** can form **multiple** mycorrhizal associations
- **Ectomycorrhizal mycelia to interconnect trees**, providing linkages for transfer of carbon and other nutrients between trees of the same or different species —> Nutrient transfer from well-illuminated overstory plants to shaded trees is thought to help **equalize resource availability**, subsidizing **young trees** and **increasing biodiversity** by promoting the **coexistence** of different species

Major features of AMF and their implications for ecosystems

- **Endomycorrhizae, a part of the fungus becomes deeply embedded within cells** comprising the root tissue, very **diverse**, some are **arbuscular mycorrhizae** (AM colonize **70–90% of all terrestrial plants**, including most **grassland** species and many **crop** species).
- AM Fungi that form a mycorrhizal symbiosis with a plant host. This is typical for certain trees and most non woody plants and is characterized **by fungal hyphae that penetrate plant cell walls, where they form highly branched structures known as arbuscules**. AM belong to a single **monopyhyletic** lineage of Glomeromycota. **They are not able to decompose biopolymers.**



Duan et al. 2024

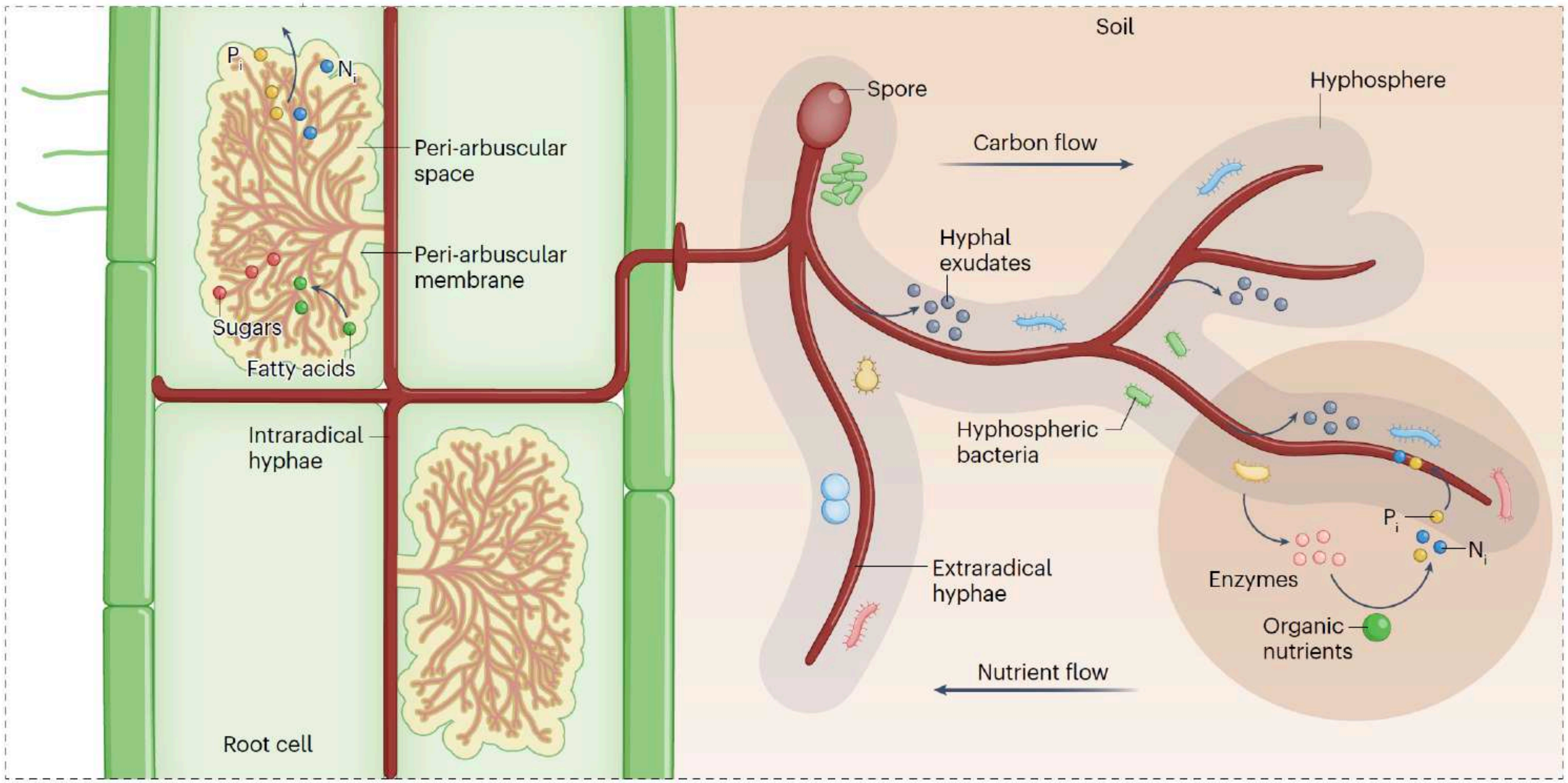
Chemical and spatial tight coupling in Plant-AM-microbe

- In AMF symbioses, **plants provide photosynthetically fixed C (including lipids and sugars) in exchange for minerals, especially phosphorus (P) and nitrogen (N)**

- **Moreover, AMF hyphae grow within and extend outside the plant root; the thin soil layer that surrounds these extraradical hyphae (ERH) forms a specialized niche called the' hyphosphere' .**

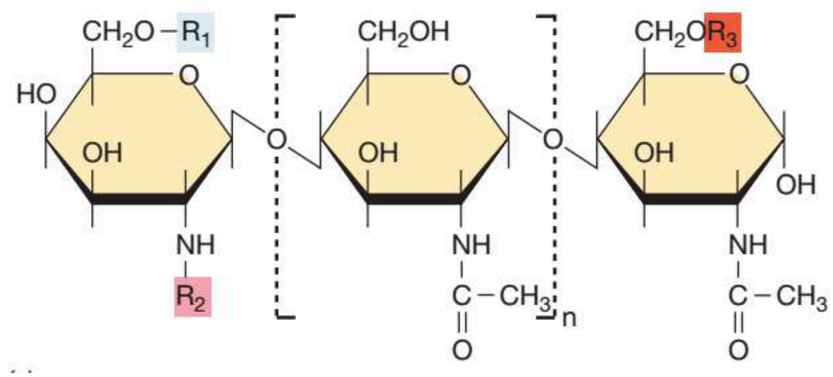
- This niche hosts a plethora of hyphospheric bacteria/microbes that feed on fungal metabolites that contain plant-derived C.

- **In return, the bacteria support the mineral nutrition of AMF by secreting extracellular enzymes, as AMF cannot decompose polymer nutrients owing to their limited saprotrophic capability**



Duan et al. 2024

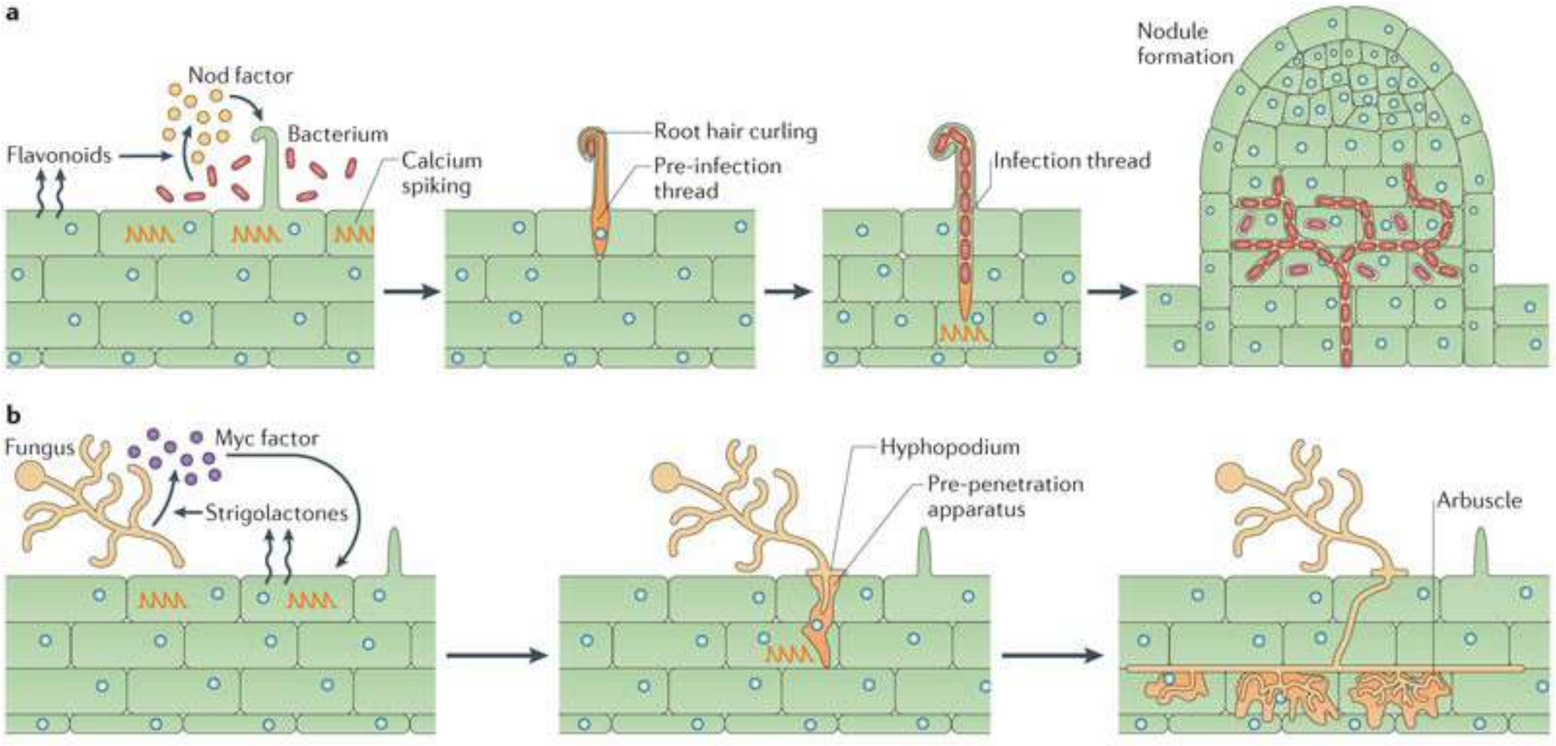
Nod & Myc Factors for chemical communication



