

Partnerský život symbiontů: výprava do světa lišejníků a korálů



Pavel Škaloud

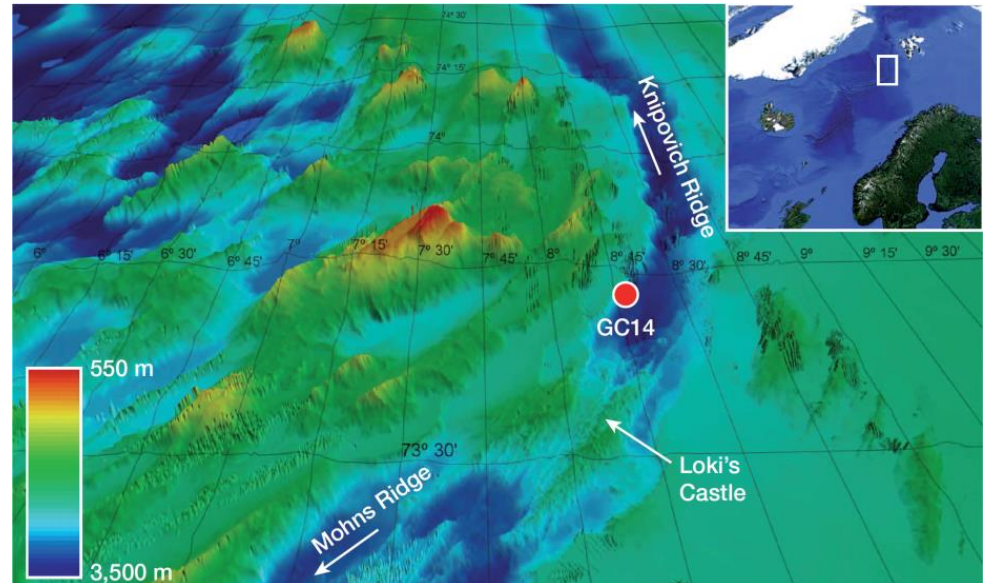
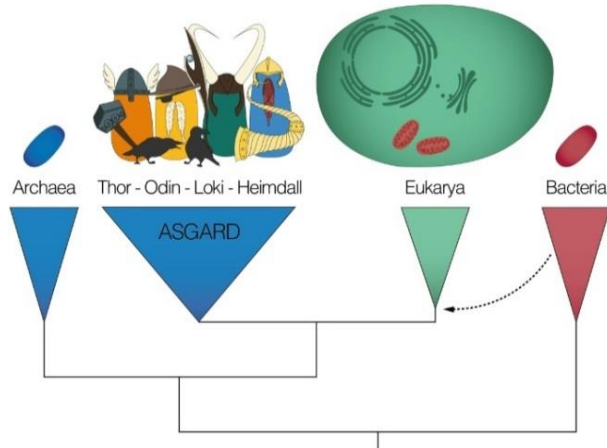
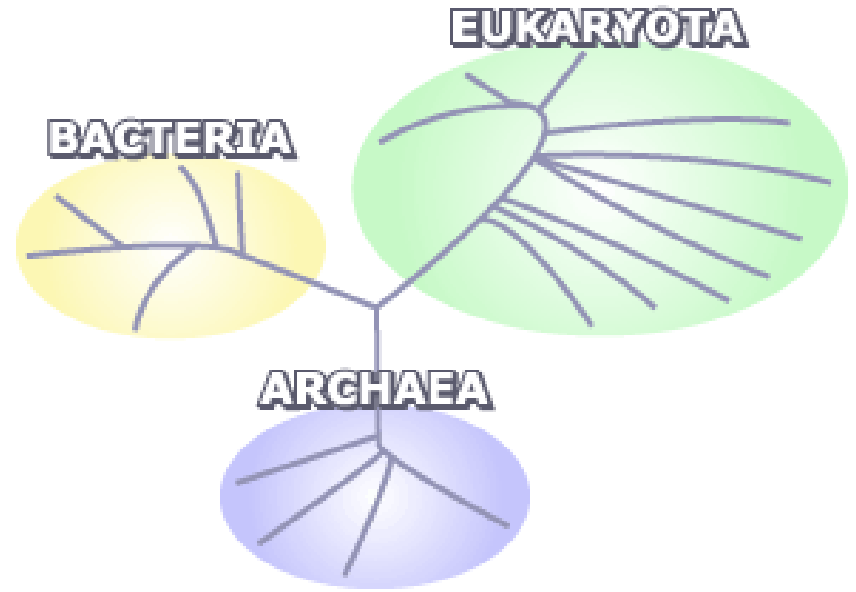
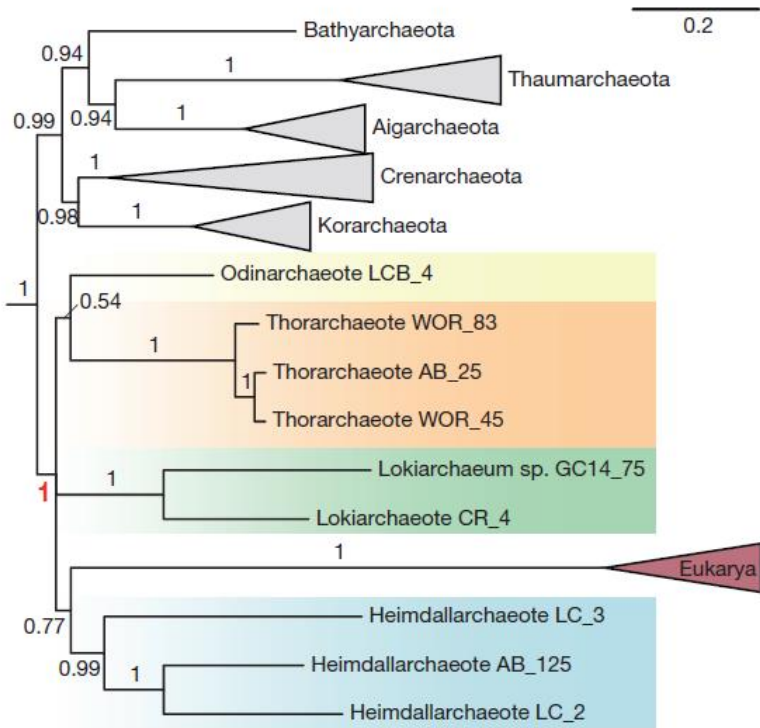


FACULTY OF SCIENCE
Charles University



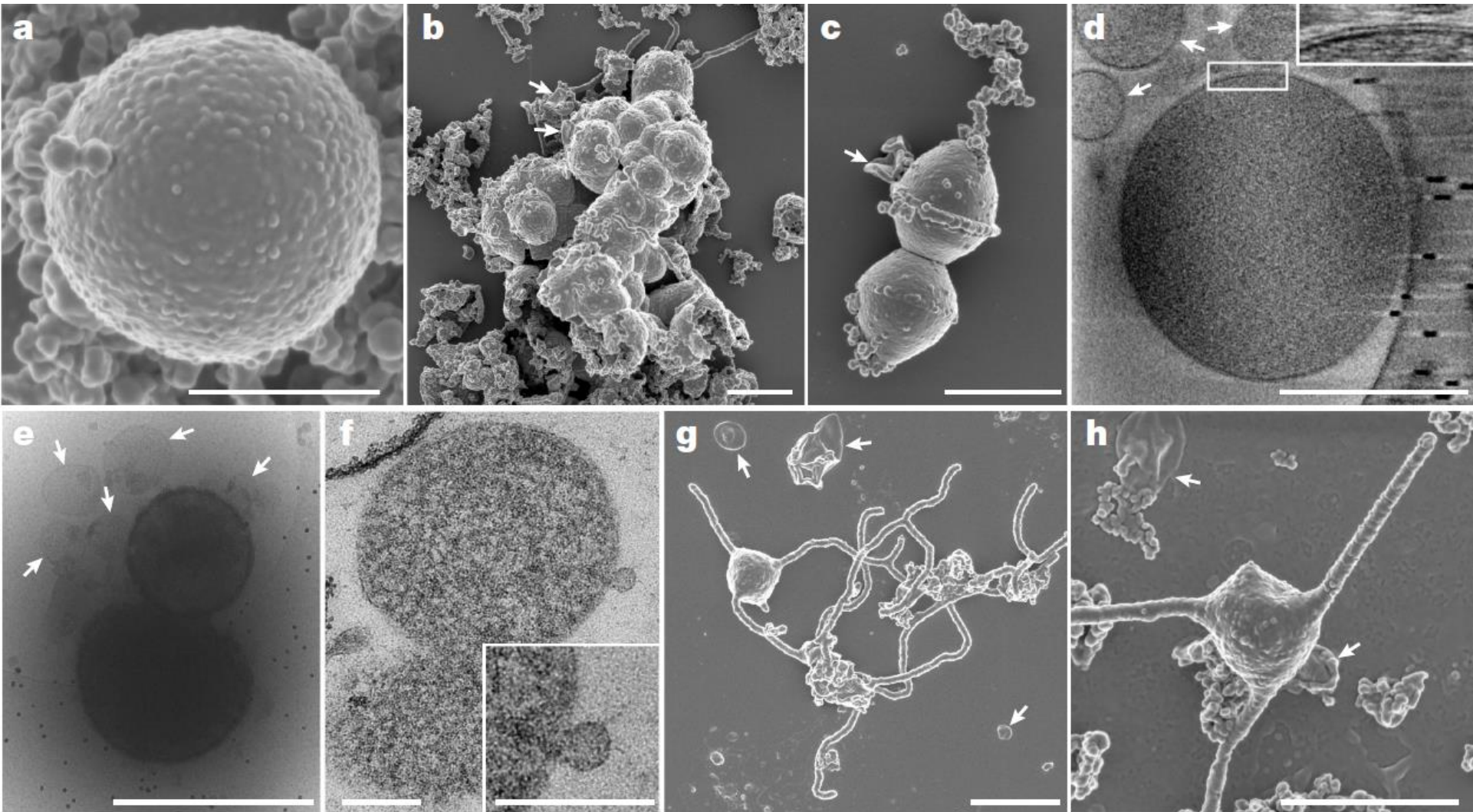
Algal speciation & evolution lab

Symbiosis - Eukaryogenesis



Symbiosis - Eukaryogenesis

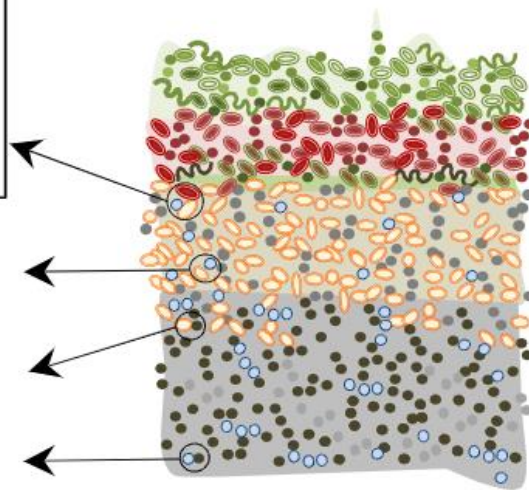
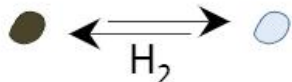
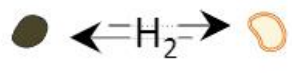
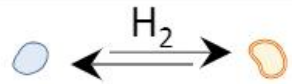
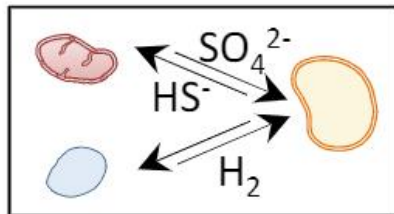
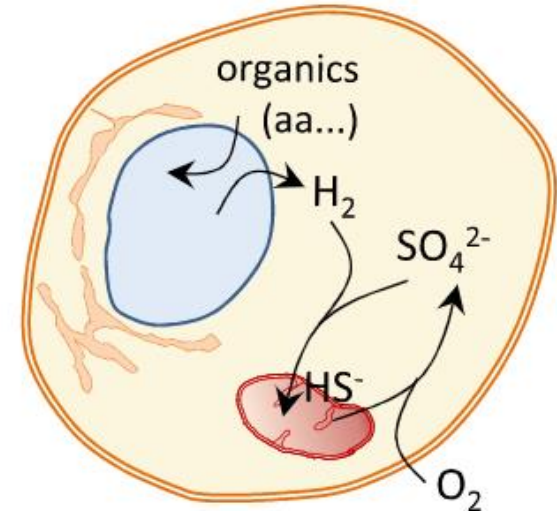
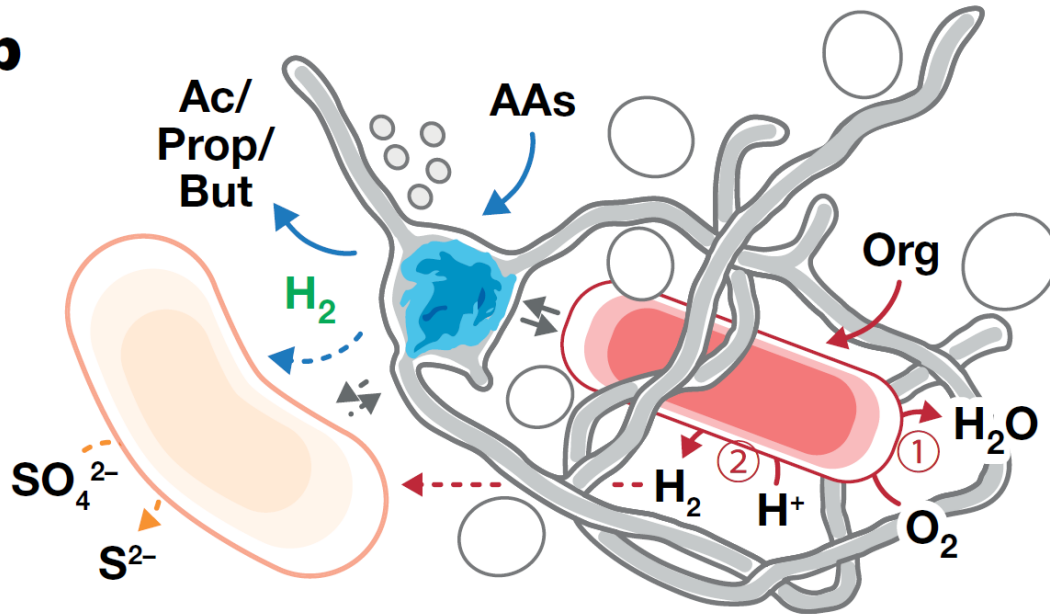
- *Prometheoarchaeum syntropicum*



Symbiosis - Eukaryogenesis

- *Prometheoarchaeum syntropicum*, syntrophy hypothesis

b

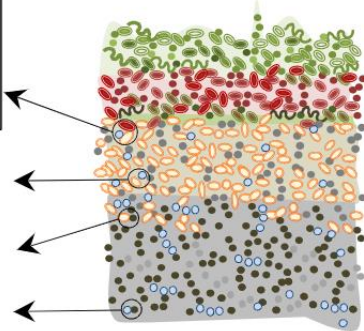
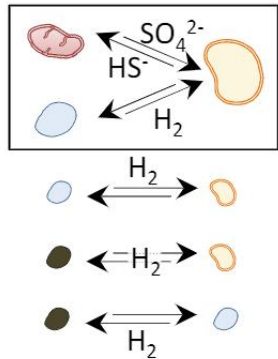
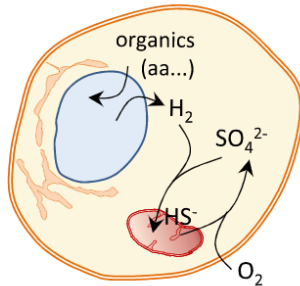


- Cyanobacteria
- Alphaproteobacteria
- Deltaproteobacteria
- Asgard archaea
- Methanogenic(/trophic) archaea
- Other bacteria

Symbiosis

- Central driver for evolution across the entire tree of life

HS - Syntrophy hypothesis

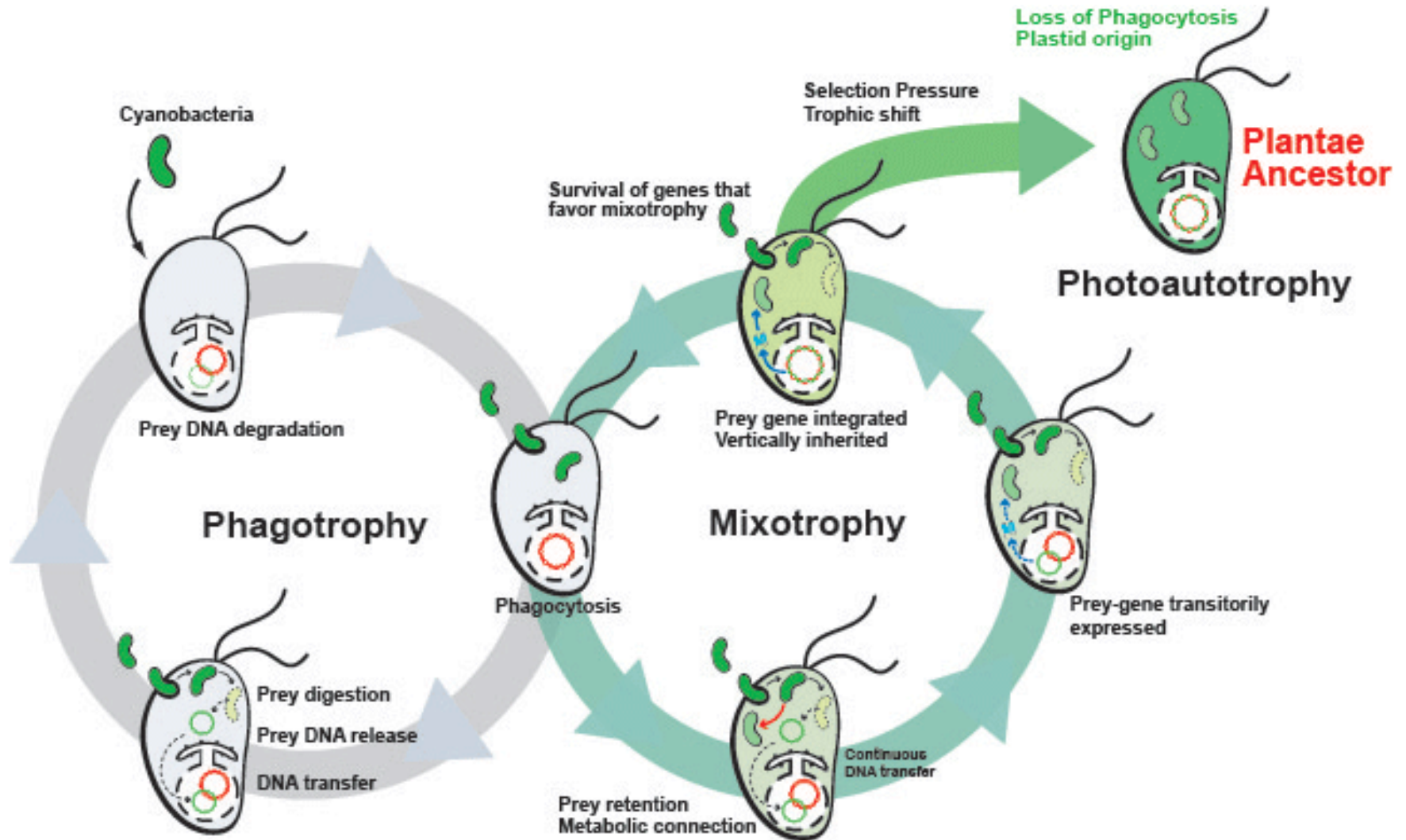


- Cyanobacteria
- Alphaproteobacteria
- Deltaproteobacteria
- Asgard archaea
- Methanogenic/(trophic) archaea
- Other bacteria



Proterozoic (P)										Phanerozoic																																		
Paleoproterozoic (X)					Mesoproterozoic (Y)					Neoproterozoic (Z)					Paleozoic (Pz)										Mesozoic (Mz)						Cenozoic (Cz)													
Siderian	Rhyacian	Orosirian	Statherian	Calymnian	Edesian	Stenian	Tonian	Cryogenian	Ediacaran	Cambrian (C)	Ordovician (O)	Silurian (S)	Devonian (D)	Carboniferous (C)		Permian (P)	Triassic (T)		Jurassic (J)		Cretaceous (K)		Tertiary (T)			Quaternary (Q)																		
														Mississippian (M)	Pennsylvanian (P)																													
2500	2300	2050	1800	1600	1400	1200	1000	850	635*	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Middle	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene													
										542.0 ± 1.0	513.0 ± 2.0	501.0 ± 2.0	488.3 ± 1.7	471.8 ± 1.6	460.9 ± 1.6	443.7 ± 1.5	428.2 ± 2.3	422.9 ± 2.5	418.7 ± 2.7	416.0 ± 2.8	397.5 ± 2.7	385.3 ± 2.6	359.2 ± 2.5	345.3 ± 2.1	328.3 ± 1.6*	318.1 ± 1.3	311.7 ± 1.1	280.4 ± 0.7	270.6 ± 0.7	251.0 ± 0.4	245.0 ± 1.5	228.7 ± 2.0*	198.6 ± 0.6	175.6 ± 2.0	161.2 ± 4.0	145.5 ± 4.0	99.6 ± 0.9	65.5 ± 0.3	55.8 ± 0.2	33.9 ± 0.1	23.03 ± 0.05	5.332 ± 0.005	2.588*	11,700 ± 89 yr*

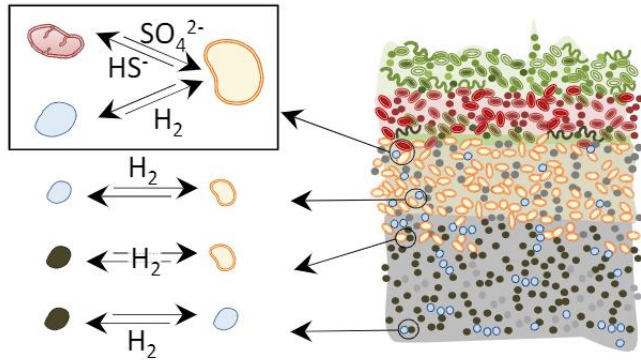
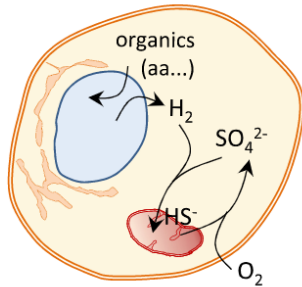
Symbiosis – primary endosymbiosis



Symbiosis

- Central driver for evolution across the entire tree of life

HS - Syntrophy hypothesis



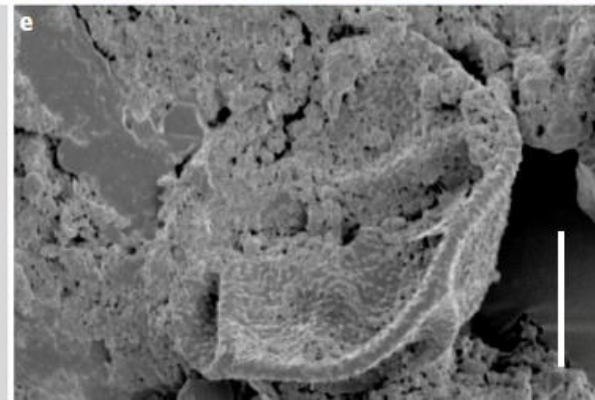
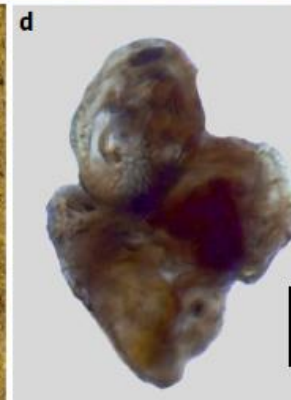
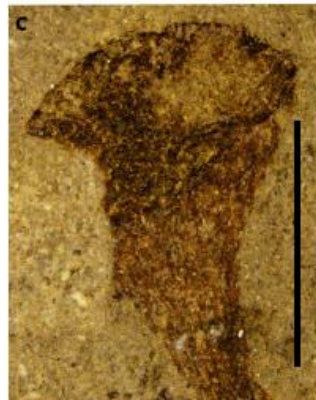
- Cyanobacteria
- Alphaproteobacteria
- Deltaproteobacteria
- Asgard archaea
- Methanogenic/(trophic) archaea
- Other bacteria



Proterozoic (P)										Phanerozoic																			
Paleoproterozoic (X)					Mesoproterozoic (Y)			Neoproterozoic (Z)		Paleozoic (Pz)							Mesozoic (Mz)					Cenozoic (Cz)							
Siderian	Rhyacian	Orosirian	Statherian	Calymnian	Edesian	Stenian	Tonian	Cryogenian	Ediacaran	Cambrian (C)	Ordovician (O)	Silurian (S)	Devonian (D)	Carboniferous (C)		Permian (P)	Triassic (Tr)		Jurassic (J)		Cretaceous (K)		Tertiary (T)			Quaternary (Q)			
														Mississippian (M)	Pennsylvanian (P)		Lower / Early	Middle	Upper / Late	Lower / Early	Middle	Upper / Late	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
2300	2300	2050	1900	1600	1400	1200	1000	850	635*	542.0 ± 1.0	488.3 ± 1.7	443.7 ± 1.5	395.3 ± 2.6	359.2 ± 2.5	345.3 ± 2.1	270.6 ± 0.7	251.0 ± 0.4	228.7 ± 2.0*	175.6 ± 2.0	161.2 ± 4.0	99.6 ± 0.9	65.5 ± 0.3	55.8 ± 0.2	33.9 ± 0.1	23.03 ± 0.05	5.332 ± 0.005	2.588*	11,700 ± 89 y*	

Symbiosis – first land plants

- *Cooksonia barrandei*



Symbiosis – first land plants

- *Cooksonia barrandei*



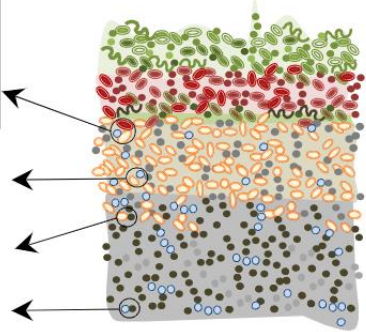
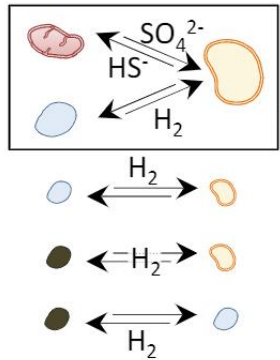
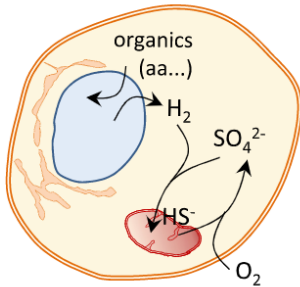
Symbiosis – first land plants



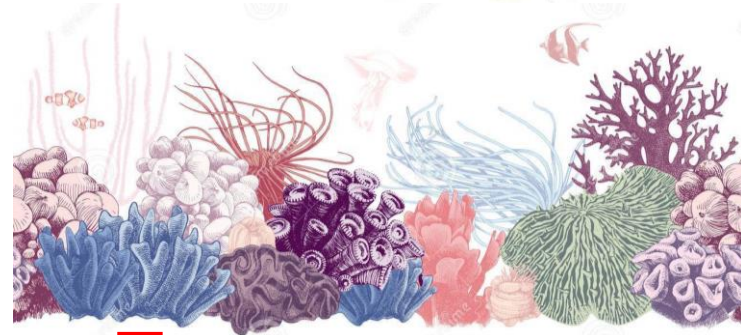
Symbiosis

- Central driver for evolution across the entire tree of life

HS - Syntrophy hypothesis



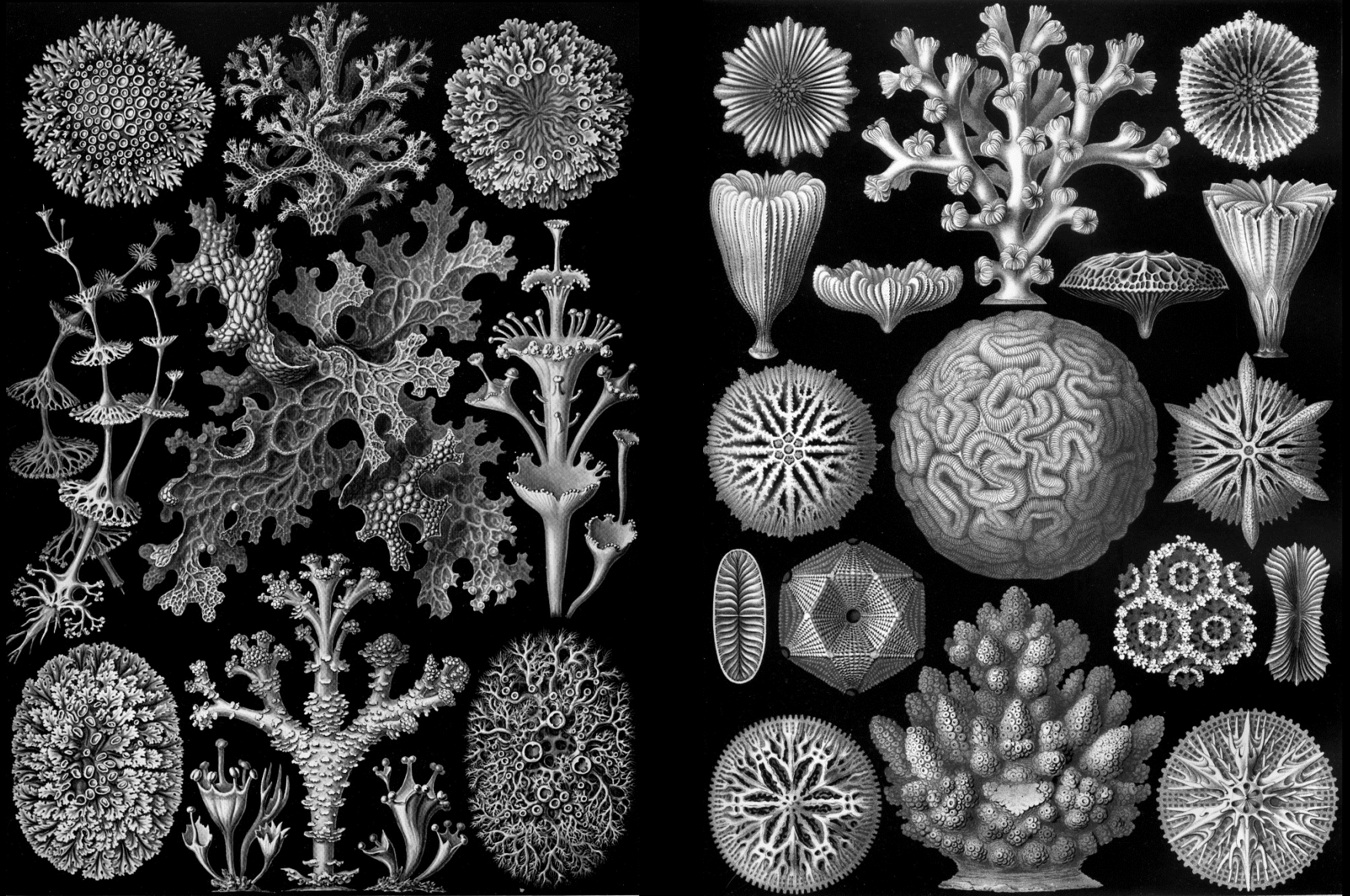
- Cyanobacteria
- Alphaproteobacteria
- Deltaproteobacteria
- Asgard archaea
- Methanogenic/(trophic) archaea
- Other bacteria



Proterozoic (P)										Phanerozoic																																		
Paleoproterozoic (X)					Mesoproterozoic (Y)			Neoproterozoic (Z)		Paleozoic (Pz)							Mesozoic (Mz)					Cenozoic (Cz)																						
Siderian	Rhyacian	Orosirian	Statherian	Calymnian	Edesian	Stenian	Tonian	Cryogenian	Ediacaran	Cambrian (C)		Ordovician (O)		Silurian (S)		Devonian (D)		Carboniferous (C)			Permian (P)		Triassic (Tr)		Jurassic (J)		Cretaceous (K)		Tertiary (T)			Quaternary (Q)												
										Lower / Early	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Lower / Early	Upper / Late	Mississippian (M)	Pennsylvanian (P)	Permian (P)	Permian (P)	Lower / Early	Middle	Upper / Late	Lower / Early	Middle	Upper / Late	Lower / Early	Upper / Late	Paleocene	Eocene	Oligocene	Neogene (N)	Pliocene	Pleistocene	Holocene								
2300	2300	2050	1900	1600	1400	1200	1000	850	635*	542.0 ± 1.0	513.0 ± 2.0	501.0 ± 2.0	488.3 ± 1.7	471.8 ± 1.6	460.9 ± 1.6	443.7 ± 1.5	428.2 ± 2.3	422.9 ± 2.5	418.7 ± 2.7	416.0 ± 2.8	397.5 ± 2.7	385.3 ± 2.6	359.2 ± 2.5	345.3 ± 2.1	328.3 ± 1.6*	318.1 ± 1.3	311.7 ± 1.1	307.2 ± 1.0*	299.0 ± 0.8	270.6 ± 0.7	280.4 ± 0.7	251.0 ± 0.4	228.7 ± 2.0*	199.6 ± 0.6	175.6 ± 2.0	161.2 ± 4.0	145.5 ± 4.0	99.6 ± 0.9	65.5 ± 0.3	55.8 ± 0.2	33.9 ± 0.1	23.03 ± 0.05	2.588*	11,700 ± 89 y*

Phototrophic symbioses

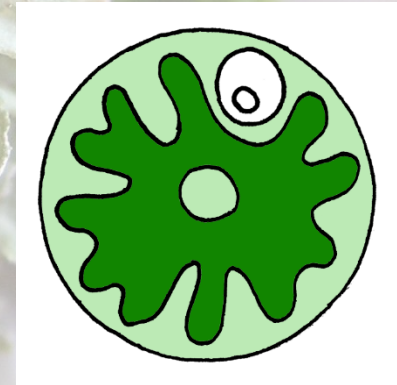
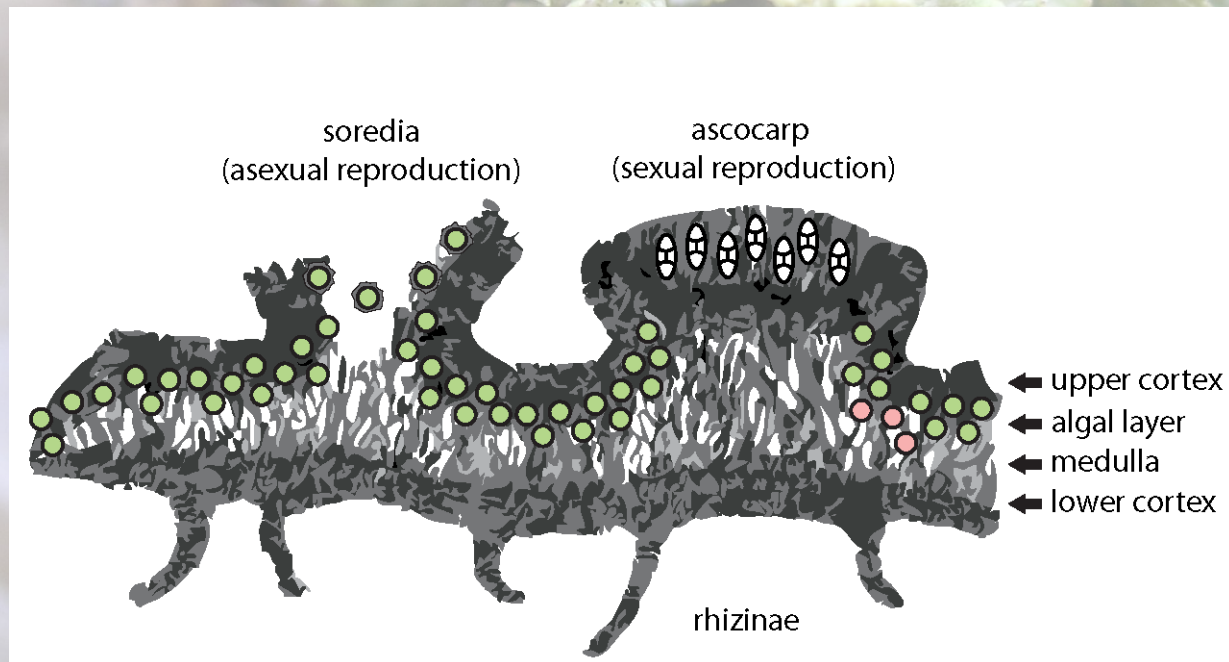
- Generally macroscopic hosts nutritionally dependent on microscopic endosymbionts providing organic carbon produced by the photosynthesis