Madigan et al. 2018

Rhizobial or AM fungus species	R_1	R_2	R_3
Sinorhizobium meliloti (alfalfa)	Ac	C16:2 or C16:3	SO_3H
Rhizobium leguminosarum biovar *viciae* (pea)	Ac	C18:1 or C18:4	H or Ac
Glomus intraradices (many agricultural crops)	H	C16 or C16:1 or C16:2 or C18 or C18:1Δ9Z	H or SO_3H

- **Nod & Myc factors are lipochitin** oligosaccharides to which various substituents are bonded that function as primary **rhizobial /mycorrhizal signaling molecules triggering** legumes/plant to develop either new plant organs: **root nodules** that host the bacteria as nitrogen-fixing bacteroids to allow the **physical interaction** with the **mycelium and formation arbuscules inter-or intra-cellularly**



Nature Reviews | Microbiology

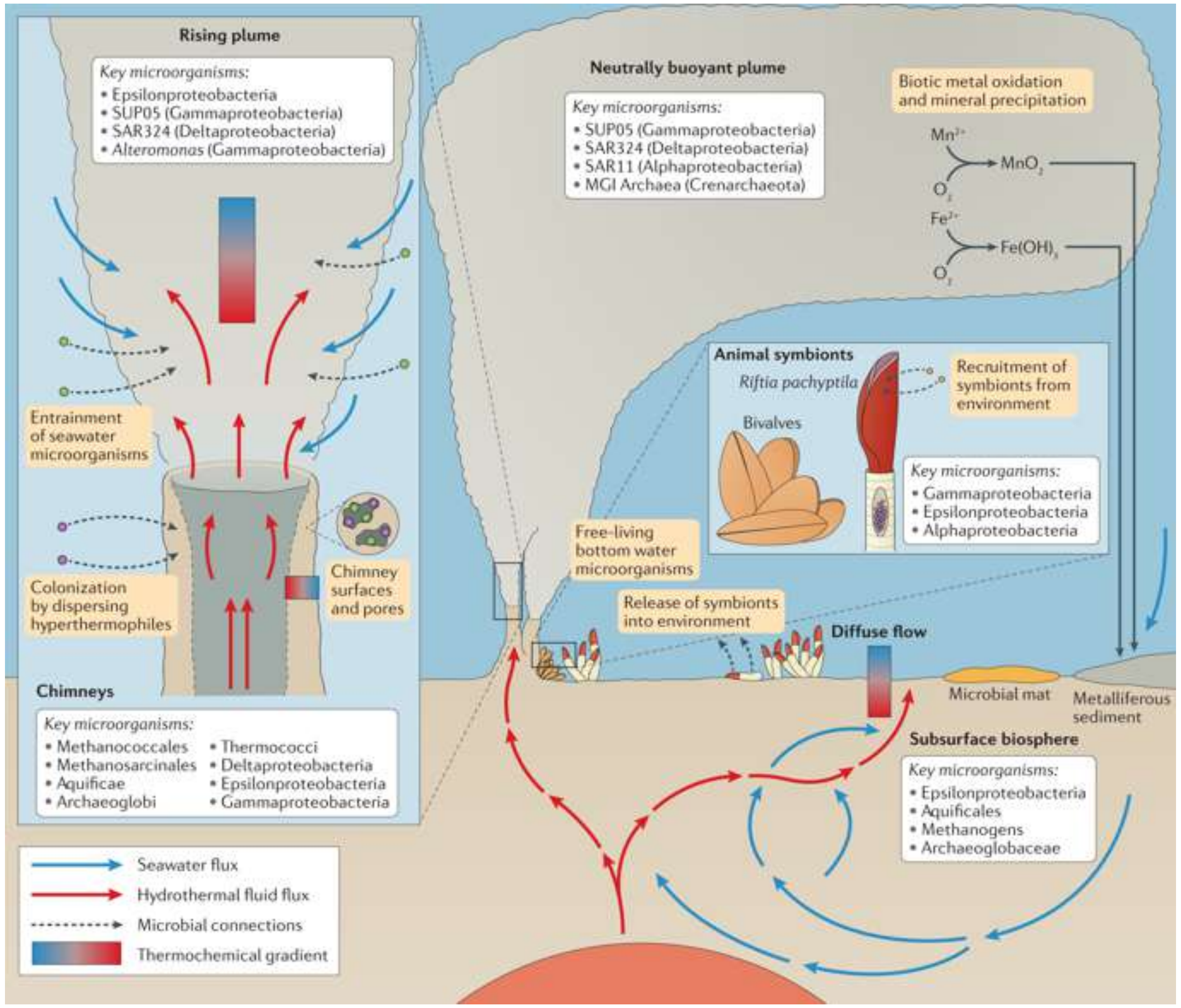
Oldroyd, 2013

Hydrothermal vent chemolithotrophs and their animal hosts

Bobtail squid and *Aliivibrio fischeri*

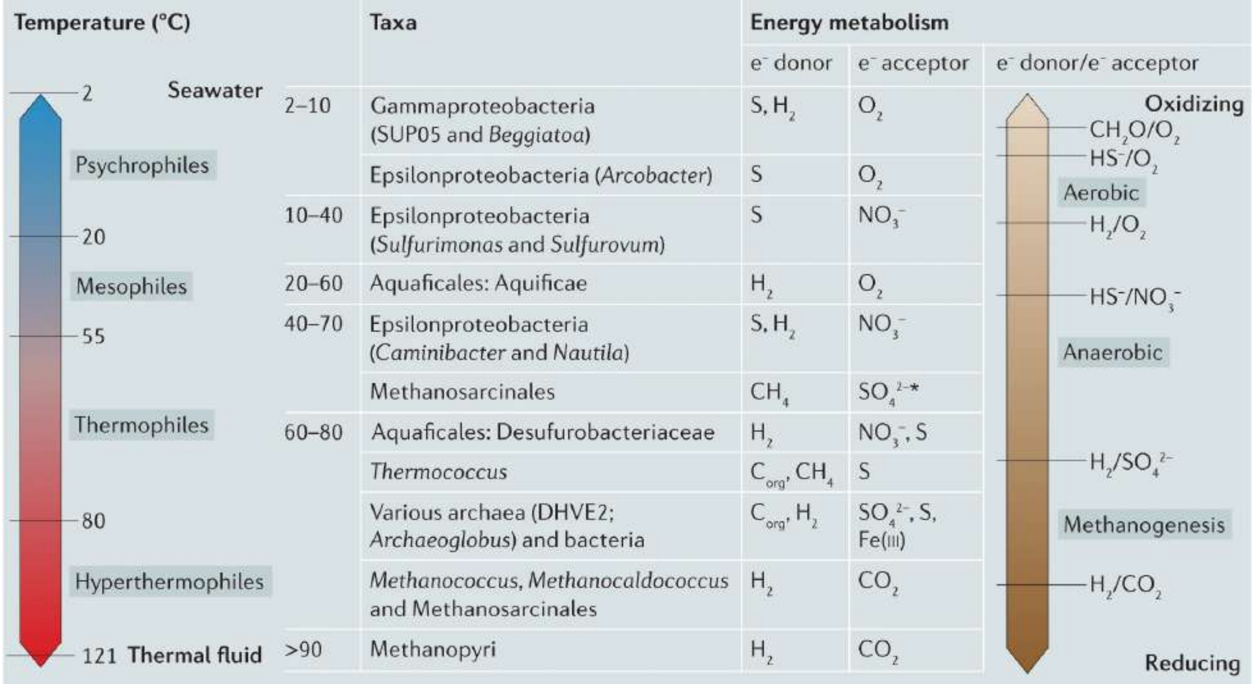
Hydrothermal vent chemolithotrophs and their animal hosts