Phototrophic symbioses

- Lichens

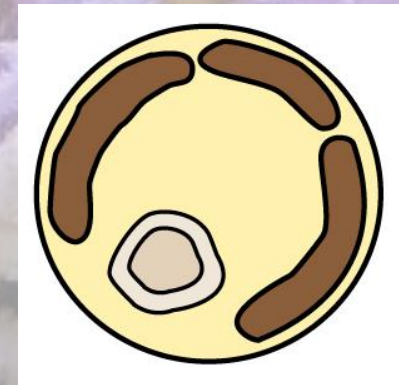
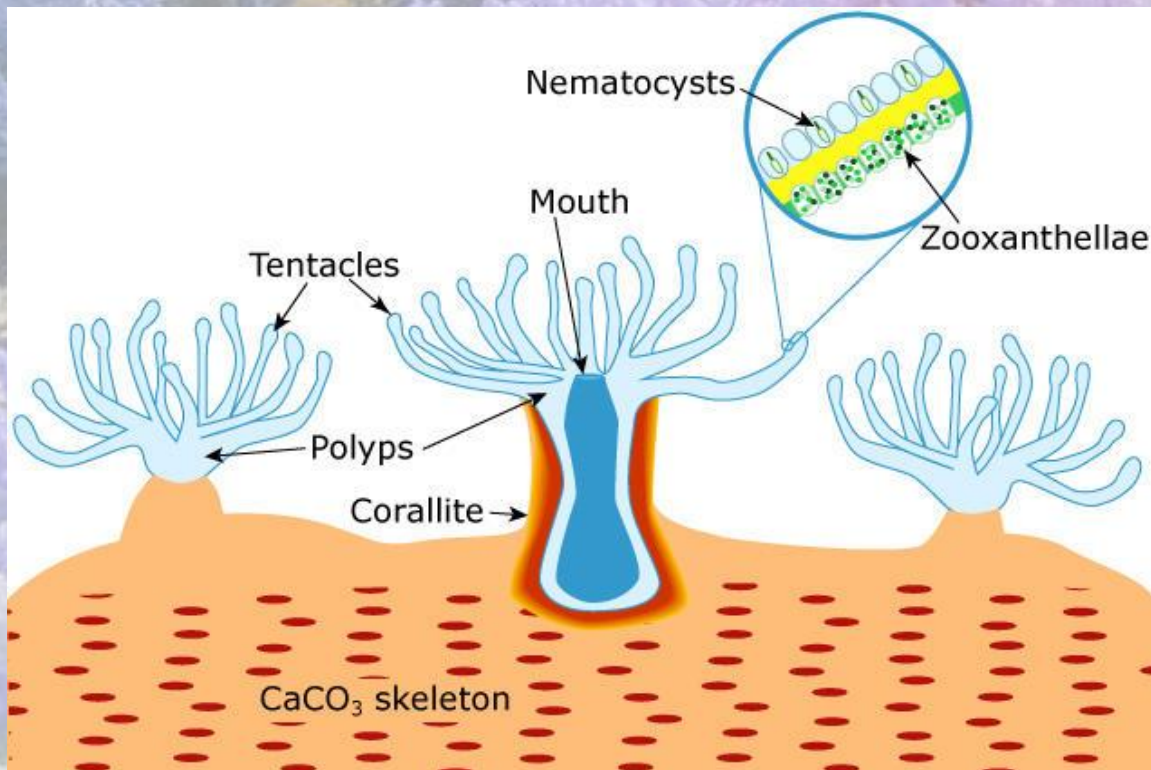
- Dominate 8% of the Earth's land surface
- Impacting global fluxes of carbon and nutrients
- Soil stabilization and development



Phototrophic symbioses

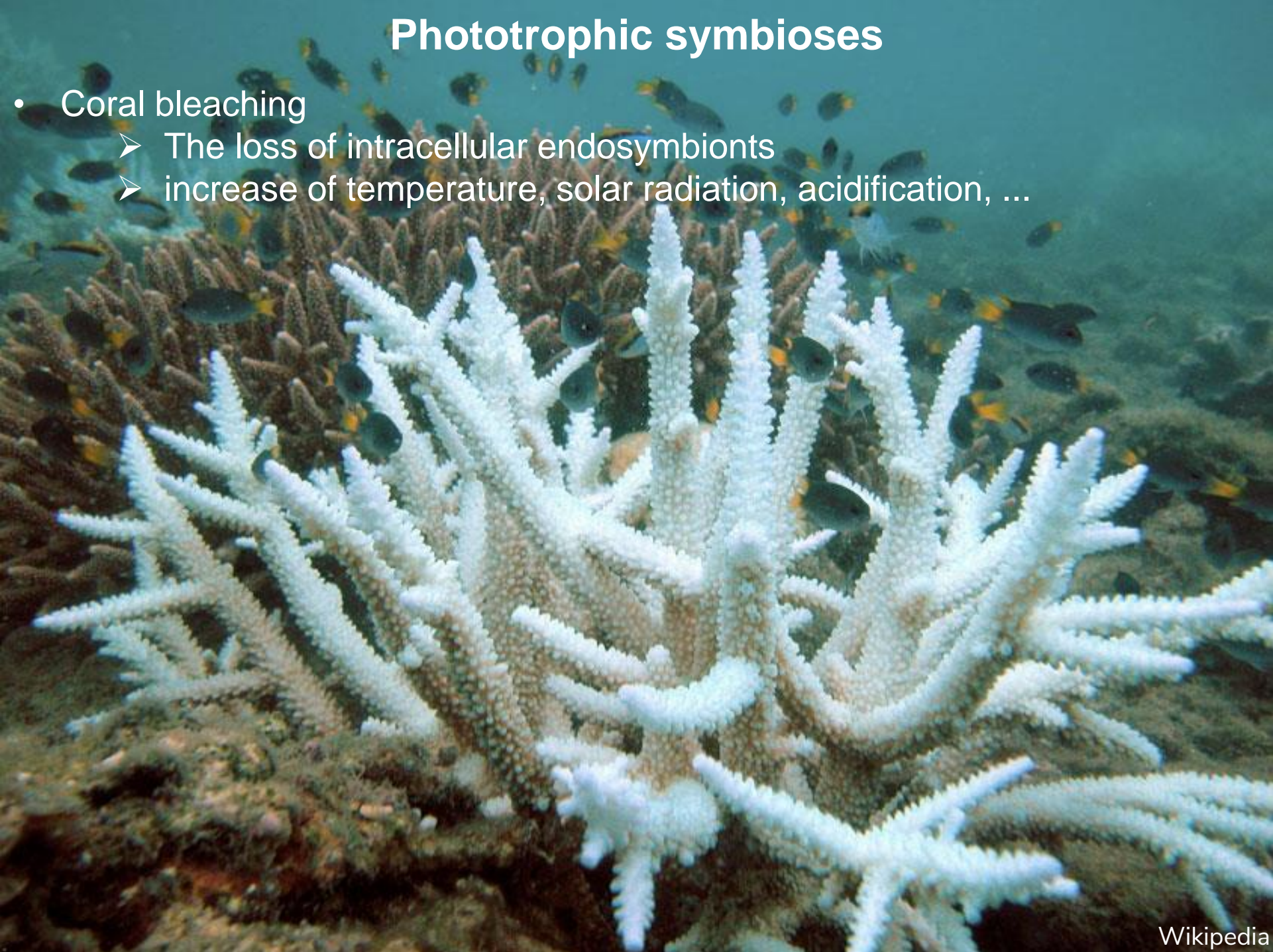
- Corals

- Cover 0.17% of the ocean surface
- Coral reefs as important planetary biodiversity hotspots



Phototrophic symbioses

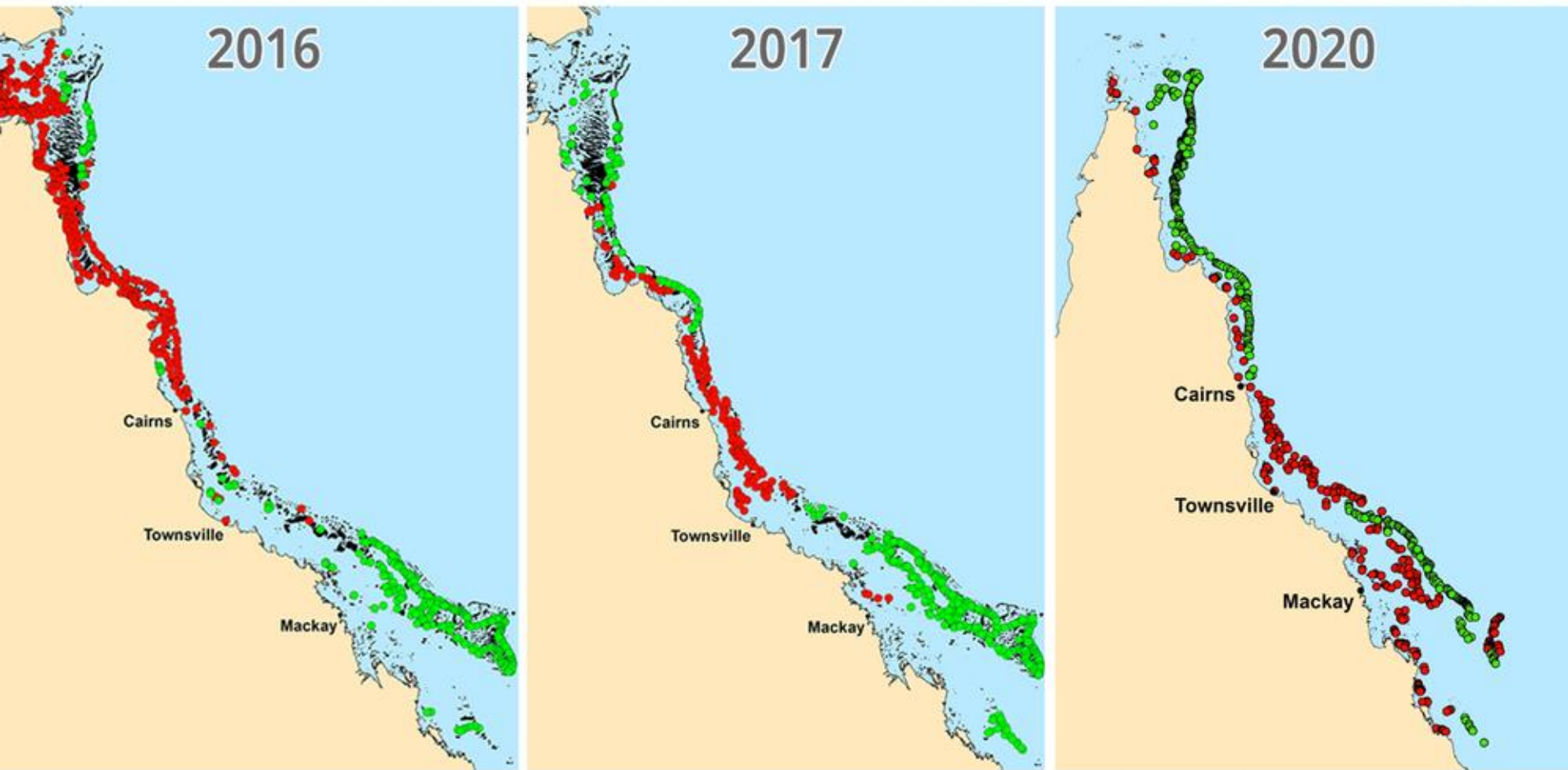
- Coral bleaching
 - The loss of intracellular endosymbionts
 - increase of temperature, solar radiation, acidification, ...



Phototrophic symbioses

- Coral bleaching
 - Great Barrier Reef – five massive bleaching events
 - The number of corals has declined by more than 50% since the 1990s

 Most severe bleaching  No or negligible bleaching



Phototrophic symbioses

- Decrease of lichens in Arctic ecosystems, climatic changes
 - Dramatic decline in reindeer populations in recent years

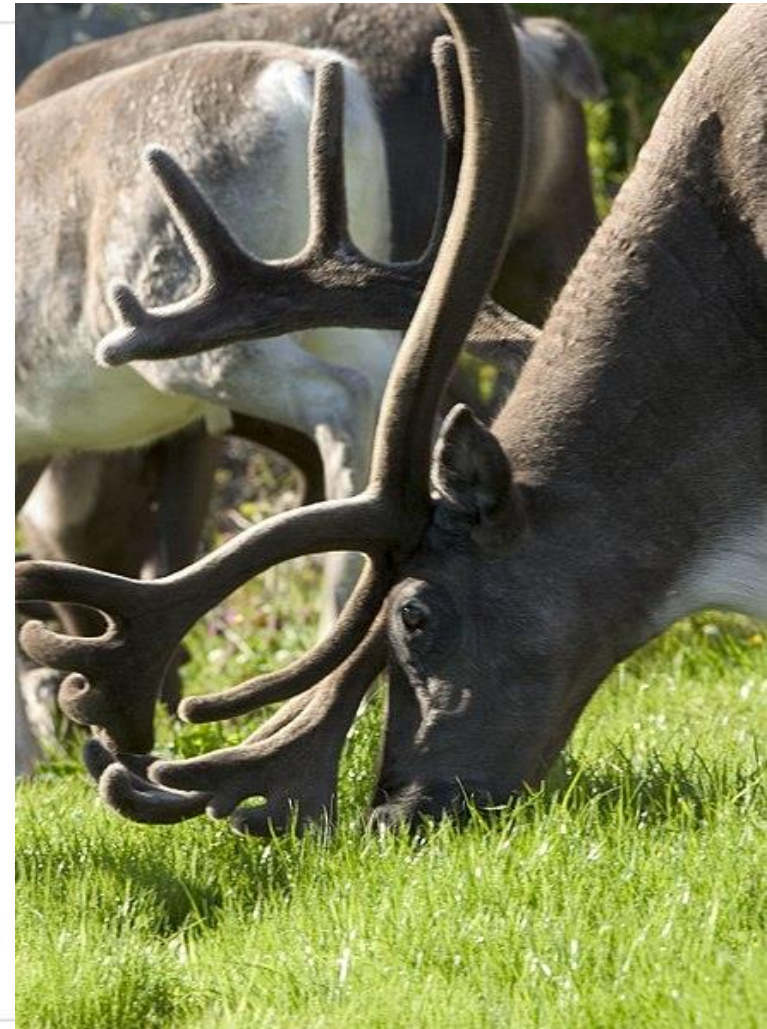
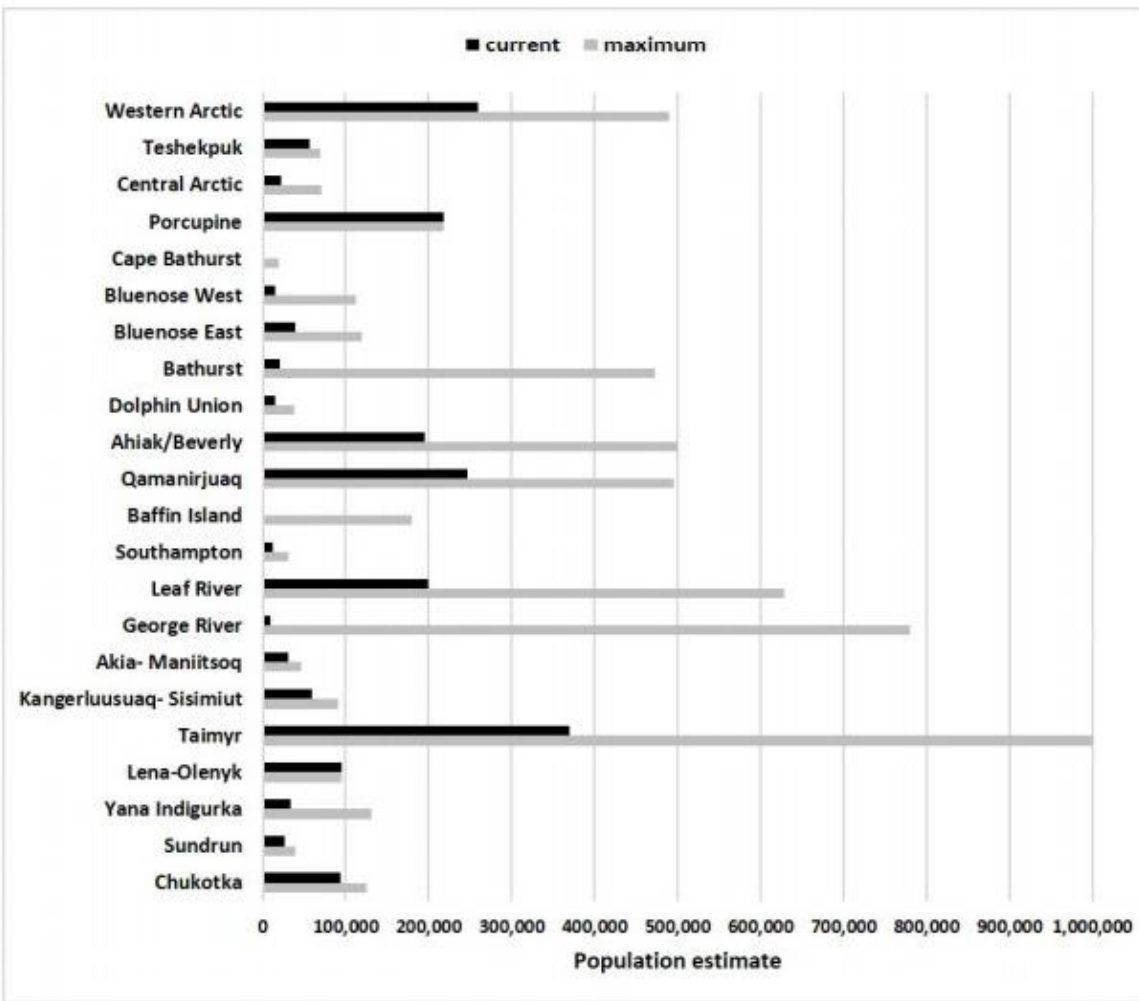
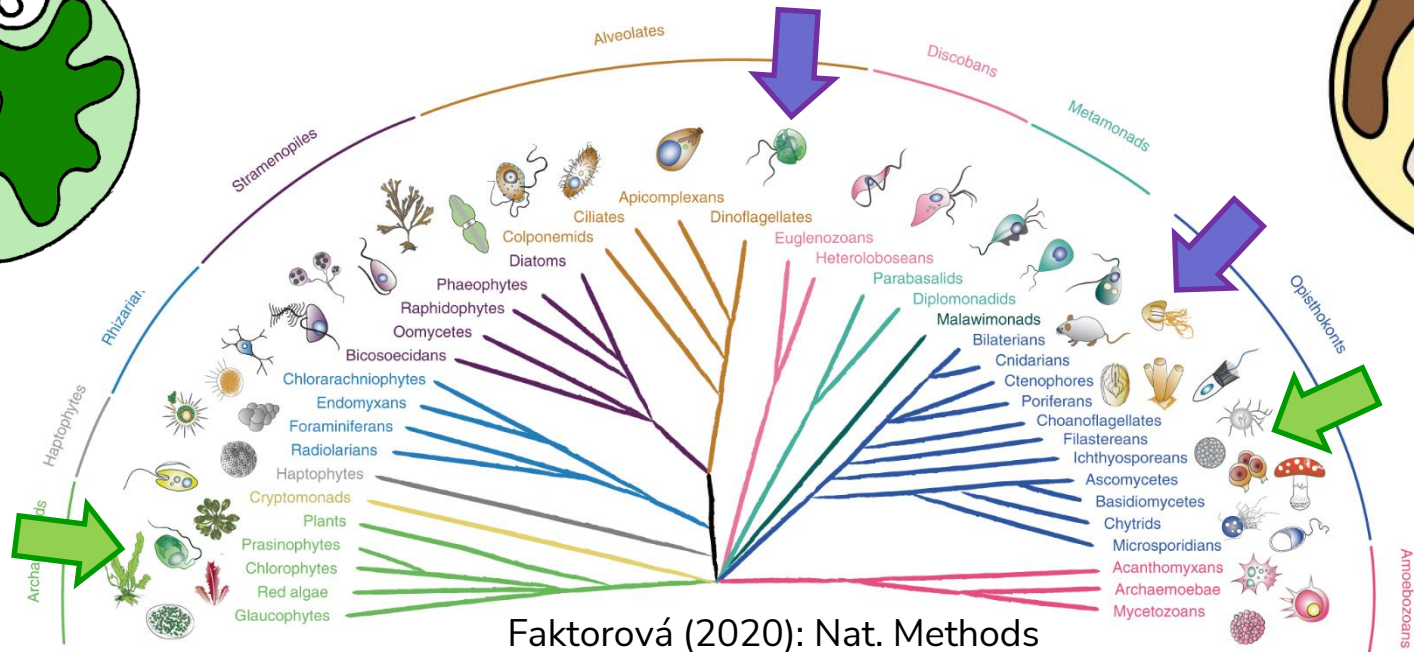
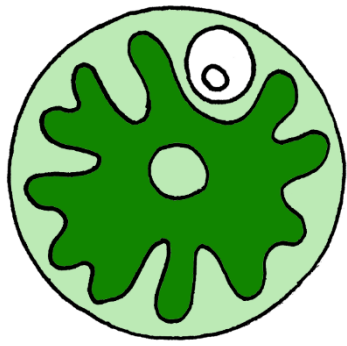


Figure 2. The current and peak estimates for migratory tundra wild reindeer/caribou herds for the 22 herds with at least three censuses. Data from CARMA's population database and covers population estimates from 1970-2017. Herds are ordered from west to east, starting in western Alaska.