- In a dark and cold ocean—> no photosynthetic C fixation —> **chemolithoautotrophy**
- Hydrothermal vents with **sharp contrasts in physical and chemical conditions** between these various habitats and their dynamic, **extreme** and **geographically isolated nature**
- **Hydrothermal fluids** contain large amounts of **reduced inorganic materials**, including H_2S, Mn^{2+}, H_2, and CO (carbon monoxide), and some vents contain high levels of ammonium (NH_4^+) instead of H_2S; all of these are **good electron donors for chemolithotrophs**
- **Mutualistic chemolithotrophs are either tightly attached to the animal surface (epibionts) or actually live within the animal tissues**, supplying organic compounds to the animals in exchange for a safe residence and ready access to the electron donors needed for their energy metabolism —> fix CO_2/biomass



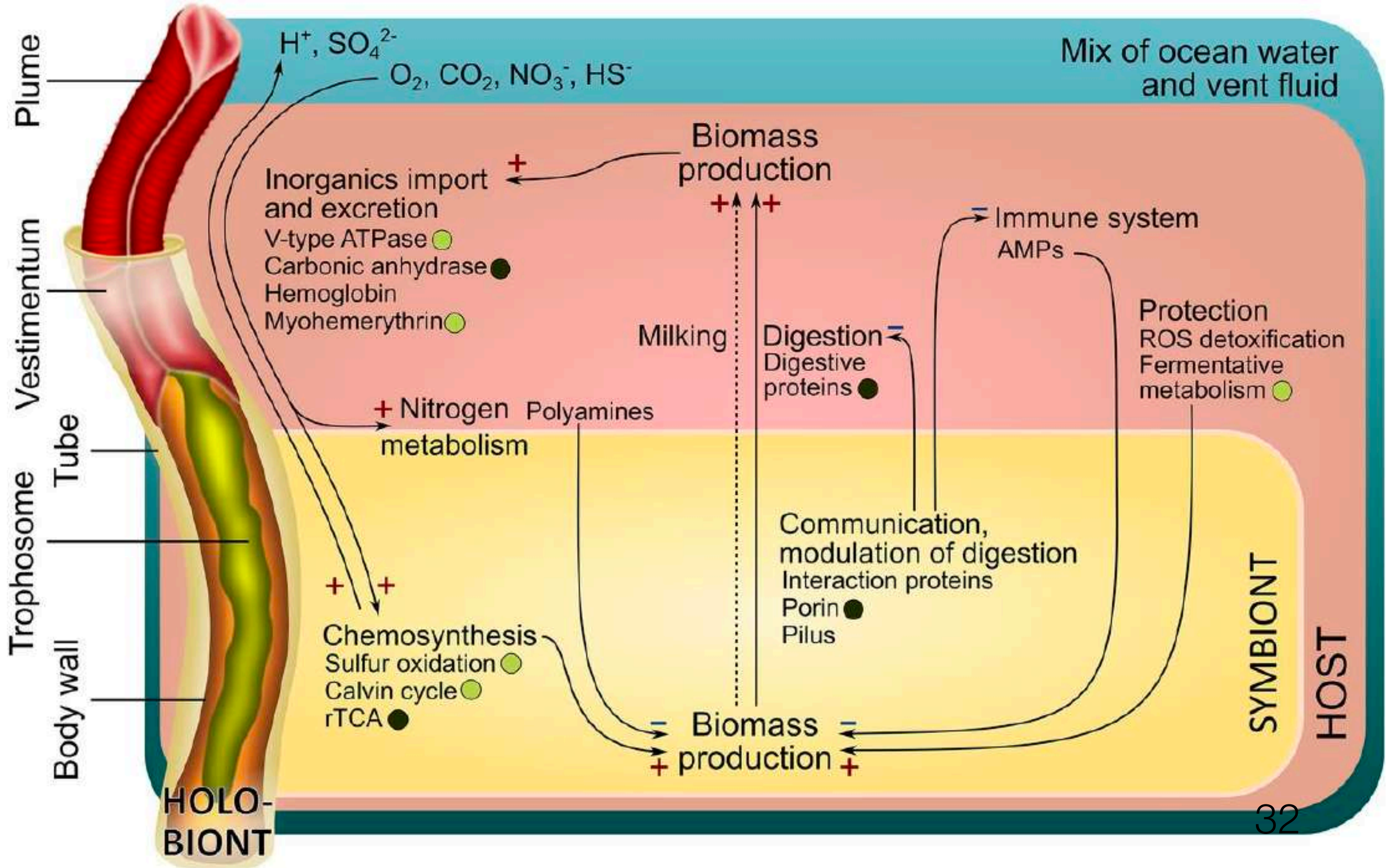
Dick, 2019

Biochemical REDOX coupling for primary production at vent sites



Temperature (°C)	Taxa	Energy metabolism: e⁻ donor	Energy metabolism: e⁻ acceptor
2–10	Gammaproteobacteria (SUP05 and *Beggiatoa*)	S, H_2	O_2
	Epsilonproteobacteria (*Arcobacter*)	S	O_2
10–40	Epsilonproteobacteria (*Sulfurimonas* and *Sulfurovum*)	S	NO_3^-
20–60	Aquificales: Aquificae	H_2	O_2
40–70	Epsilonproteobacteria (*Caminibacter* and *Nautila*)	S, H_2	NO_3^-
	Methanosarcinales	CH_4	SO_4^{2-}*
60–80	Aquificales: Desufurobacteriaceae	H_2	NO_3^-, S
	Thermococcus	C_{org}, CH_4	S
	Various archaea (DHVE2; *Archaeoglobus*) and bacteria	C_{org}, H_2	SO_4^{2-}, S, Fe(III)
	Methanococcus, *Methanocaldococcus* and Methanosarcinales	H_2	CO_2
>90	Methanopyri	H_2	CO_2

Dick, 2019



Hinzie et al., 2019

Riftia pachyptila:

- ★ Energy is obtain from oxidation of reduced inorganic compounds O_2
- ★ Electron donor: reduced inorganic compounds HS^-
- ★ Carbon sources: inorganic CO_2
- ★ Specialized structure where the symbiotic microbes live, trophhosome

Biochemical diversity for C fixation

Chemolithoautotrophic growth
The growth of bacteria or archaea using an inorganic, chemical source of energy (for example, reduced forms of iron, sulfur, hydrogen and ammonia) to fix inorganic carbon into organic carbon

Microbial Primary productivity

Reductive tricarboxylic acid cycle
(rTCA). A metabolic pathway for carbon fixation in which two molecules of **carbon dioxide** are converted **into acetyl coenzyme A**; it uses most of the same enzymes as the oxidative tricarboxylic acid cycle but runs it in reverse by using three alternative enzymes: fumarate reductase, 2-oxoglutarate synthase and ATP citrate lyase.

Calvin–Benson–Bassham cycle
A carbon fixation pathway in which **carbon dioxide** is converted into **glyceraldehyde-3-phosphate** using the key enzyme Rubisco.

Wood–Ljungdahl pathway
A metabolic pathway for carbon fixation in which two molecules of **carbon dioxide** are converted into **acetyl coenzyme A** by the key enzyme carbon monoxide dehydrogenase–acetyl coenzyme A synthase.

Dicarboxylate–4-hydroxybutyrate pathway
A recently described carbon fixation pathway in Archaea in which a molecule of **bicarbonate** (HCO_3^-) is fixed onto **acetyl coenzyme A** via a combination of enzymes from the reductive tricarboxylic acid cycle and the 4-hydroxybutyrate part of the 3-hydroxypropionate–4-hydroxybutyrate cycle.

Bobtail squid and *Aliivibrio fischeri*

Bioluminescence

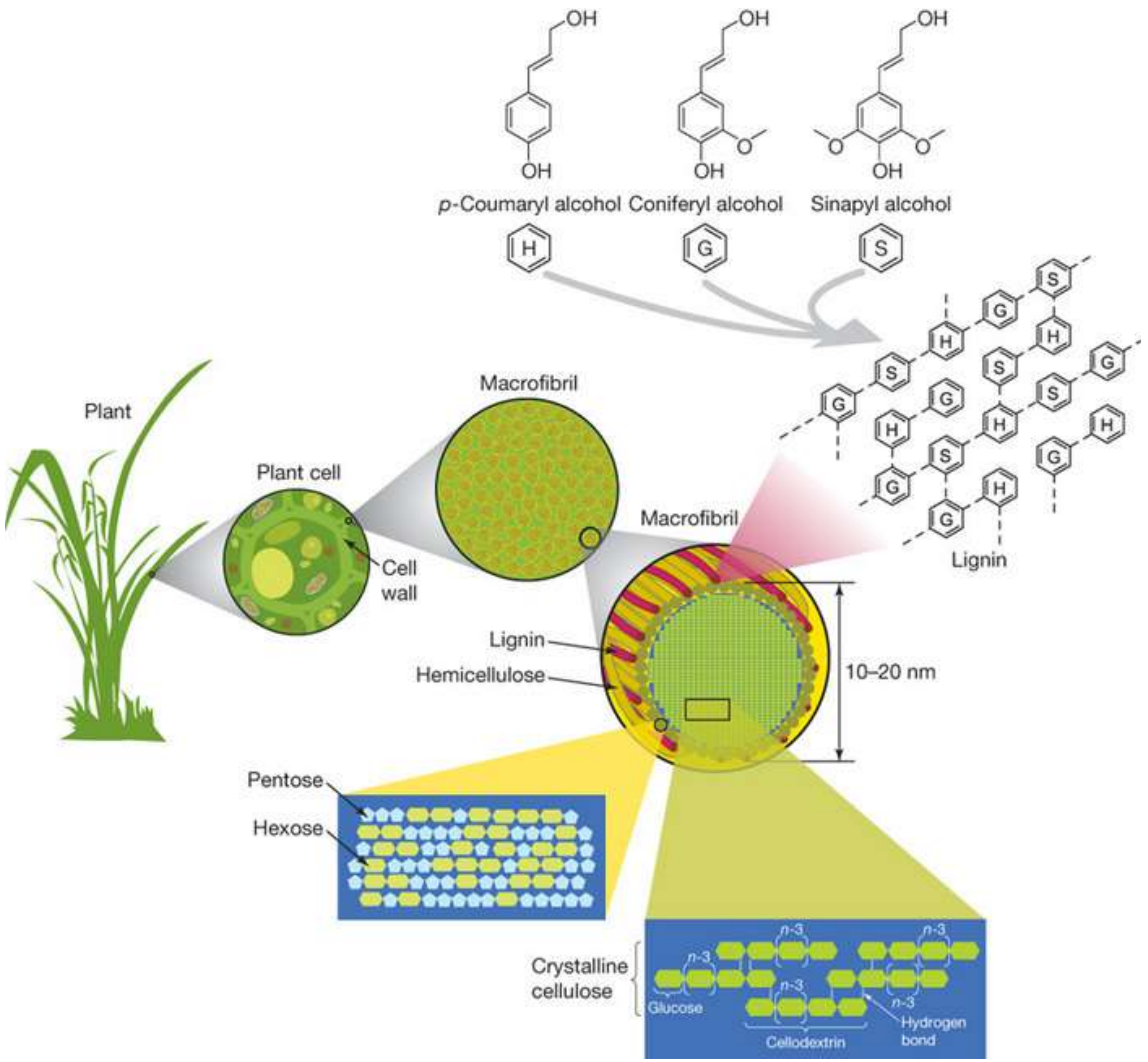
- Hawaiian bobtail squid, *Euprymna scolopes*, is a small marine invertebrate that harbors a large population of the bioluminescent gram-negative gammaproteobacterium *Aliivibrio fischeri* (unique species) in a light organ located on its ventral side
- Bacteria emit light that resembles moonlight penetrating marine waters, and this is thought to camouflage the squid from predators that strike from beneath
- Several other species of *Euprymna* inhabit marine waters near Japan and Australia and in the Mediterranean, w. *Aliivibrio* symbionts
- Transmission of bacterial cells to juvenile squid is a horizontal (environmental) rather than a vertical (parent to offspring) event
- Almost immediately after juveniles emerge from eggs, cells of *A. fischeri* in surrounding seawater begin to colonize them, entering through ciliated ducts that end in the immature light organ, 2h
- In light organ, 10^8-10^9 cells, coevolution in the presence of the microbes
- Animal in some way recognizes and accepts *A. fischeri* cells and excludes those of other species, lose flagellum
- Nitric oxide produced by the squid repel other bacteria
- Squid matures into an adult in ~ 2 months and then lives a strictly nocturnal existence in which it feeds mostly on small crustaceans; during the day, the animal buries itself and remains quiescent in the sand
- Each morning at dawn the squid nearly empties its light organ of *A. fischeri* cells and begins to grow a new population of the bacterium
- *A. fischeri* grows faster in the squid than in the ocean
- *A. fischeri* quorum sensing —> light production

Gut microbiota - Termites and Mammals

Termites

- Microorganisms are primarily responsible for the degradation of wood and cellulose in natural environments in tropical and subtropical
- Degradation of **lignocellulosic** materials
- **Insect gut provides a protective niche for microbial symbionts**, and in return, the **insect gains access to nutrients derived from an otherwise indigestible** carbon source
- Posterior alimentary tract of **higher termites** (most advanced, family Termitidae, ~3/4 of termite species) contains a dense and diverse community of **mostly anaerobic bacteria, including cellulolytic species**
- **Lower termites** (primitive) harbor diverse populations of both anaerobic bacteria and cellulolytic protists —> **Bacteria of lower termites participate little** or not at all in cellulose digestion; only the **protists phagocytize and degrade the wood particles ingested**
- **Higher vs lower** termites have **diverse gut architecture**
- Gut is **microbial bioreactor** that efficiently converts polymeric substrates to **acetate and variable amounts of methane, with hydrogen** as a central intermediate
- **Diverse food —> diverse gut microbiome (wood, fungus, soil)**

Structure of lignocellulose



https://www.nature.com/scitable/content/structure-of-lignocellulose-14464273/

The **main component** of lignocellulose is **cellulose, a beta(1–4)-linked chain of glucose molecules**. Hydrogen bonds between different layers of the polysaccharides contribute to the resistance of crystalline cellulose to degradation

Hemicellulose, the second most abundant component of lignocellulose, is composed of **various 5- and 6-carbon sugars such as arabinose, galactose, glucose, mannose and xylose**

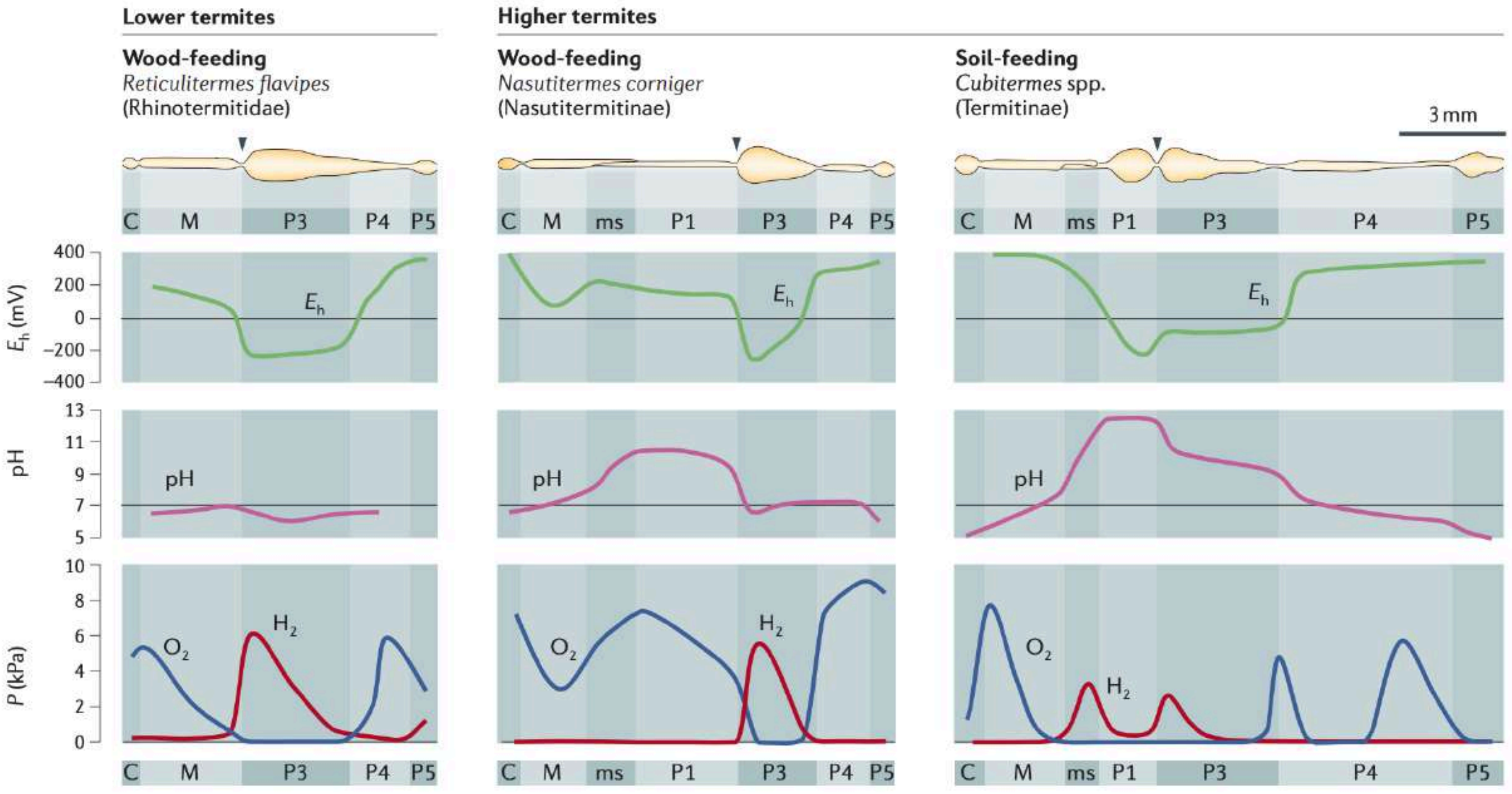
Lignin is composed of three major **phenolic** components, namely p-coumaryl alcohol (H), coniferyl alcohol (G) and sinapyl alcohol (S)