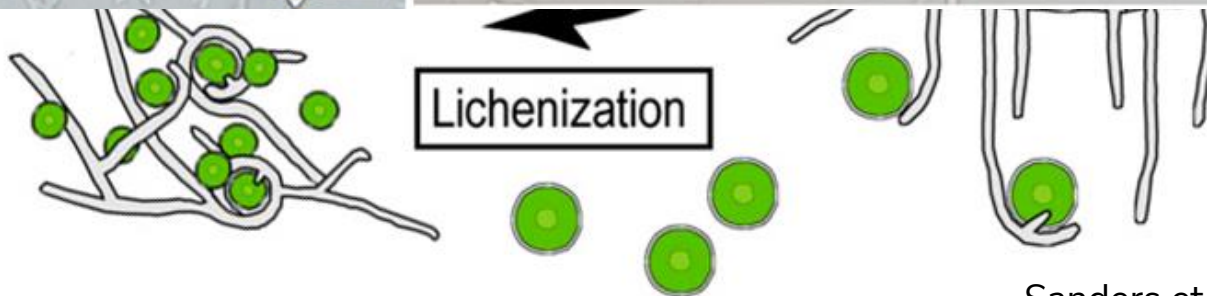
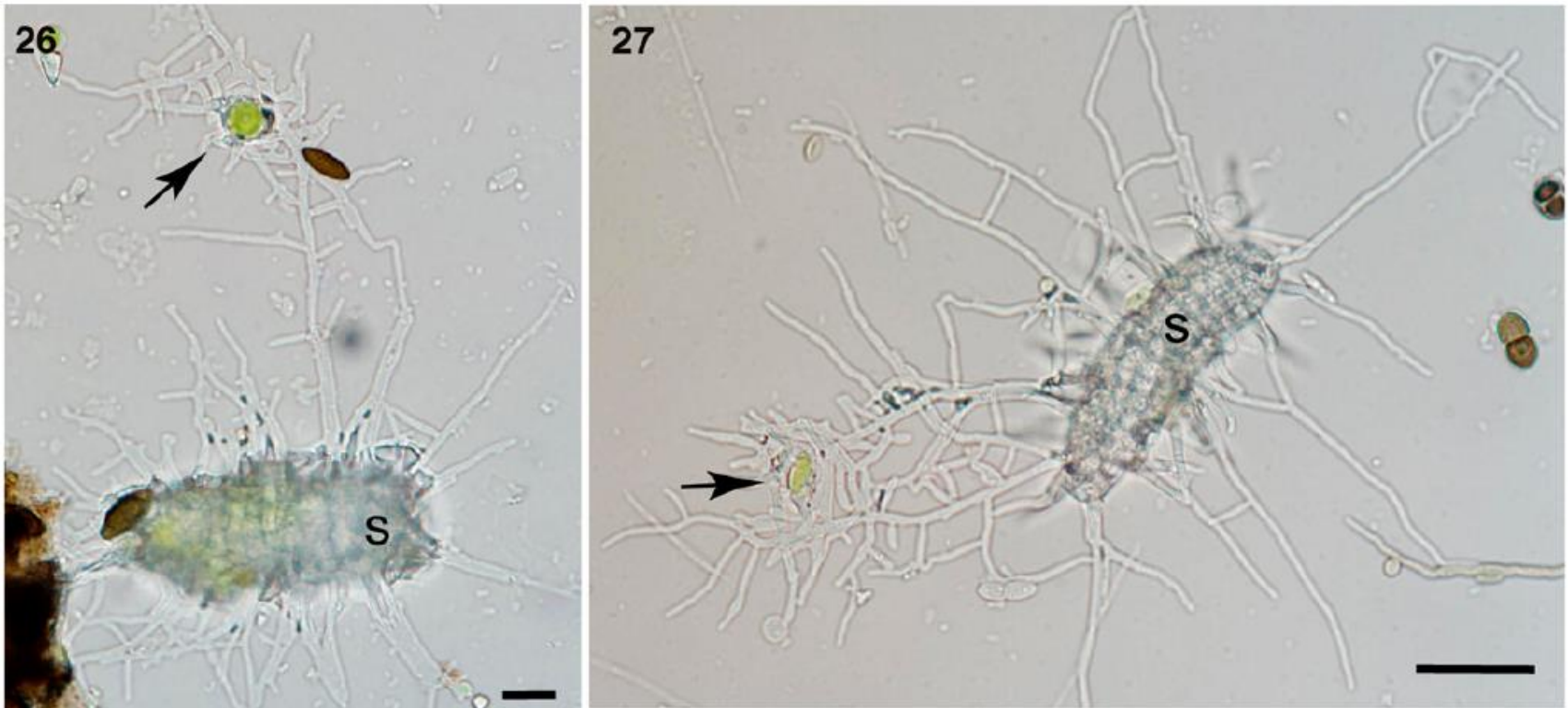


Phototrophic symbioses



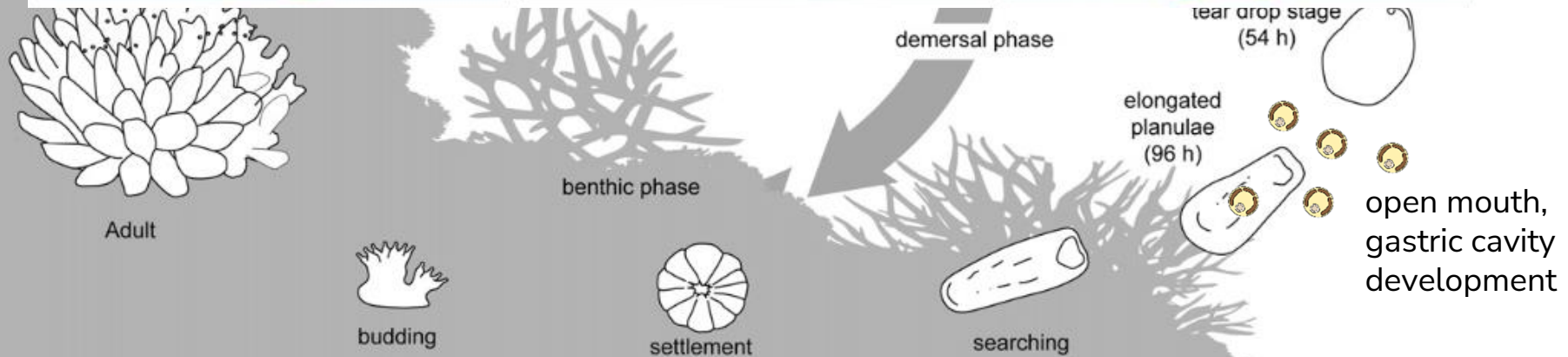
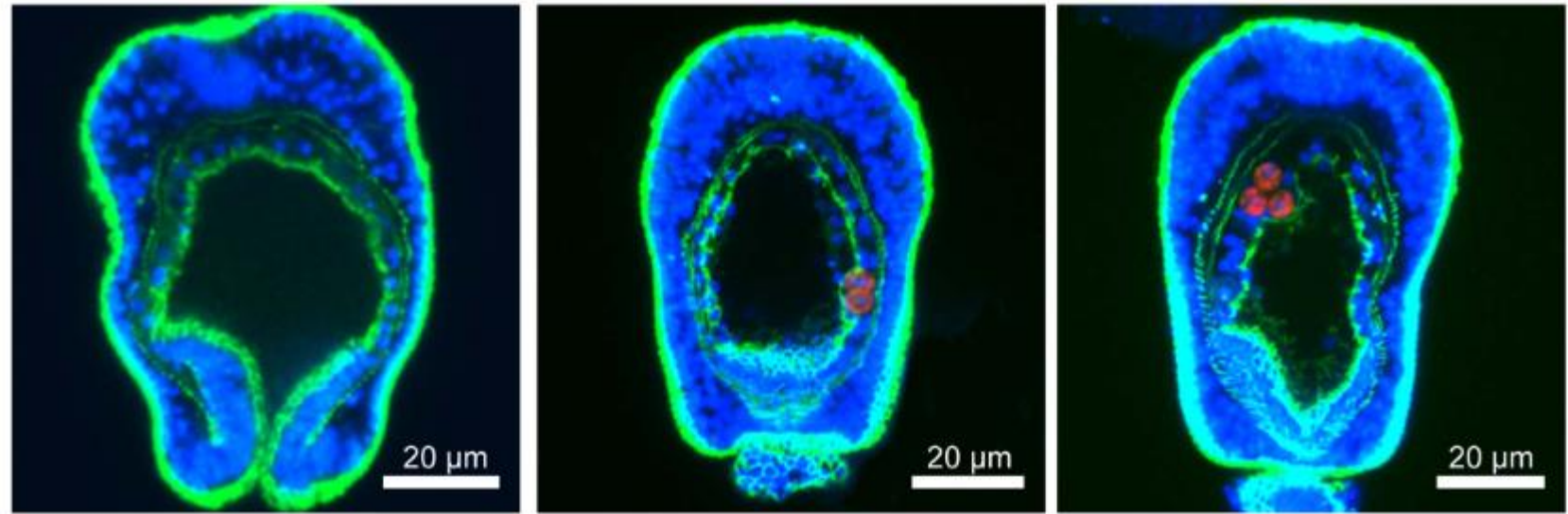
Horizontal transmission

- The majority of heterotrophic hosts disperse without their symbionts by sexually propagated offspring, and thus have to re-establish the symbiotic state at each reproductive cycle



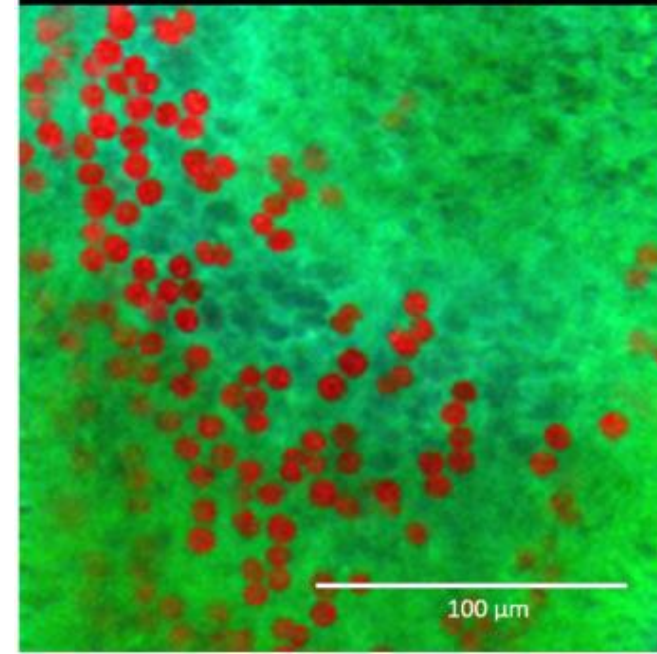
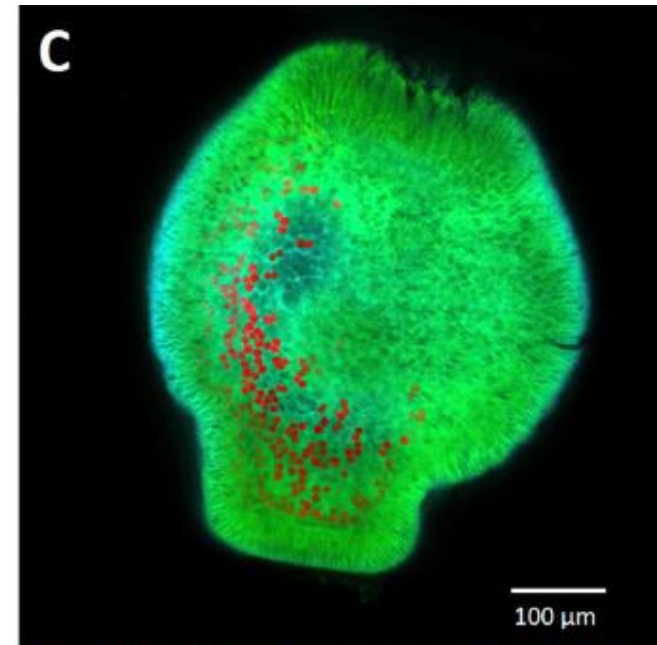
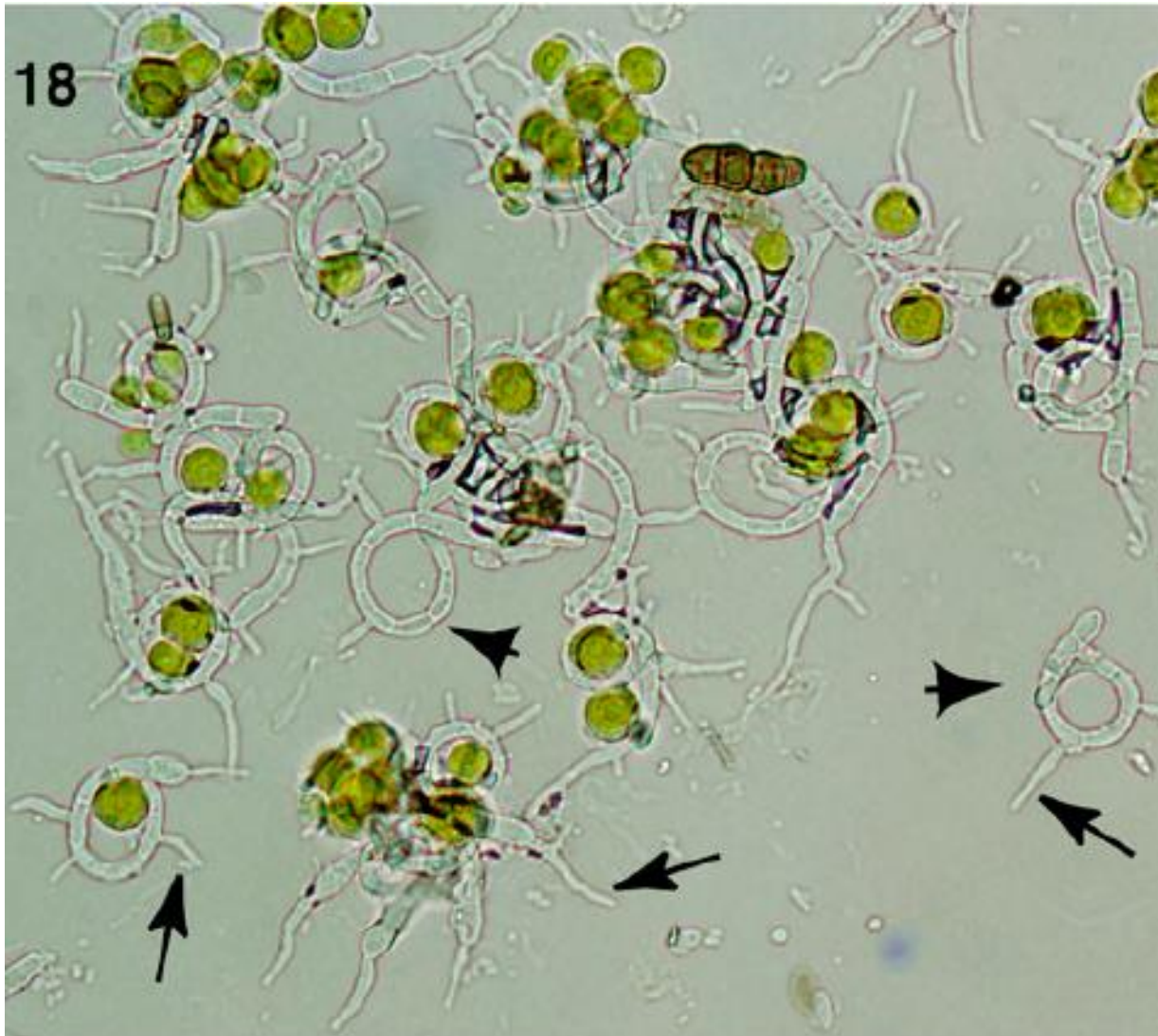
Horizontal transmission

- The majority of heterotrophic hosts disperse without their symbionts by sexually propagated offspring, and thus have to re-establish the symbiotic state at each reproductive cycle



Vertical transmission

- Co-dispersal of both symbionts



Enormous disparity in species richness

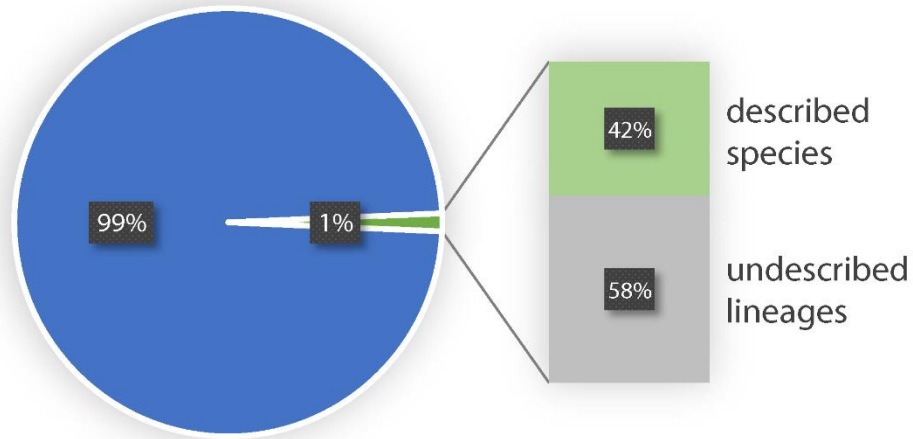
- Lichens:

- ~ 17,000 host species
- ~ 233 algal symbiotic lineages

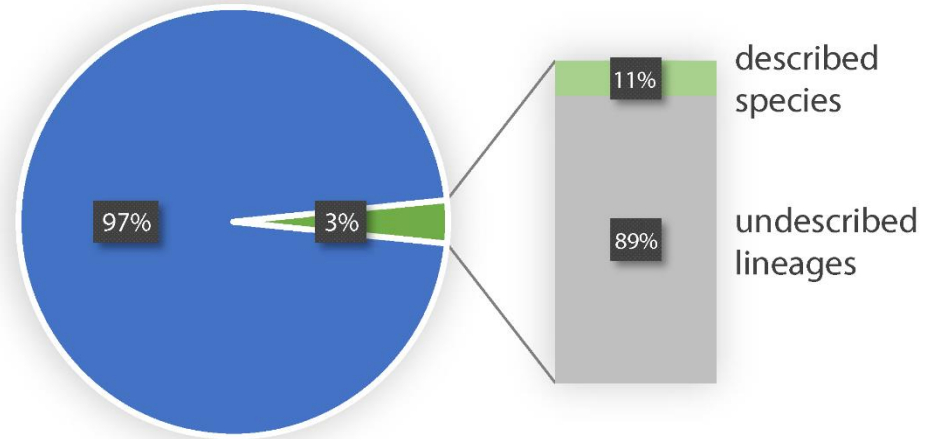
- Corals:

- ~ 6,000 host species
- ~ 200 algal symbiotic lineages

lichens



corals



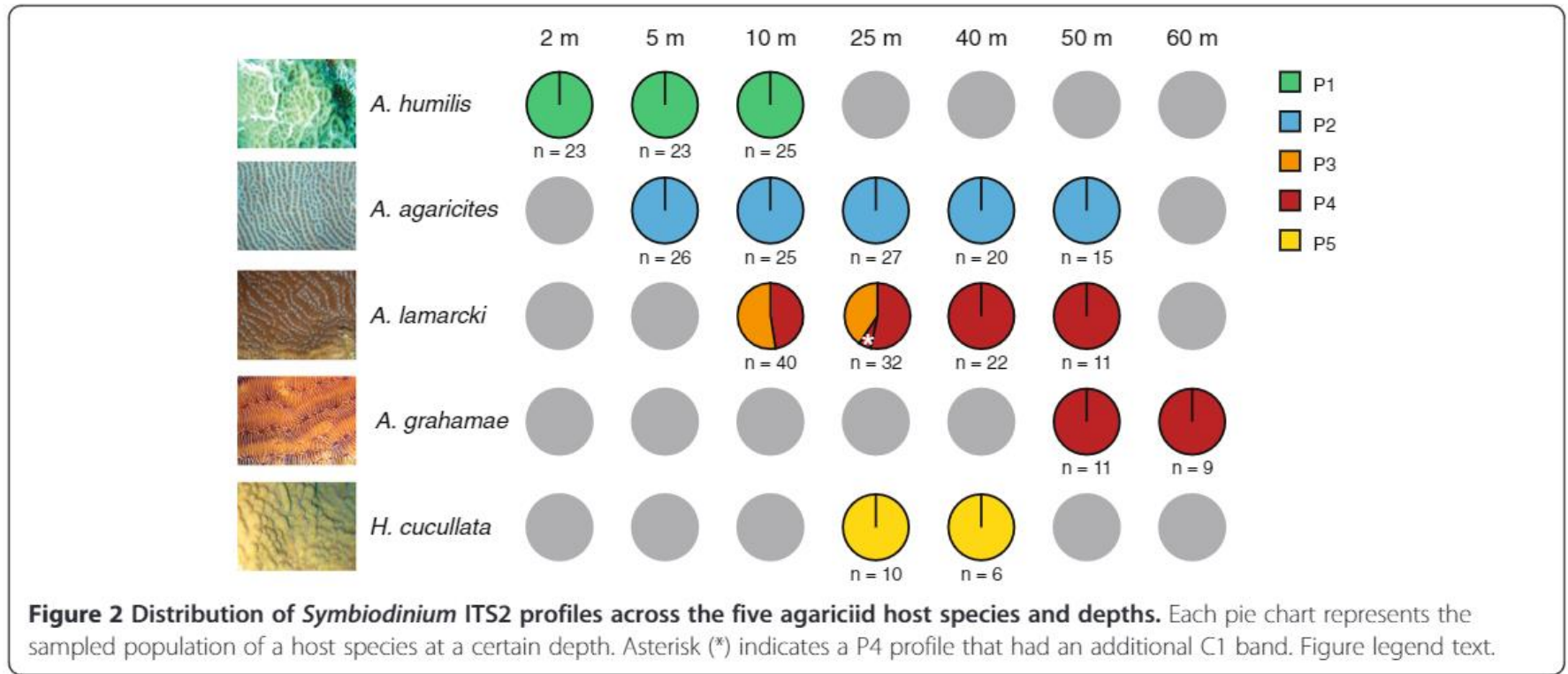
■ hosts

■ algal symbionts

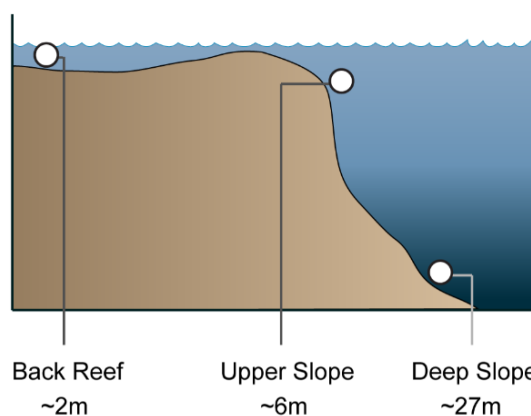
High specialization of symbionts

- Strong algal host specificity

Bongaerts et al. (2013) BMC Evol. Biol.



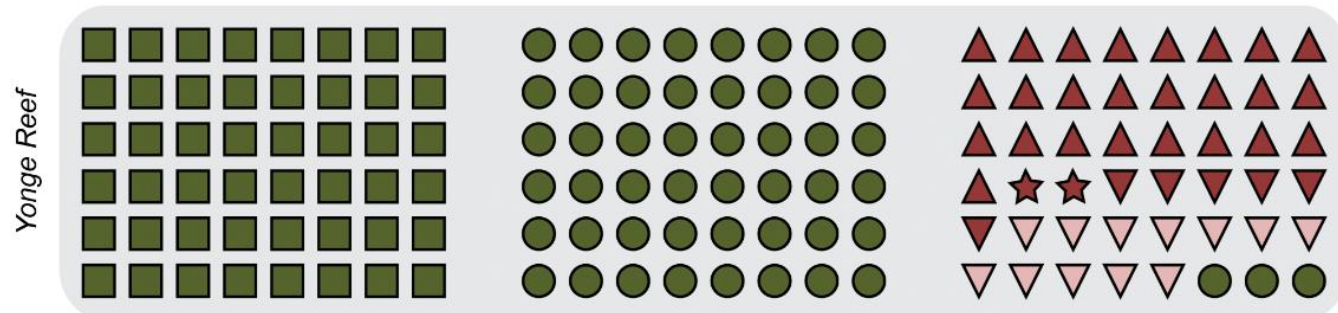
C - Habitats



'Back Reef' (~2 m)

'Upper Slope' (~6 m)

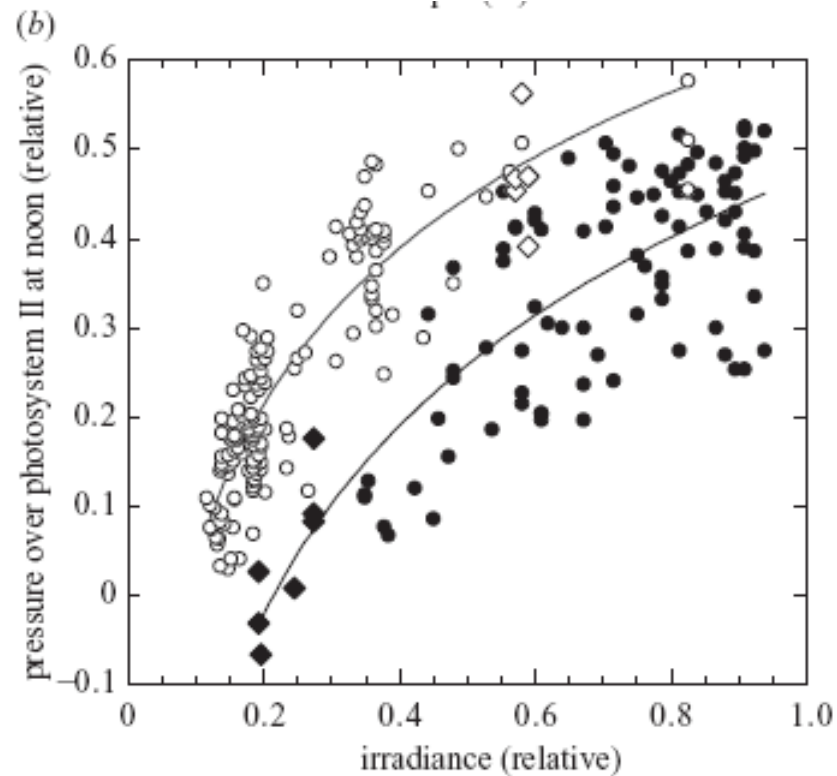
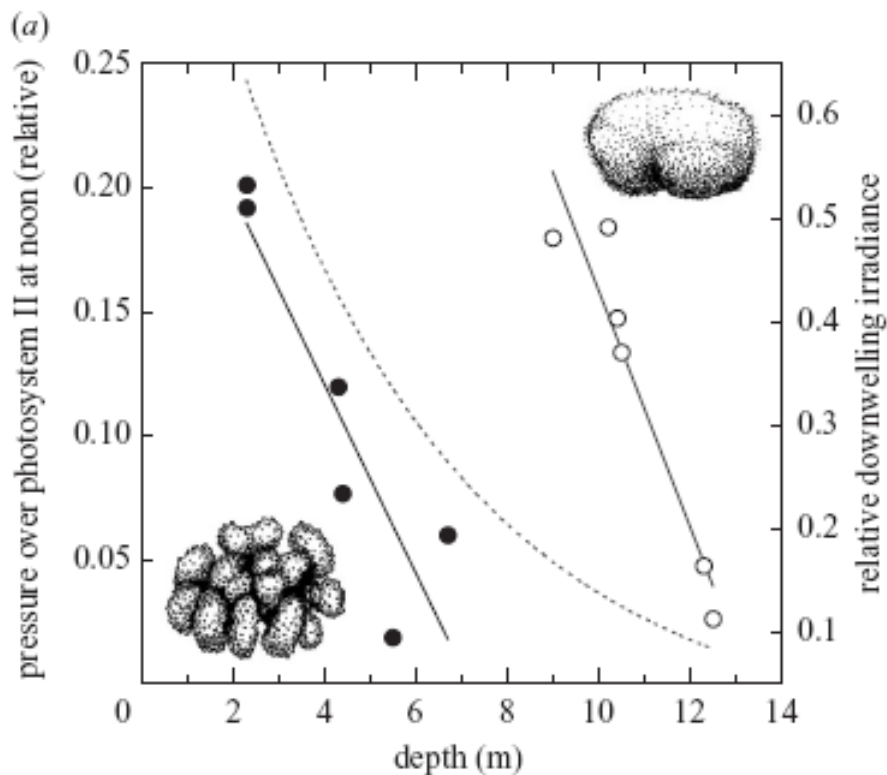
'Deep Slope' (~27 m)



Bongaerts et al. (2010) Plos ONE

High specialization of symbionts

- Narrow ecological niches of algal symbionts



Pocillopora

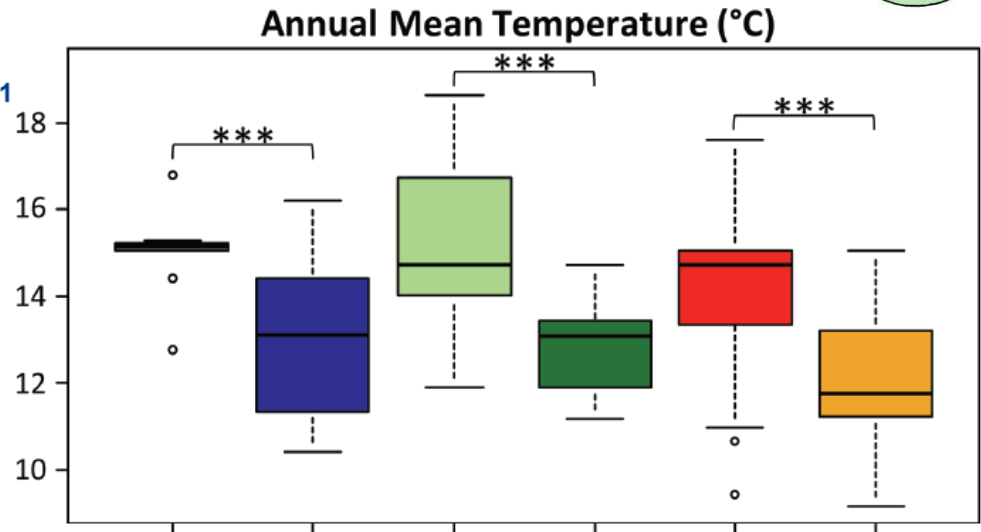
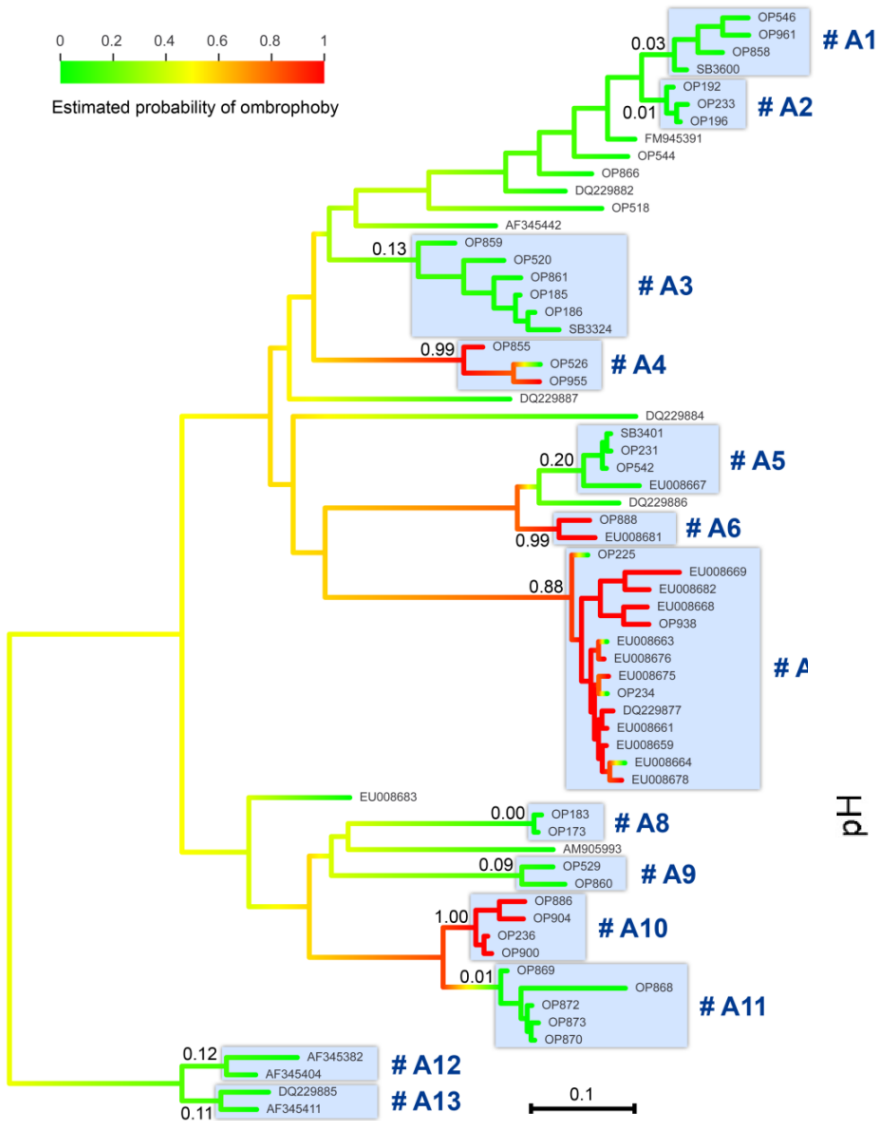