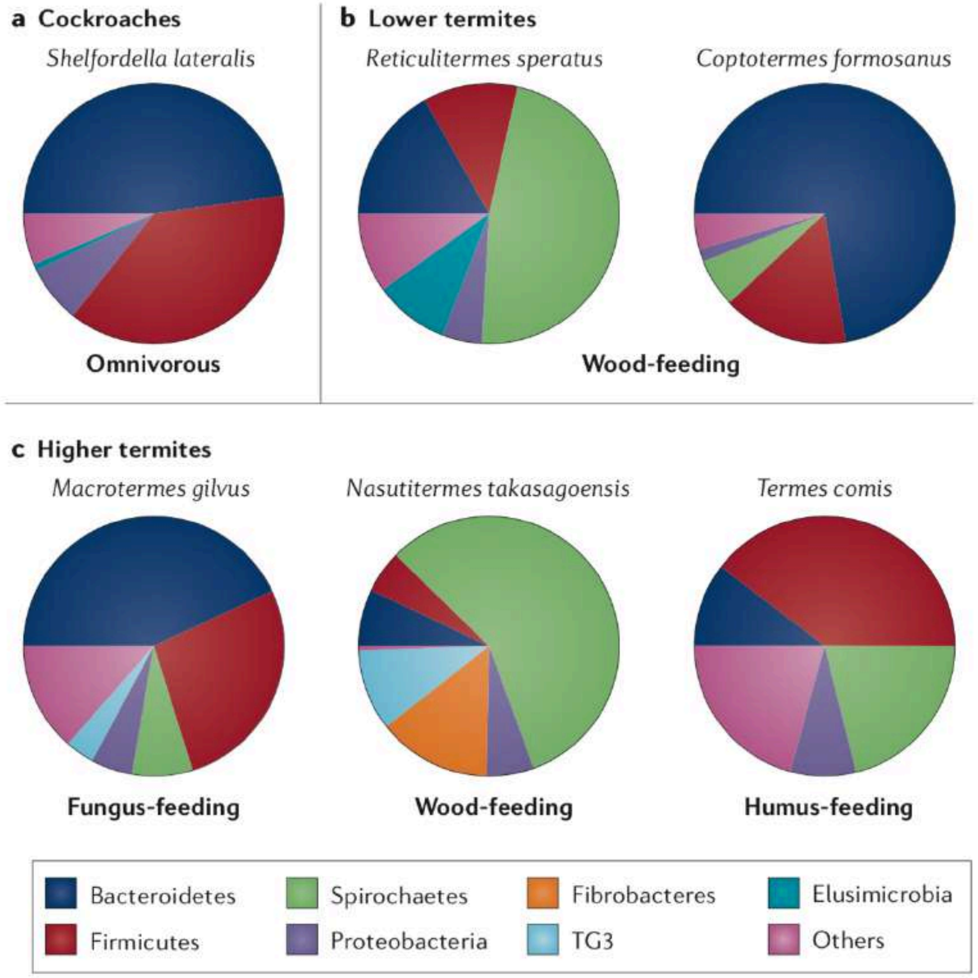
Lignin is synthesized by **polymerization** of these components and their ratio within the polymer varies between different plants, wood tissues and cell wall layers.

Cellulose, hemicellulose and lignin form structures called microfibrils, which are organized **into macrofibrils** that mediate structural stability in the plant cell wall

Termite gut

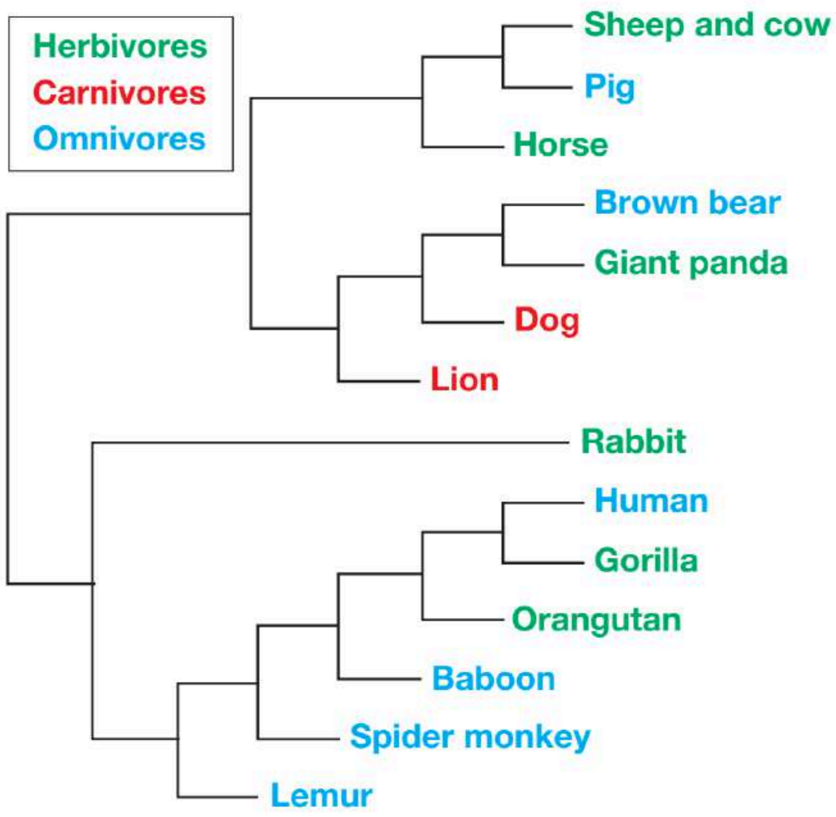
- **Metanogenesis** and **reductive acetogenesis** only in **absence of O_2**
- Within **gut local conditions select for microbial communities**