Pavona

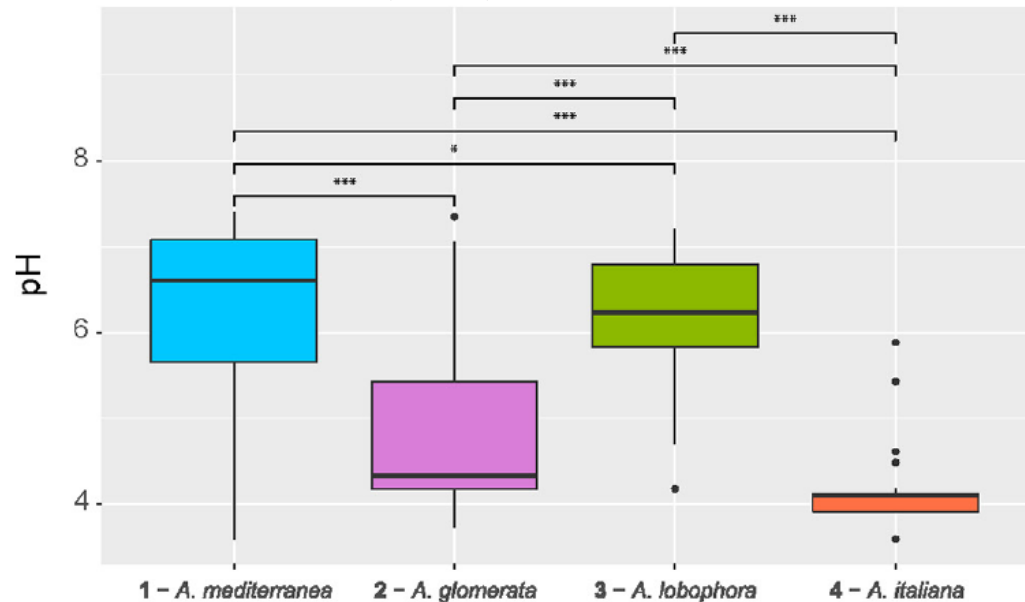
High specialization of symbionts



- Strong algal host specificity



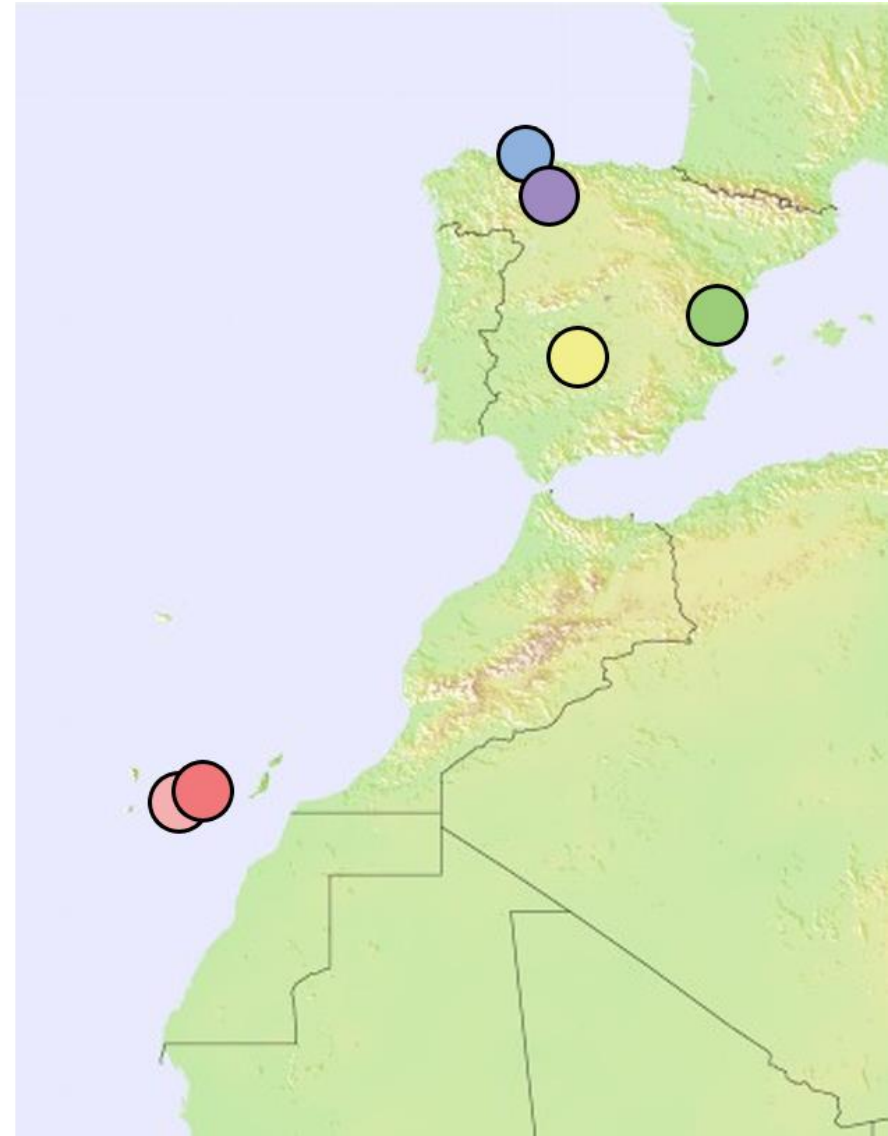
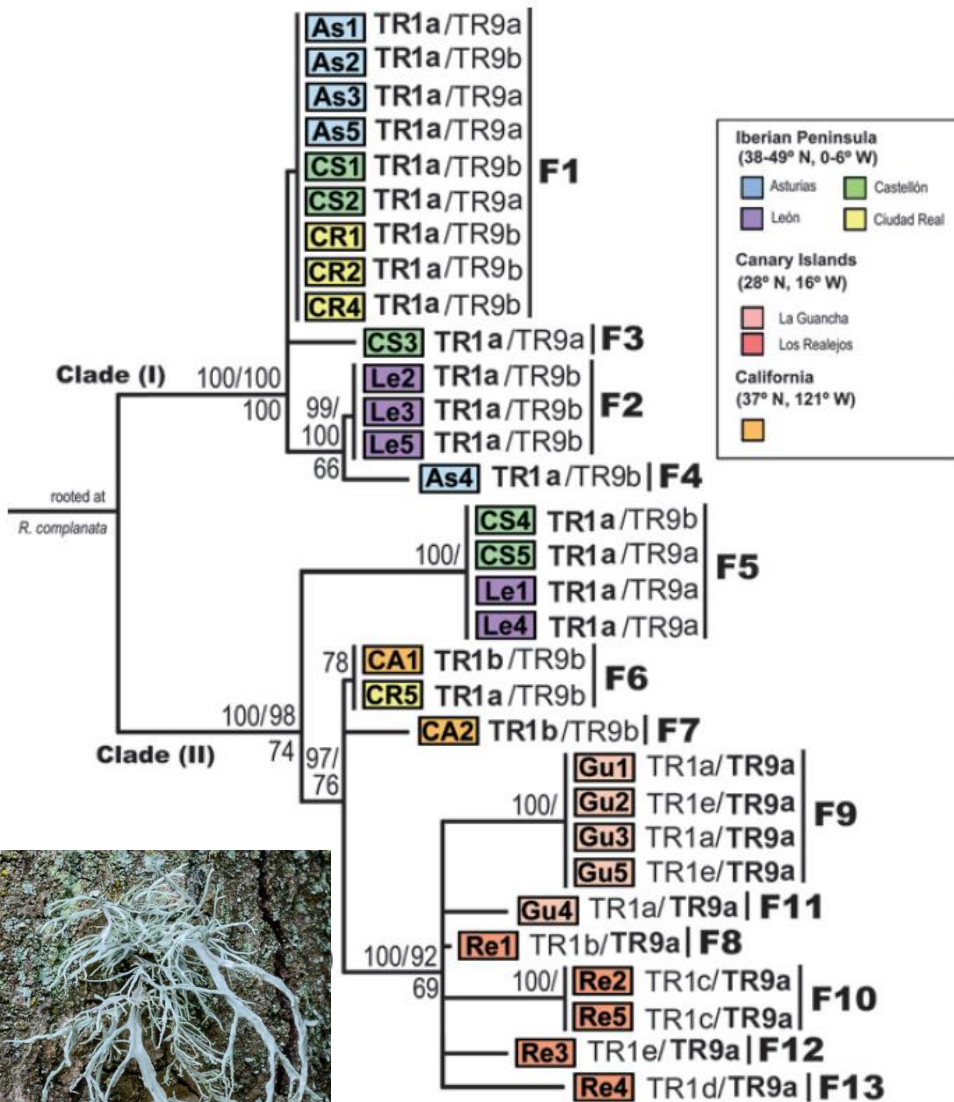
Vančurová et al. (2021): *Frontiers Microb.*