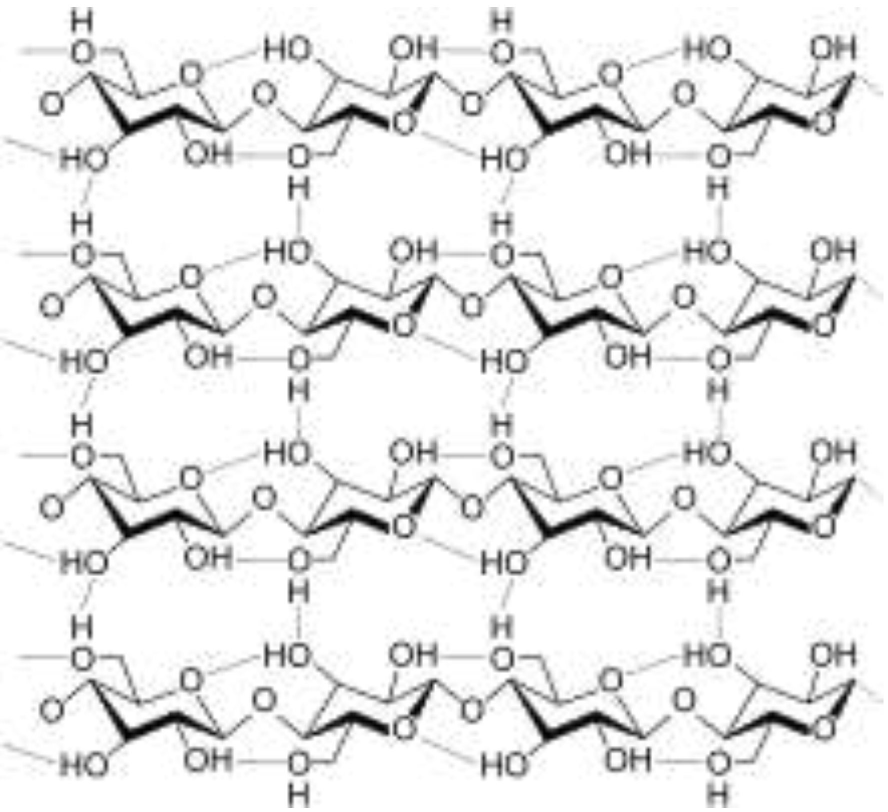


Brune, 2014

Gut microbes-Mammals symbiosis

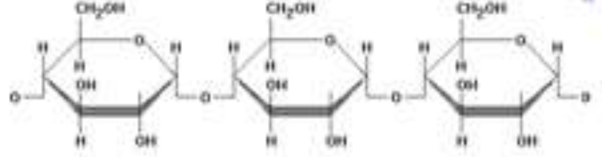
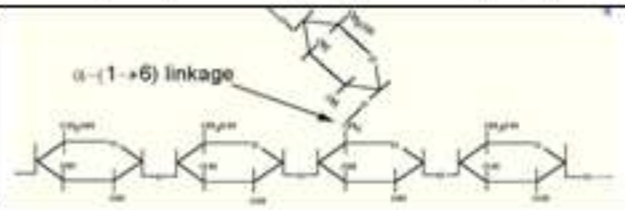
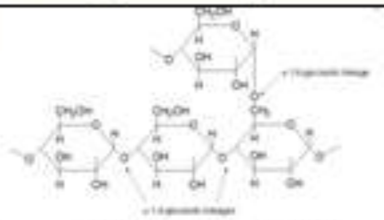
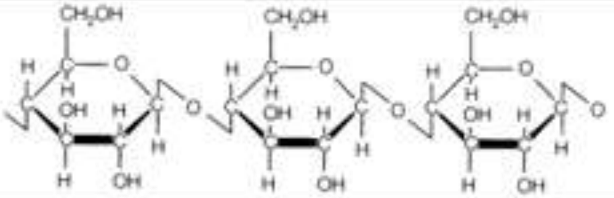


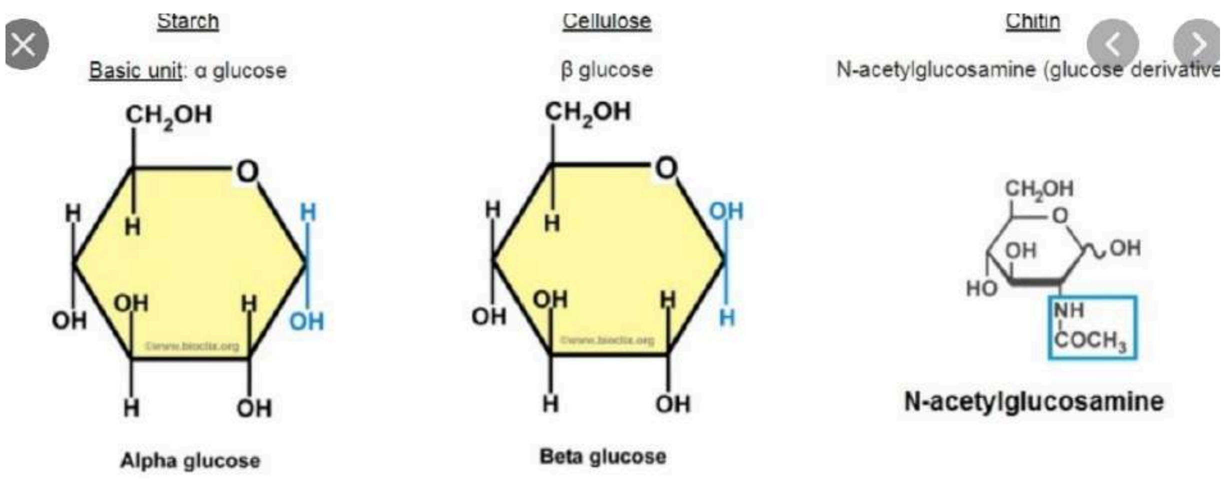
Madigan et al. 2018



- Gut microbiome has evolved **strategy to utilize complex and insoluble polysaccharides** (e.g. cellulose, beta-glucose only unit)
- Microbes have genes encoding the glycoside hydrolases and polysaccharide lyases required to decompose these polysaccharides
- Most mammalian species evolved **gut structures that foster mutualistic associations with microorganisms**
- As anatomical differences evolved, microbial fermentation remained important or essential in mammalian digestion
- Herbivory has evolved many times in Mammals

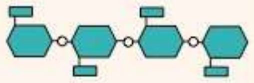
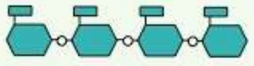
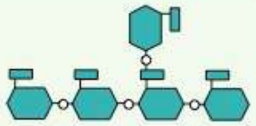
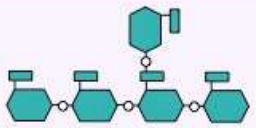
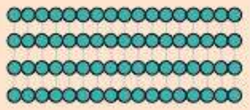
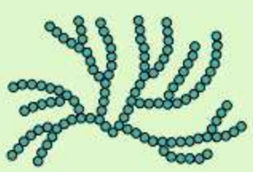
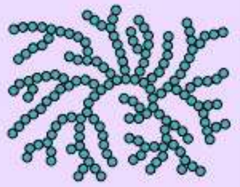
Sugar polymers

Polysacc	Monosac	Bonds	Diagram
Starch: Amylose	α - glucose	1-4	
Starch: Amylopectin	α - glucose	1-4 and 1-6	
Glycogen (**NOT starch**!)	α - glucose	1-4 and 1-6 (more 1-6 than amylopectin)	
Cellulose	β - glucose	1-4	