Škvorová et al. (2022): *Frontiers Microb.*

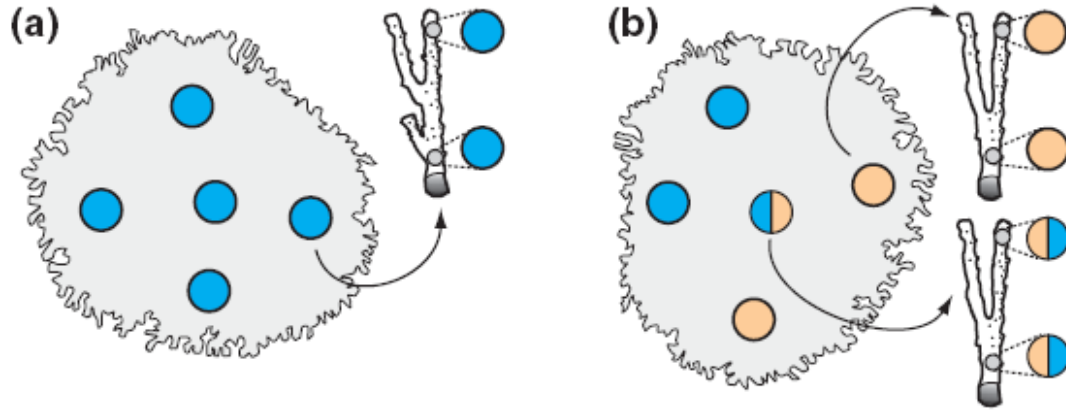
Peksa & Škaloud (2011): *Mol. Ecol.*

Multiple symbionts

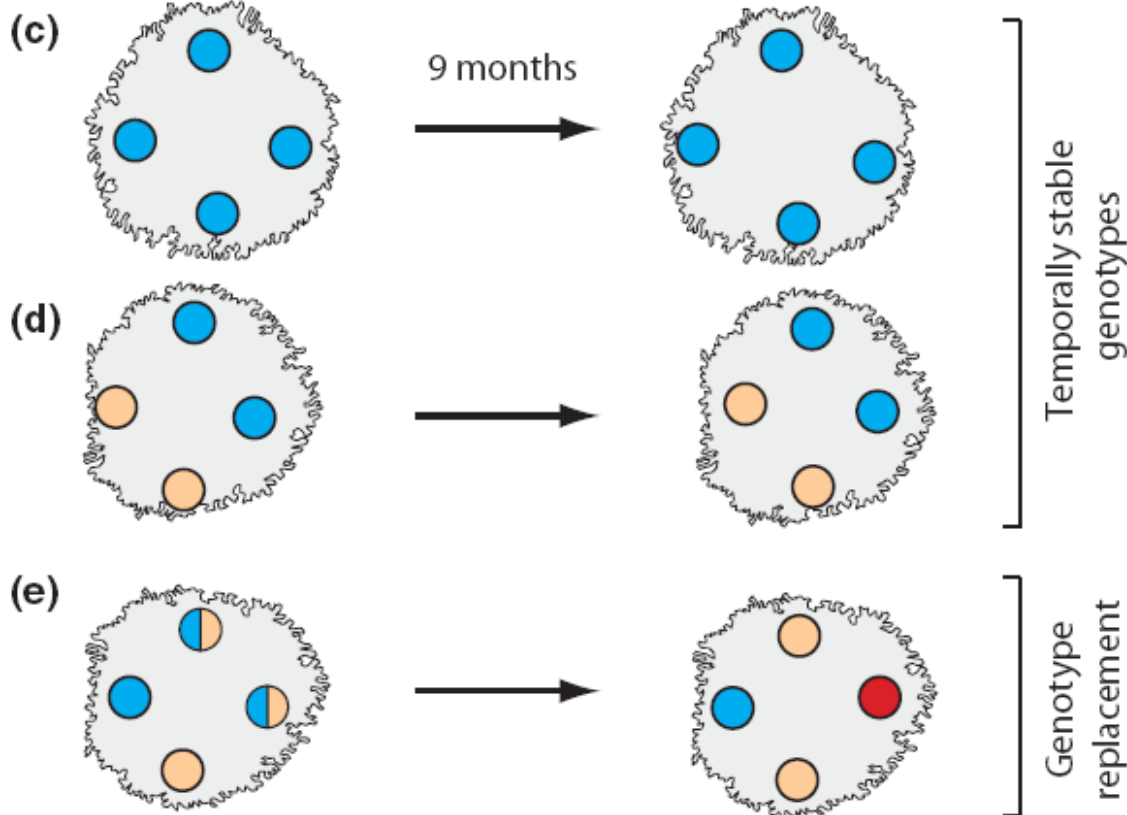


Ramalina farinacea

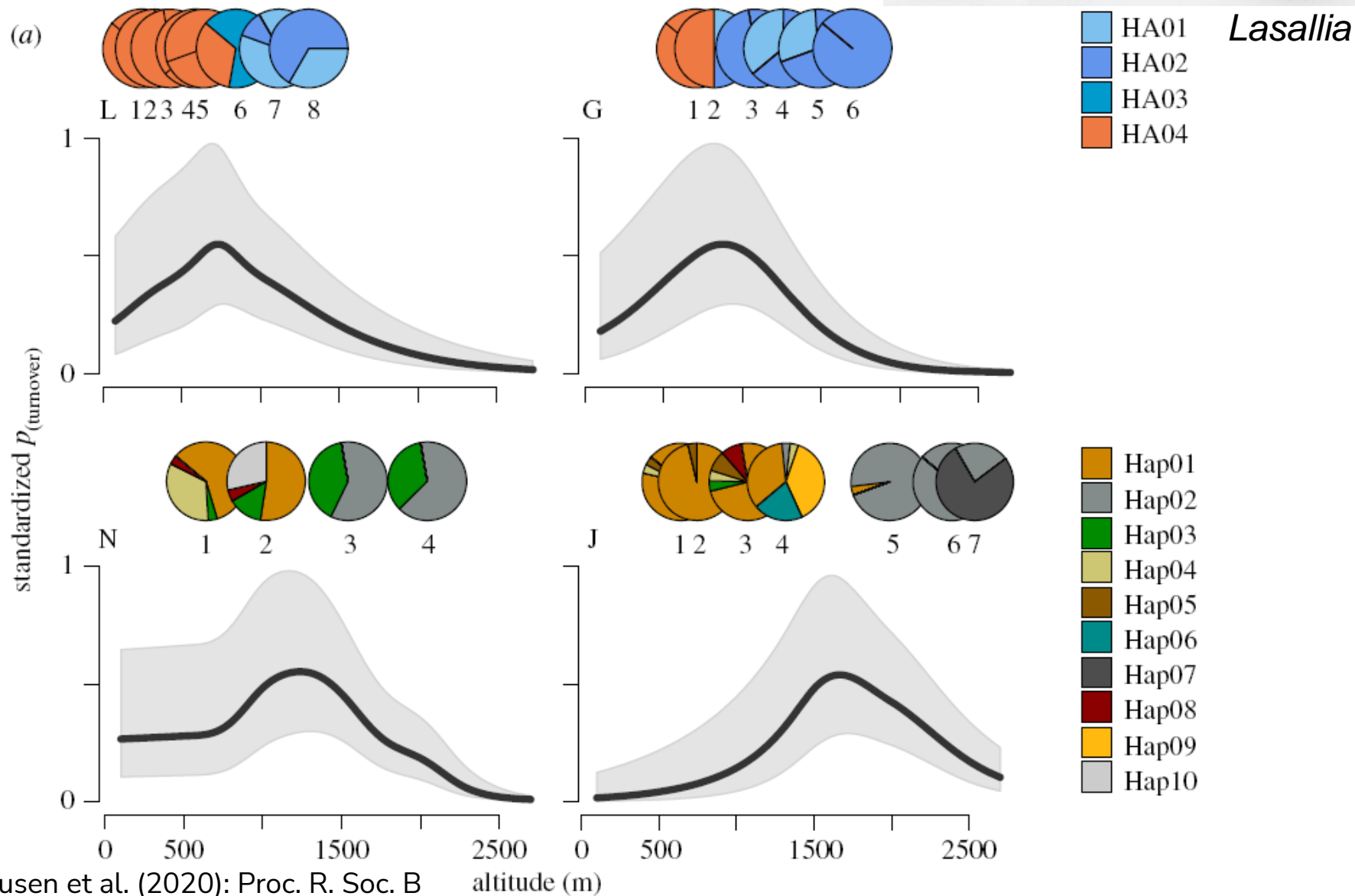
Multiple symbionts



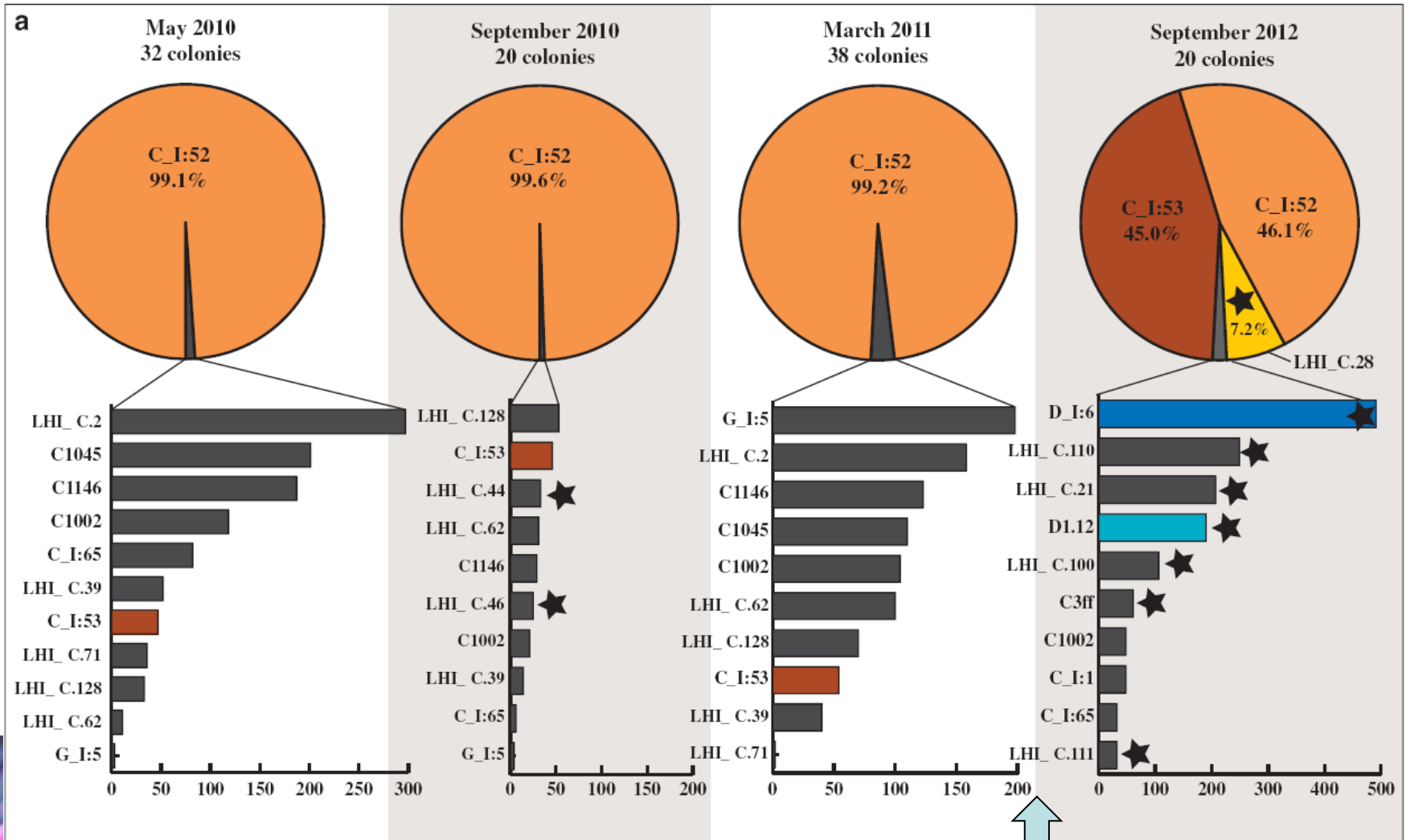
Pocillopora



Symbiont switching



Symbiont switching



bleaching event

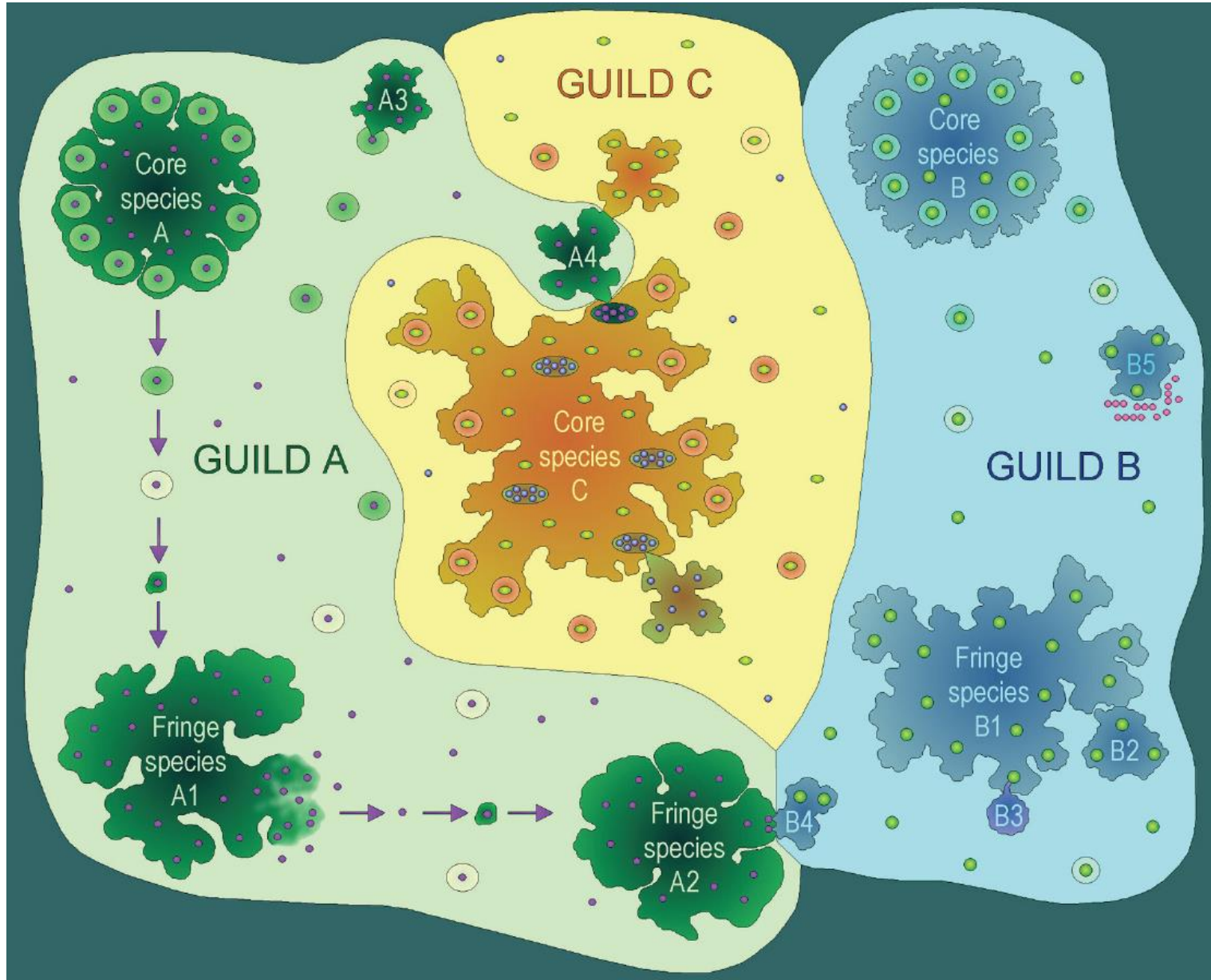


Stylophora pistillata

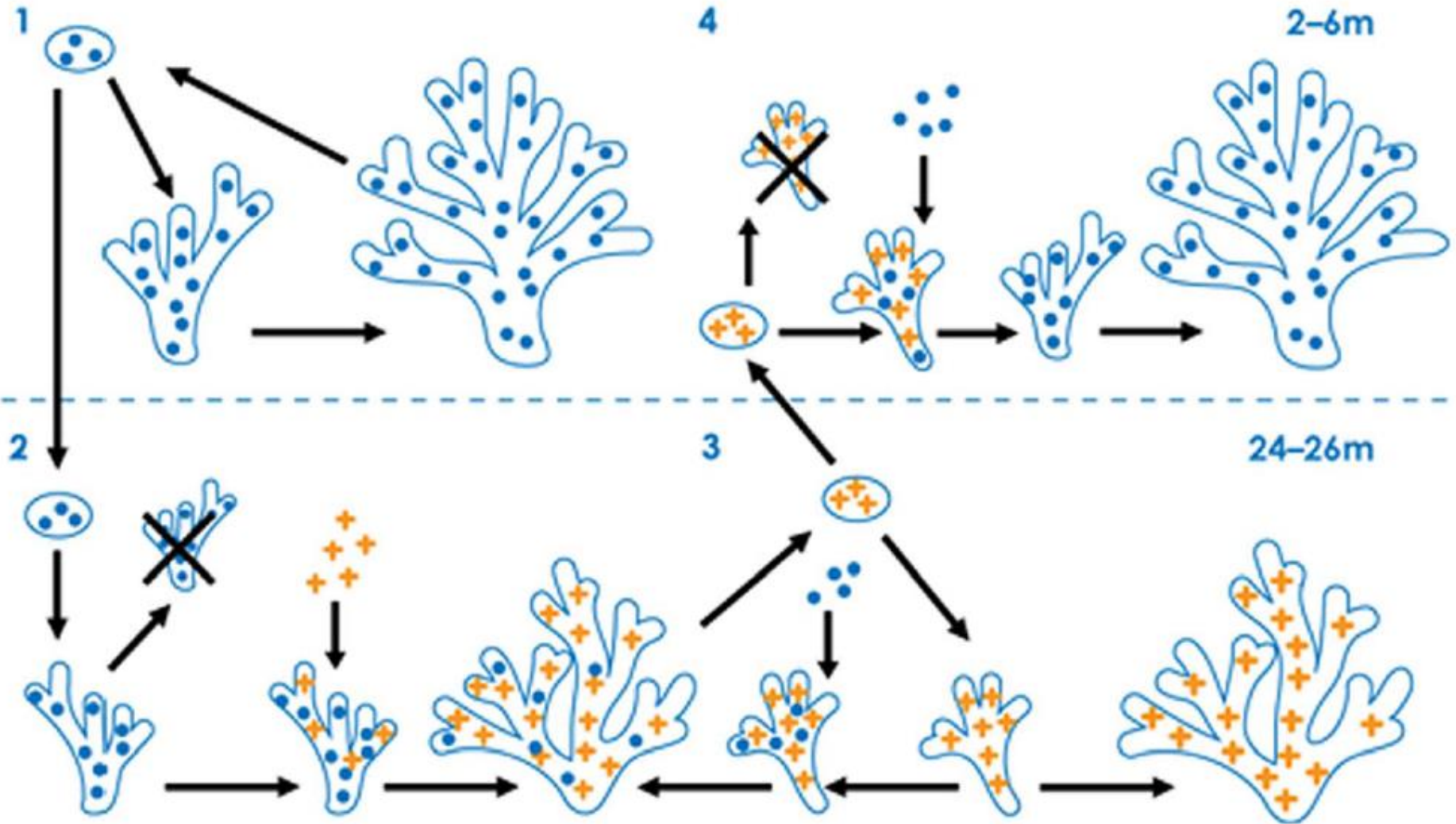
Boulotte et al. (2016): ISME J

Habitat adapted symbiosis

- Core (vertical transmission) and fringe (horizontal transmission) species

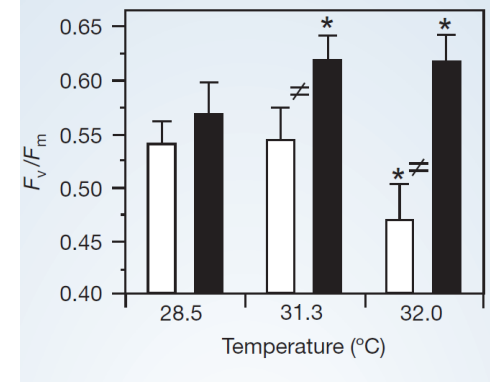
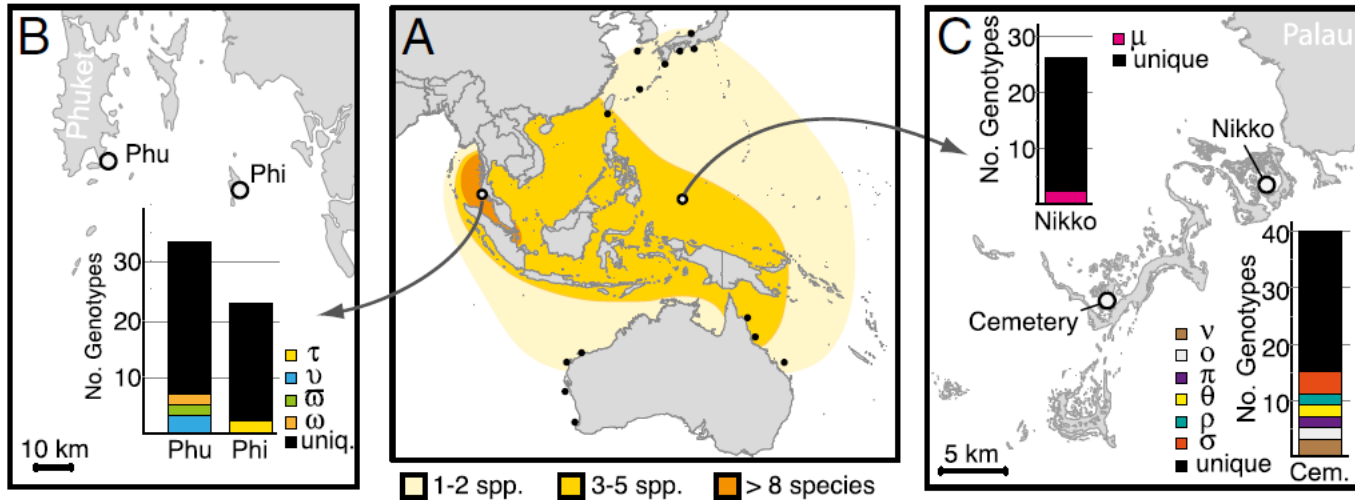


Habitat adapted symbiosis

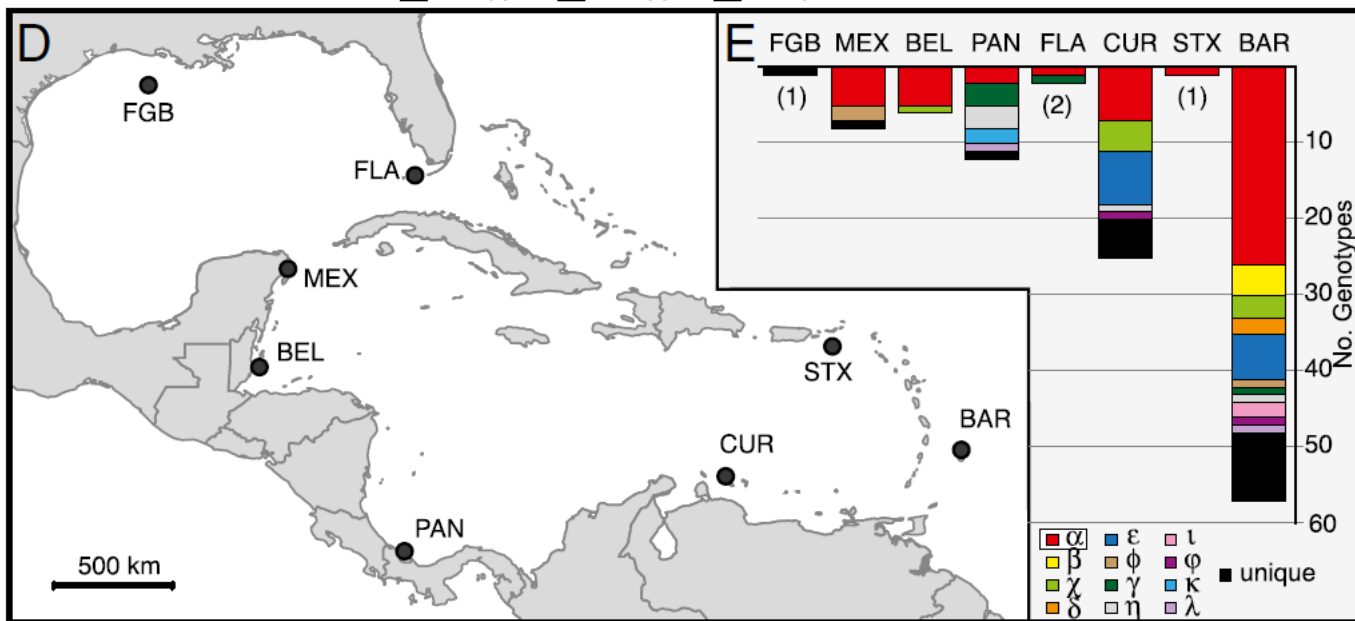


Habitat adapted symbiosis

- Avoiding coral bleaching by a symbiont switch?
 - Invasion of the Caribbean, heat-tolerant symbiont in the Gulf of Mexico



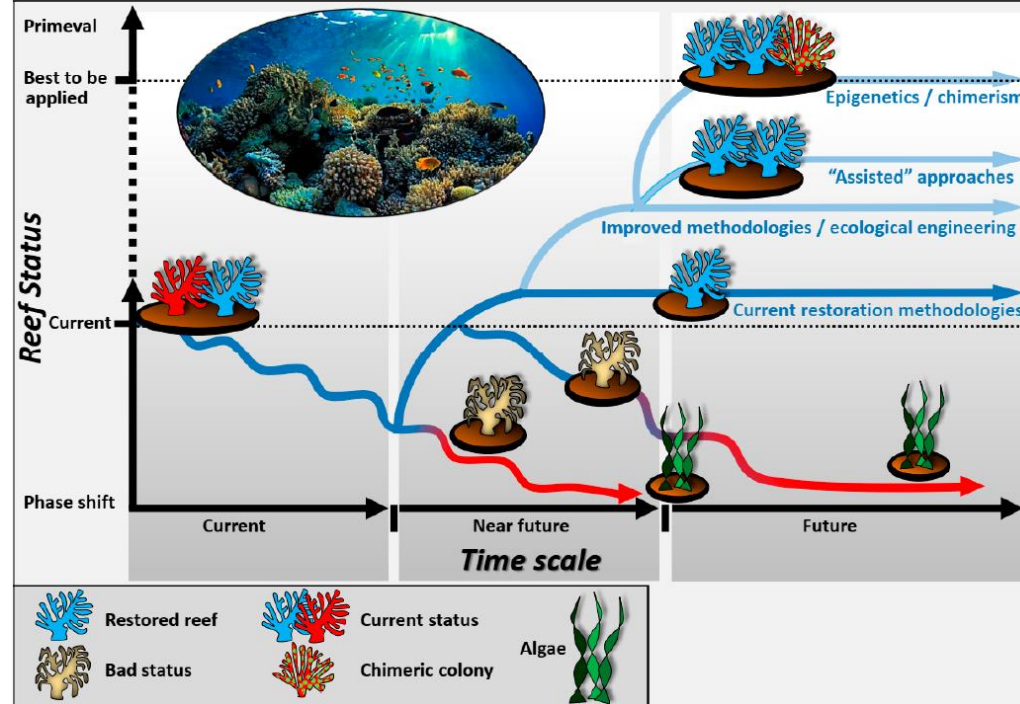
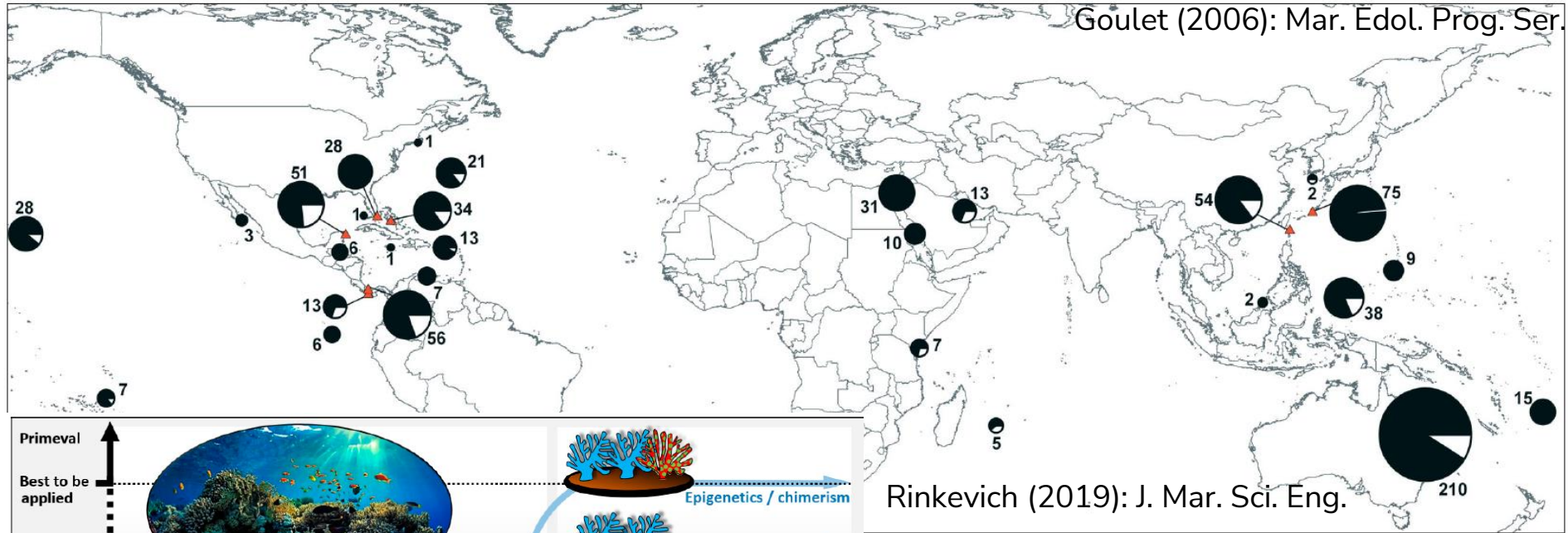
Rowan (2004): Nature



Pettay et al. (2015): PNAS

Habitat adapted symbiosis

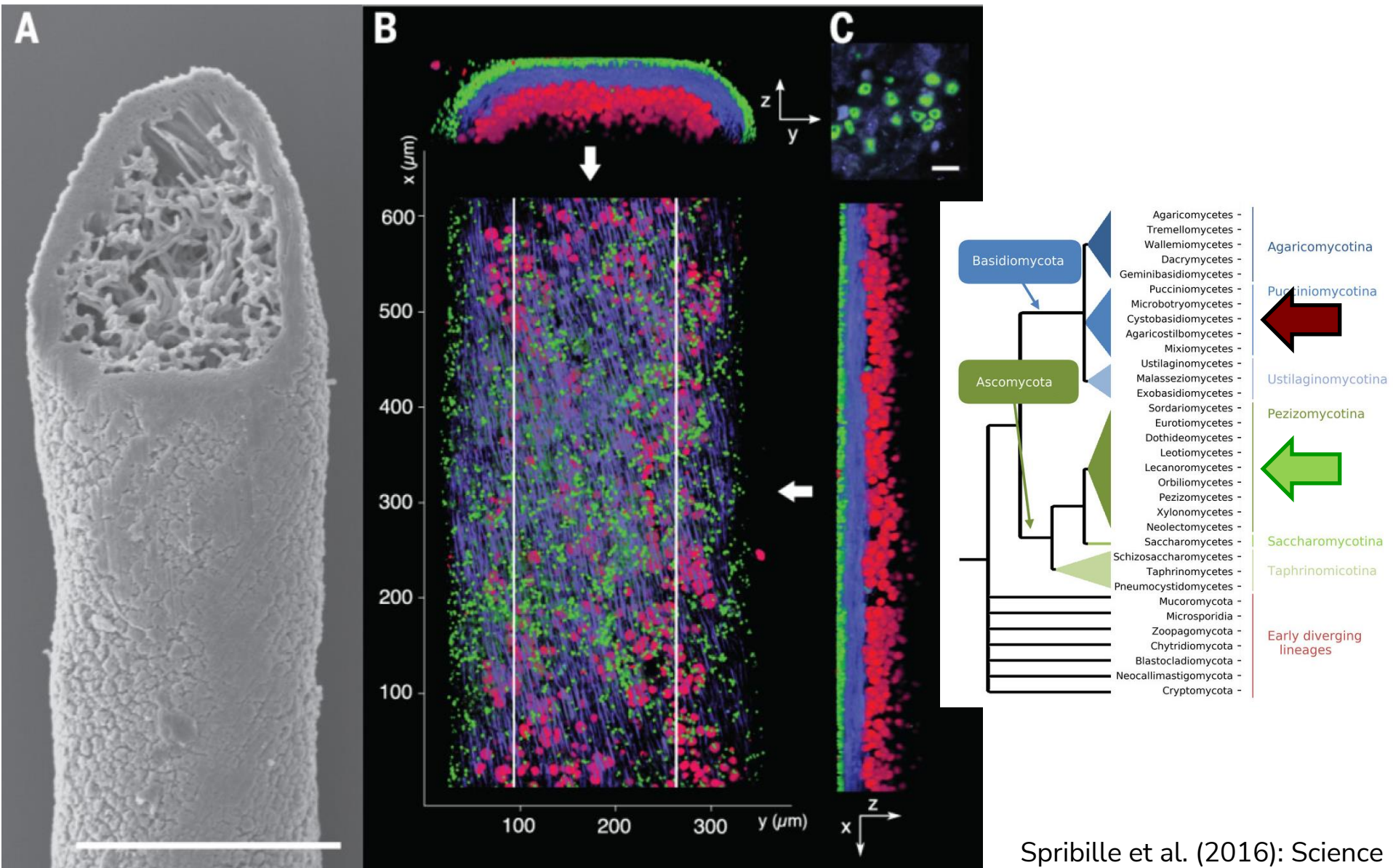
- Only 23% of coral species host multiple symbions