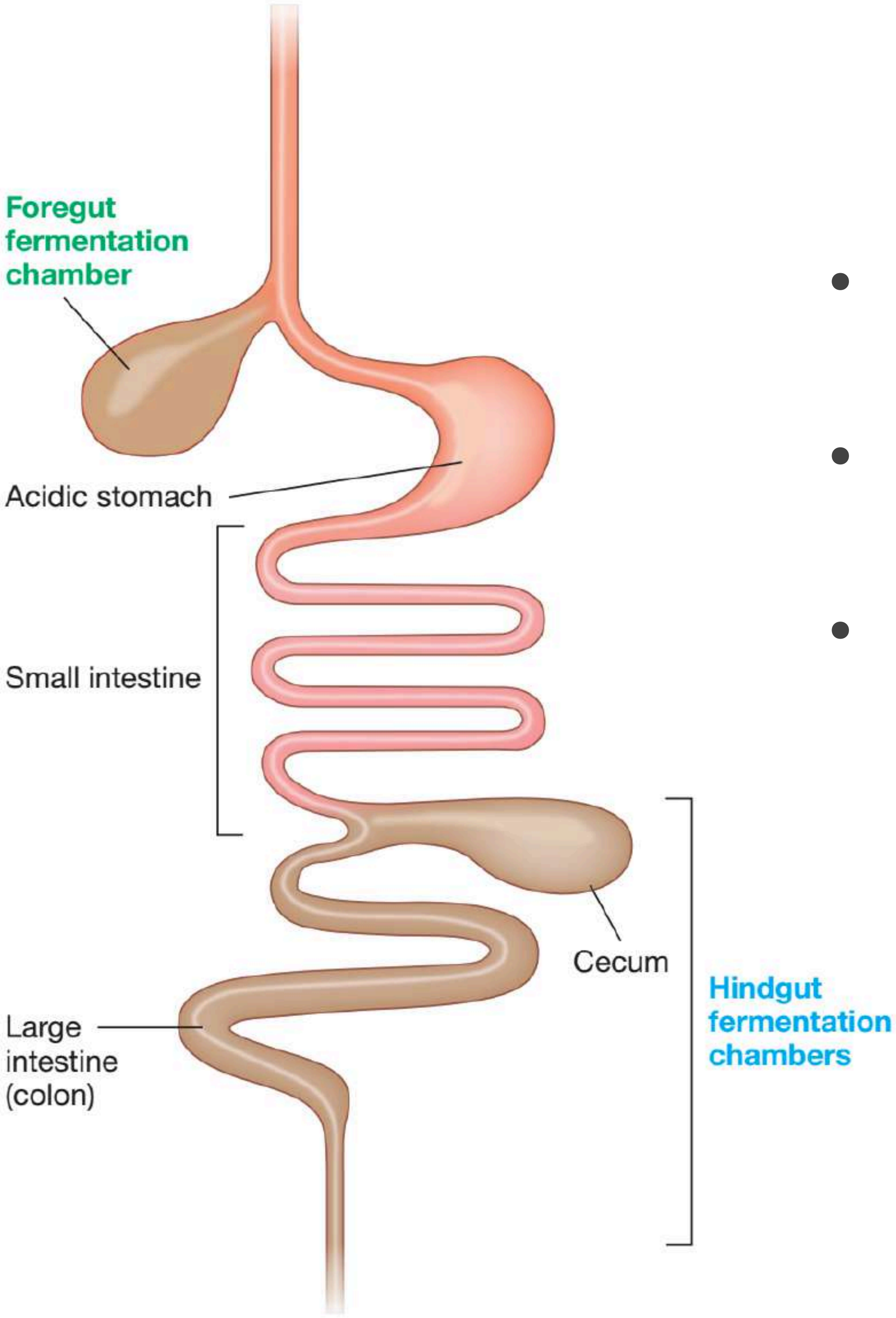
Alpha glucose

Beta glucose

	Cellulose	Starch		Glycogen
		Amylose	Amylopectin	
Source	Plant	Plant	Plant	Animal
Subunit	β-glucose	α-glucose	α-glucose	α-glucose
Bonds	1-4	1-4	1-4 *and* 1-6	1-4 *and* 1-6
Branches	No	No	Yes (~per 20 subunits)	Yes (~per 10 subunits)
Diagram				
Shape				

Google search

Fermentation in the gut



Madigan et al. 2018

Foregut fermenters Examples: Ruminants (photo 1), colobine monkeys, macropod marsupials, hoatzin (photo 2)

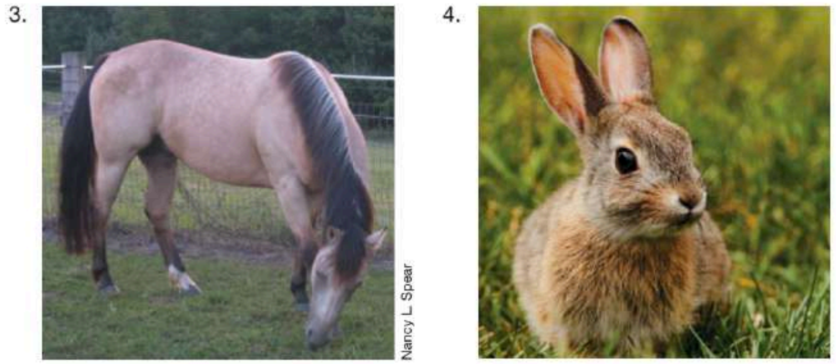
Bernard Swain

Madigan et al. 2018

Cows

- (1) **Enlarged anoxic fermentation chamber** for holding ingested plant material
- (2) **Extended retention time**—the time that ingested material remains in gut
- A longer retention time allows for a longer association of microorganisms with ingested material and thus a more complete degradation of plant polymers

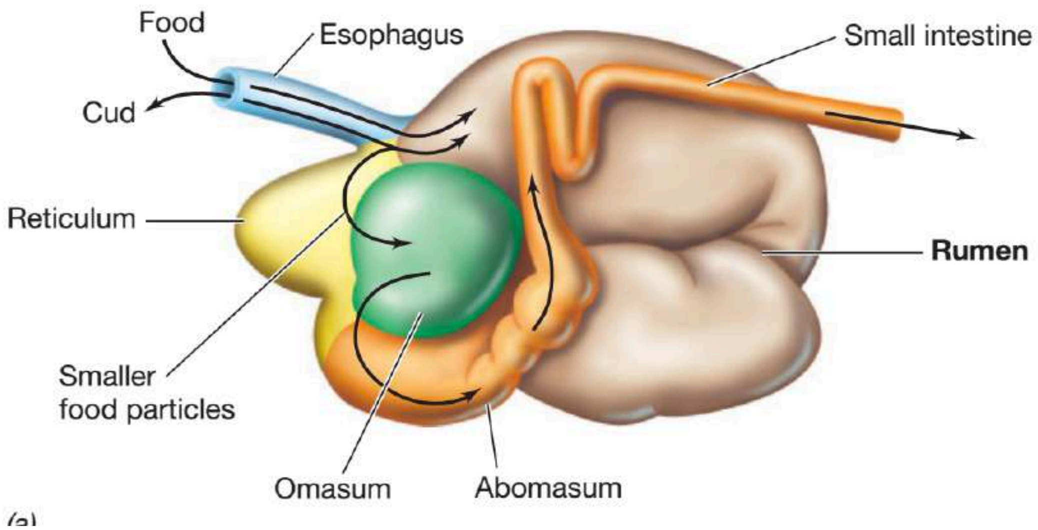
Hindgut fermenters Examples: Cecal animals (photos 3 and 4), primates, some rodents, some reptiles



Nancy L. Spear

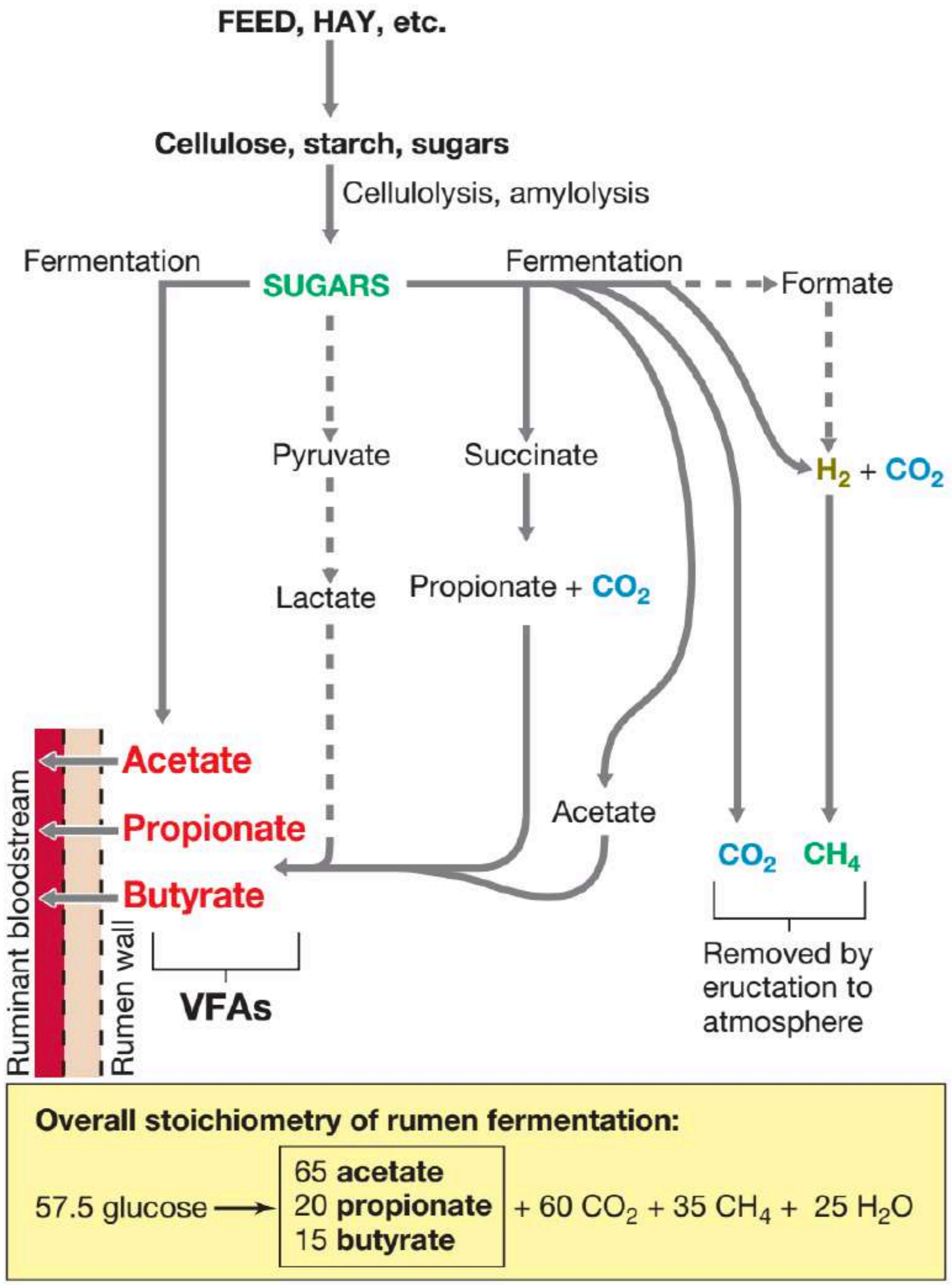
Madigan et al. 2018

Many chambers to maximize energy



Madigan et al. 2018

- 20-50 h food in the rumen
- Fermentation
- Anerobic bacteria dominate rumen
- Some anaerobic eukaryotes
- Cellulose diet: *Fibrobacter succinogenes, Ruminococcus albus*
- Starch diet: *Ruminobacter amylophilus, Succinomonas amylolitica*



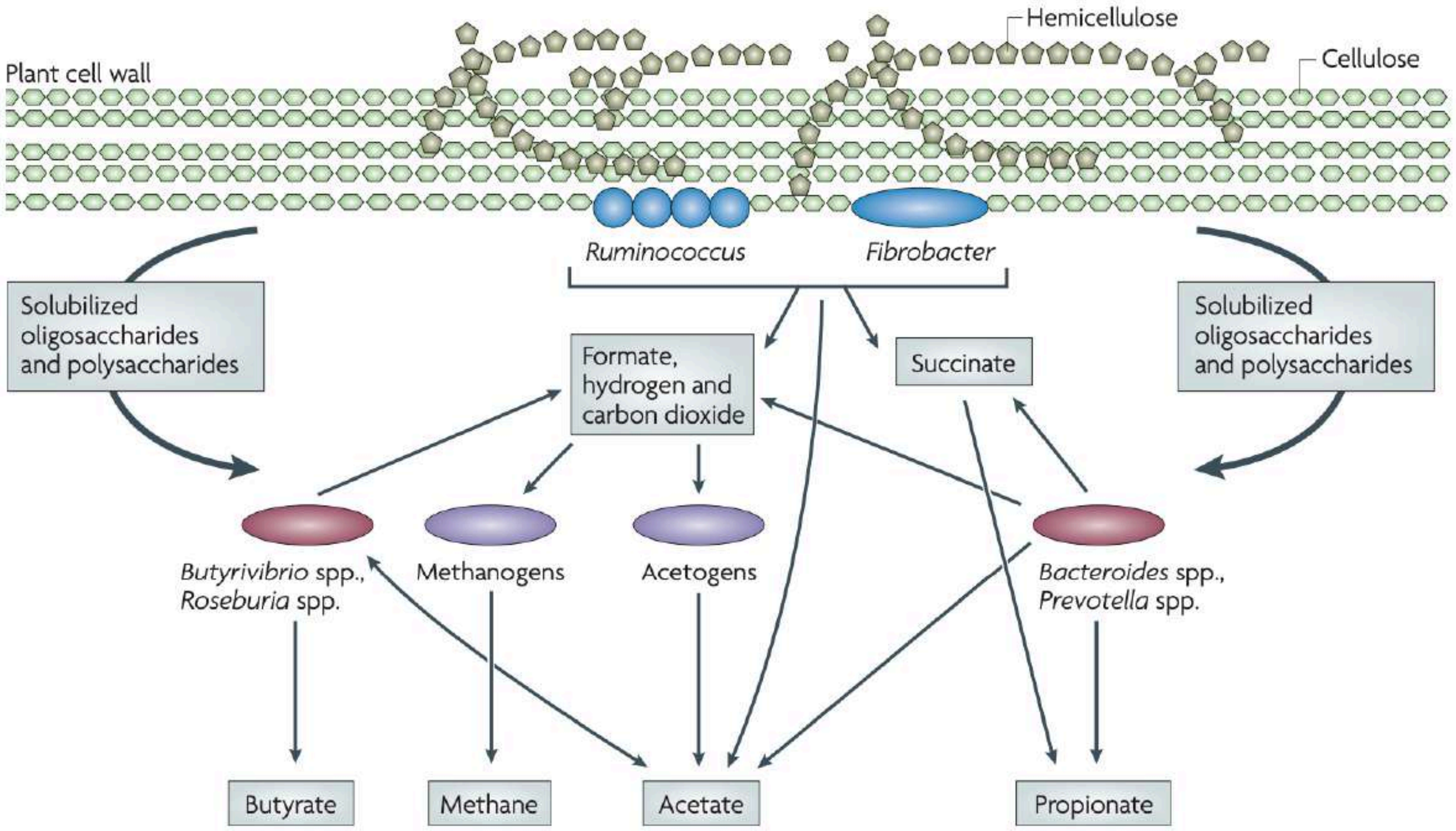
Overall stoichiometry of rumen fermentation:

57.5 glucose ⟶ 65 **acetate**, 20 **propionate**, 15 **butyrate** + 60 CO_2 + 35 CH_4 + 25 H_2O

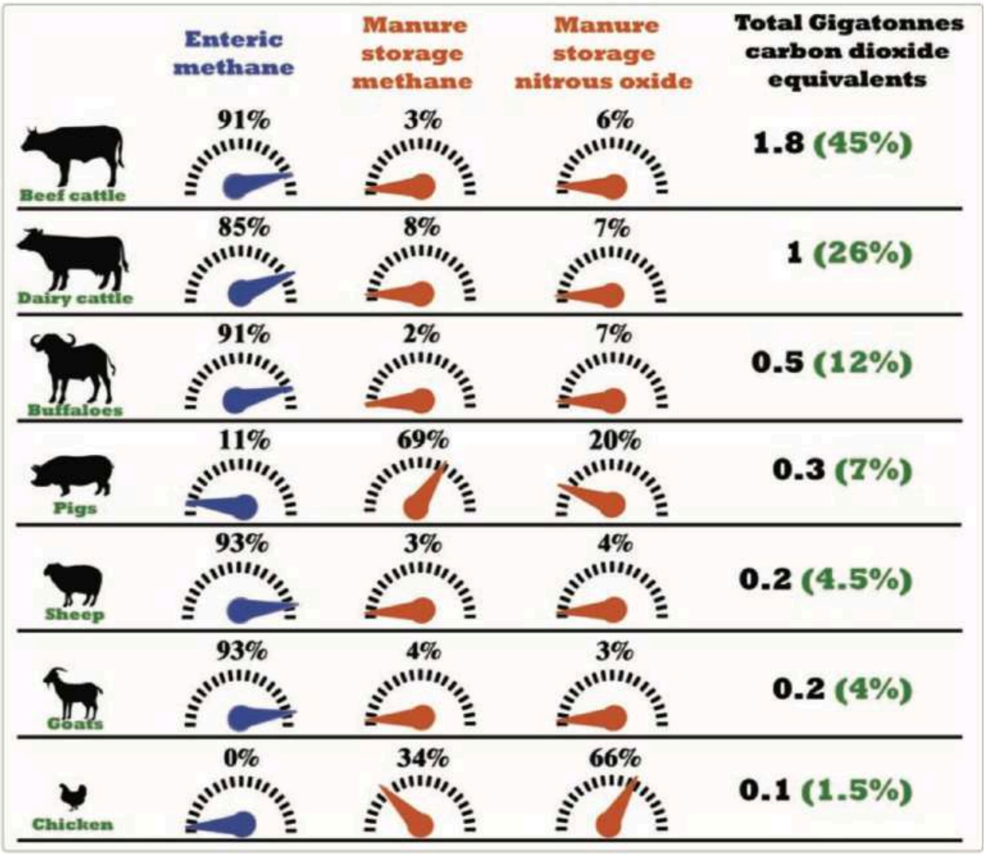
Madigan et al. 2018

Carbon budget

- Global emission ~ 37 Gt CO_2 in 2019 (https://www.globalcarbonproject.org/carbonbudget/19/highlights.htm)
- Livestock emission ~ 4.1 Gt CO_2 by FAO (http://www.fao.org/gleam/en/)



Flint et al., 2008



	Enteric methane	Manure storage methane	Manure storage nitrous oxide	Total Gigatonnes carbon dioxide equivalents
Beef cattle	91%	3%	6%	1.8 (45%)
Dairy cattle	85%	8%	7%	1 (26%)
Buffaloes	91%	2%	7%	0.5 (12%)
Pigs	11%	69%	20%	0.3 (7%)
Sheep	93%	3%	4%	0.2 (4.5%)
Goats	93%	4%	3%	0.2 (4%)
Chicken	0%	34%	66%	0.1 (1.5%)

FAO, 2017