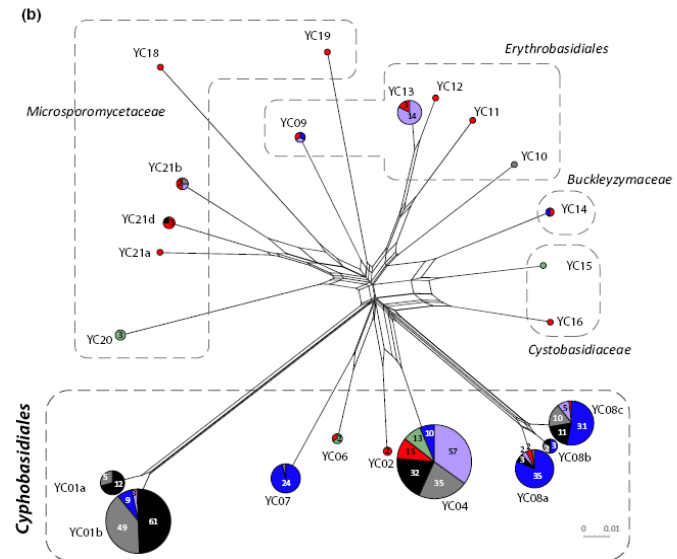
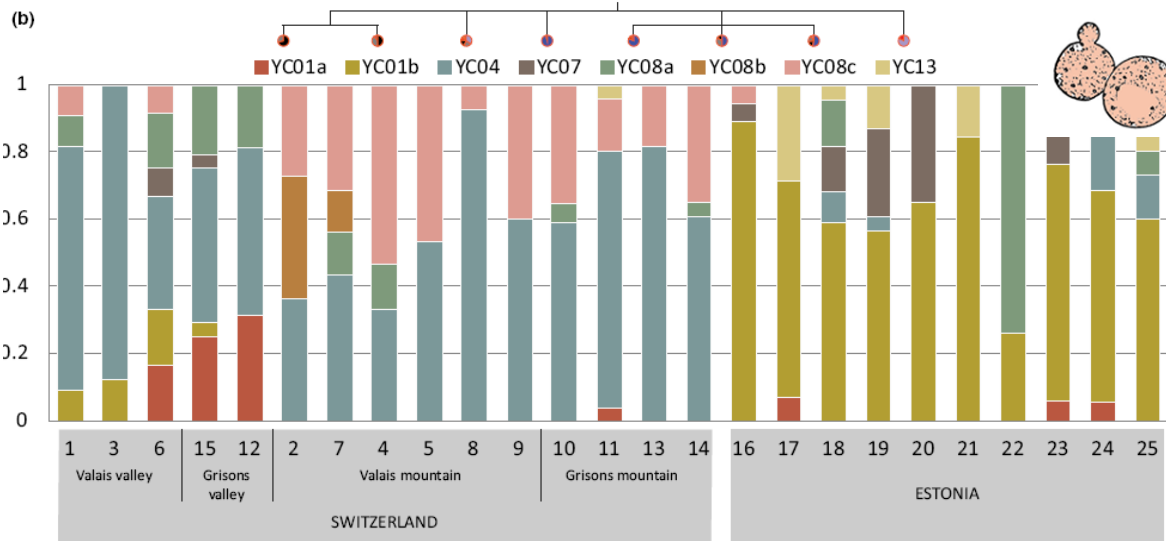
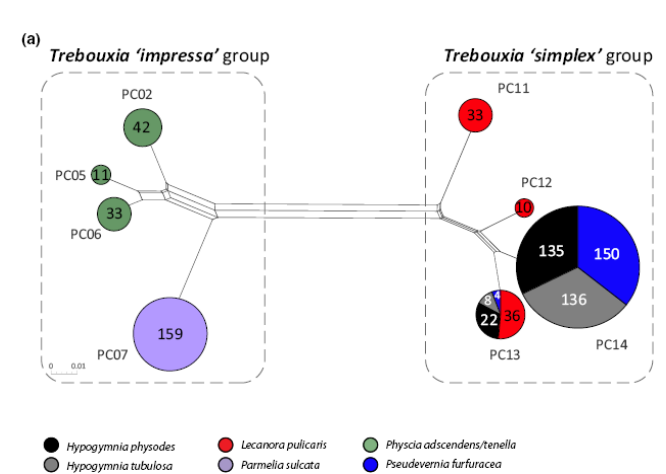
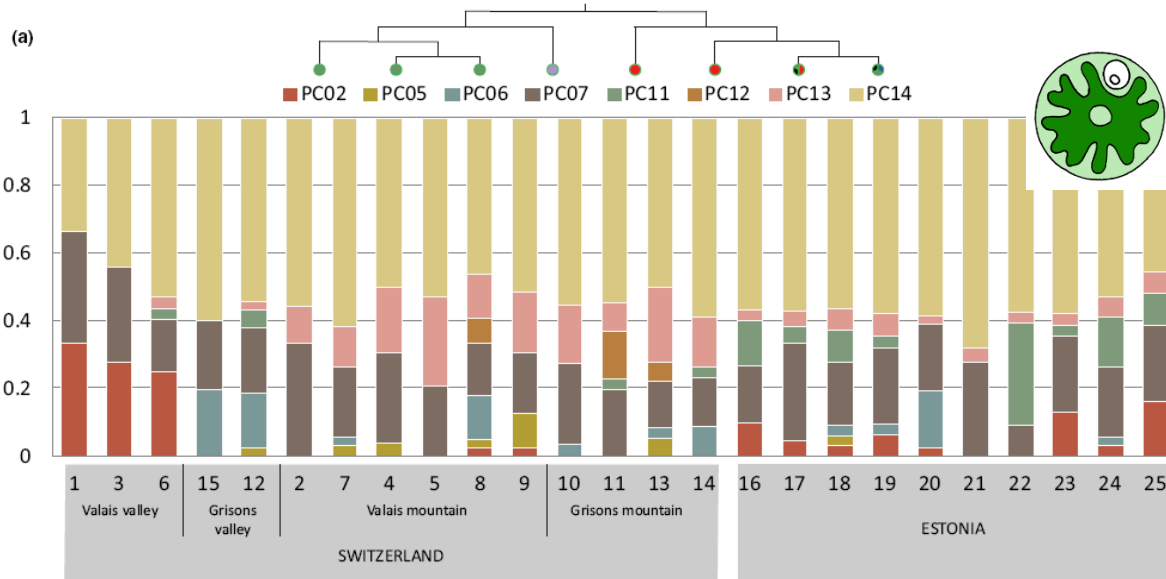
Revolution in symbiosis research

- Basidiomycete yeasts as a third partner in lichen symbiosis?



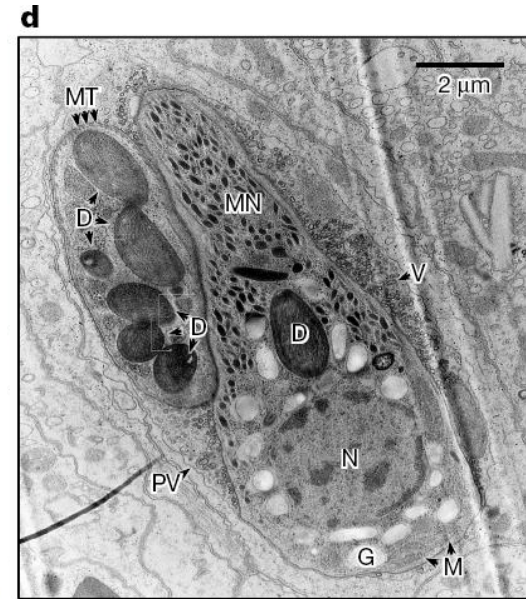
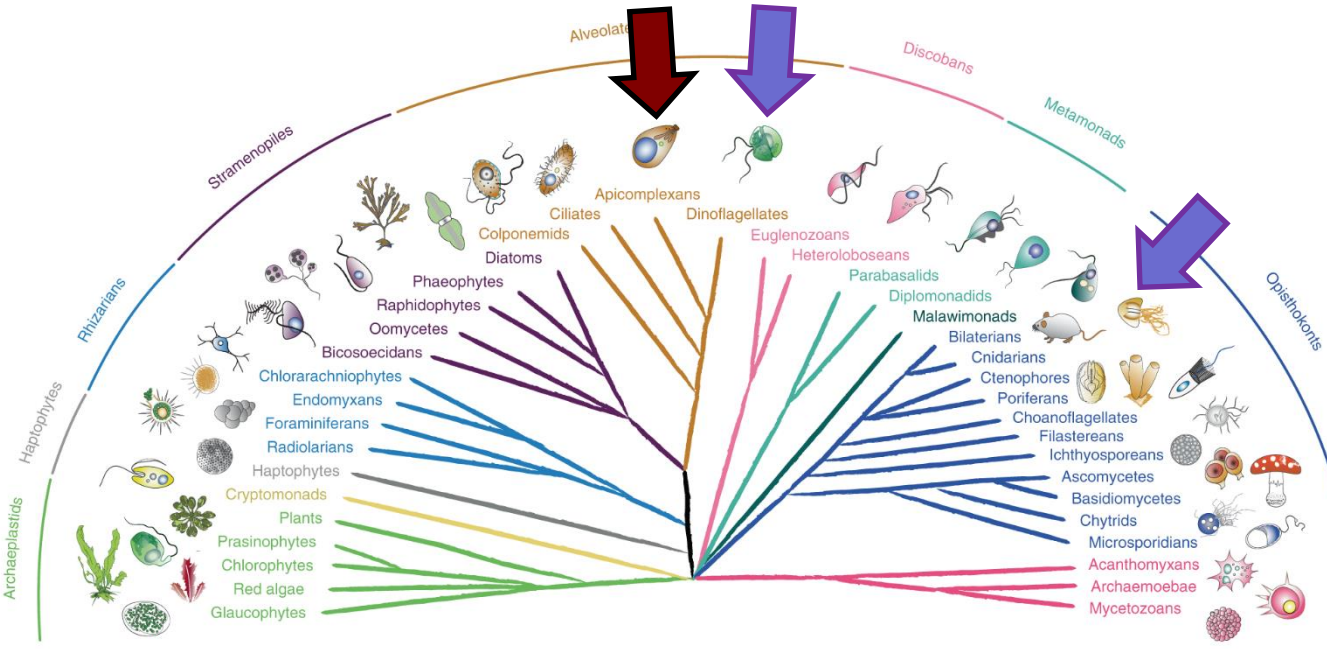
Revolution in symbiosis research

- Yeasts not omnipresent, much less lichen-specific than the included algae

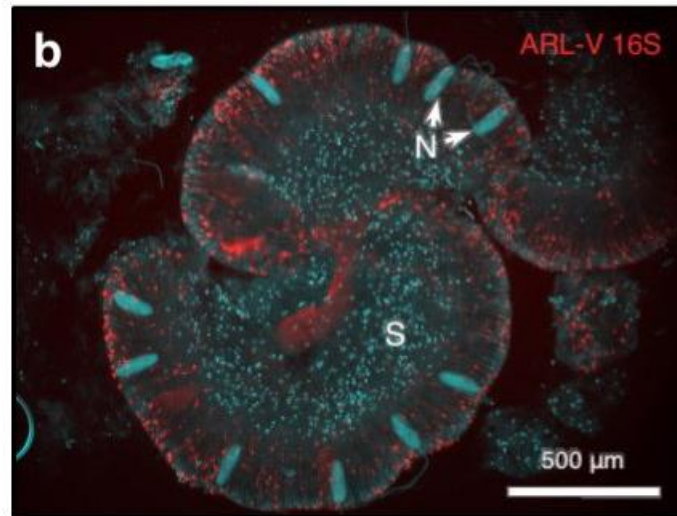
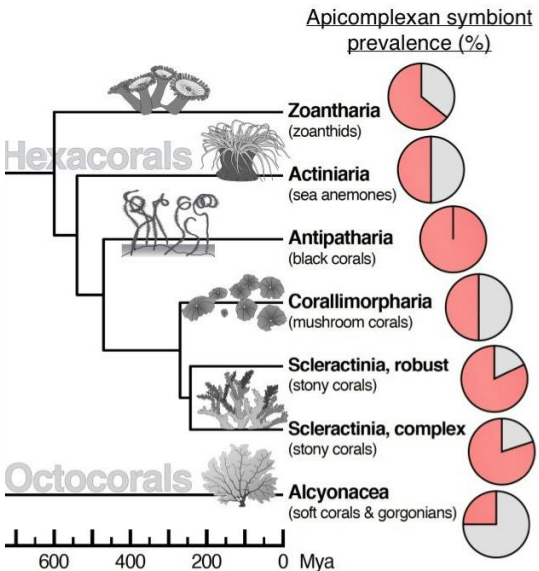


Revolution in symbiosis research

- Corallicolids – a third partner in coral symbiosis?



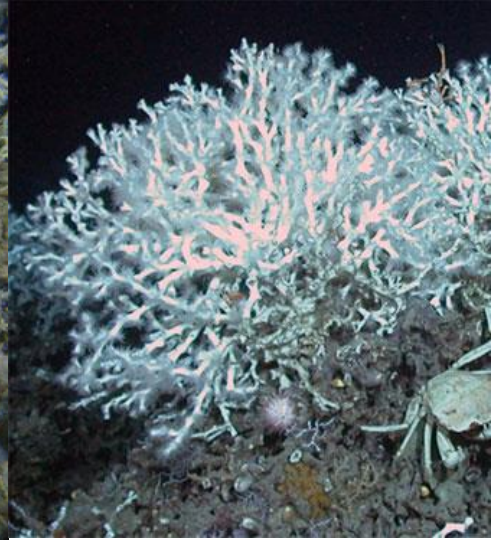
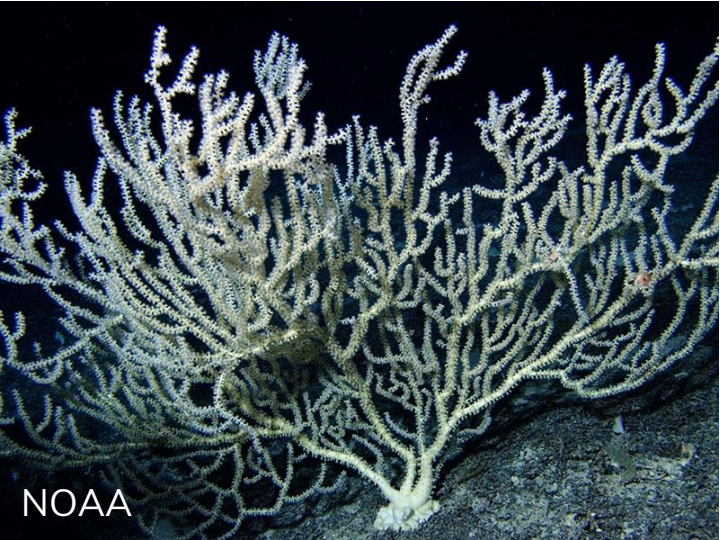
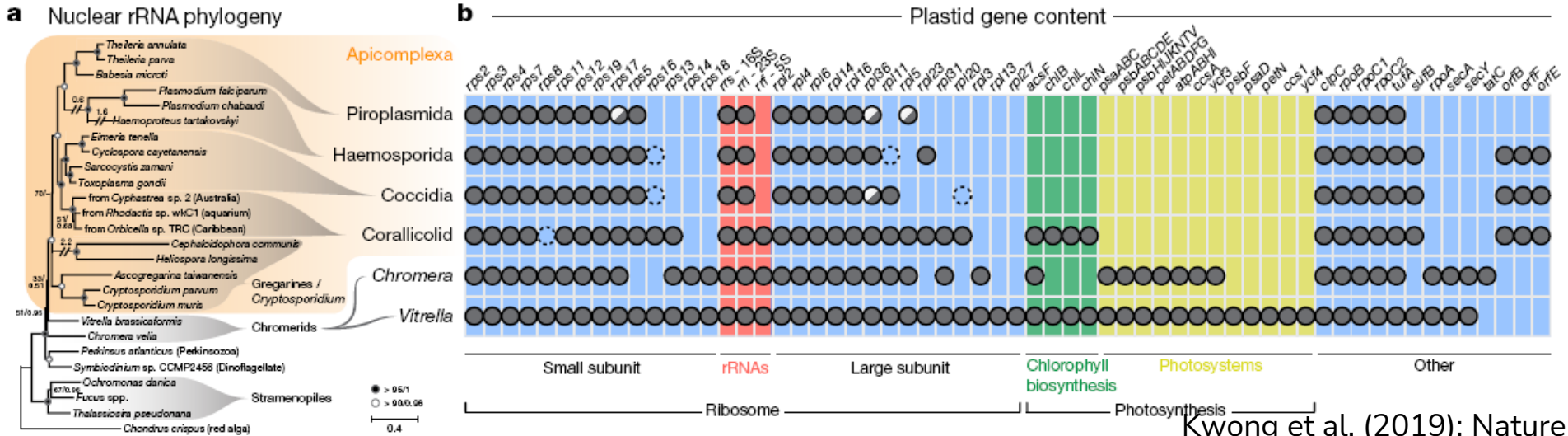
Kwong et al. (2019): Nature



Revolution in symbiosis research

- Coralicolids – a third partner in coral symbiosis?
 - Chlorophyll genes with unknown function (survival at low-oxygen environments?)

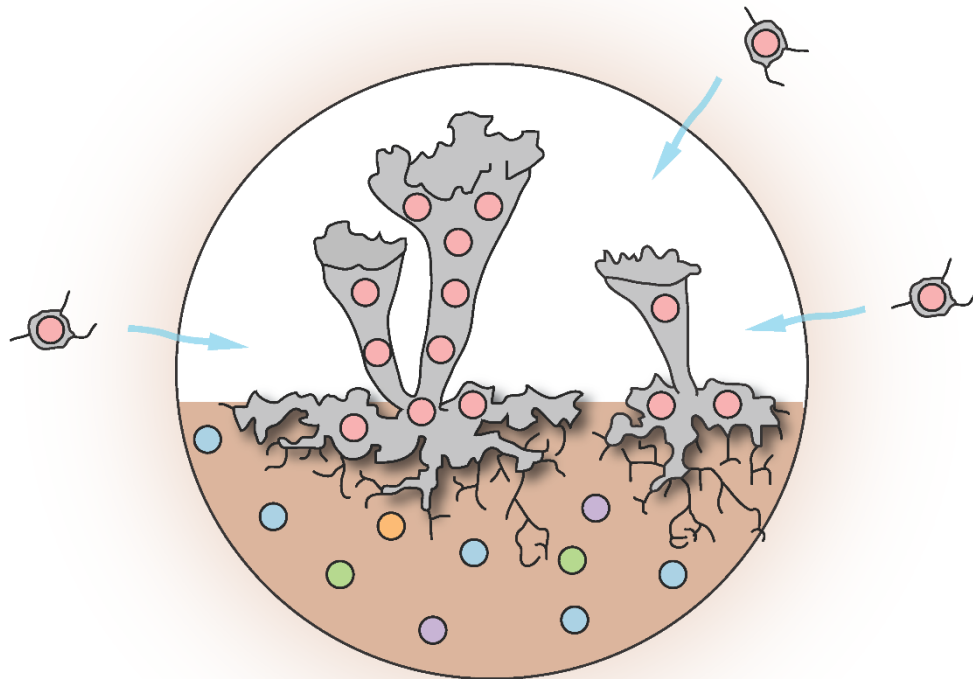
Vohsen et al. (2020): Microbiome



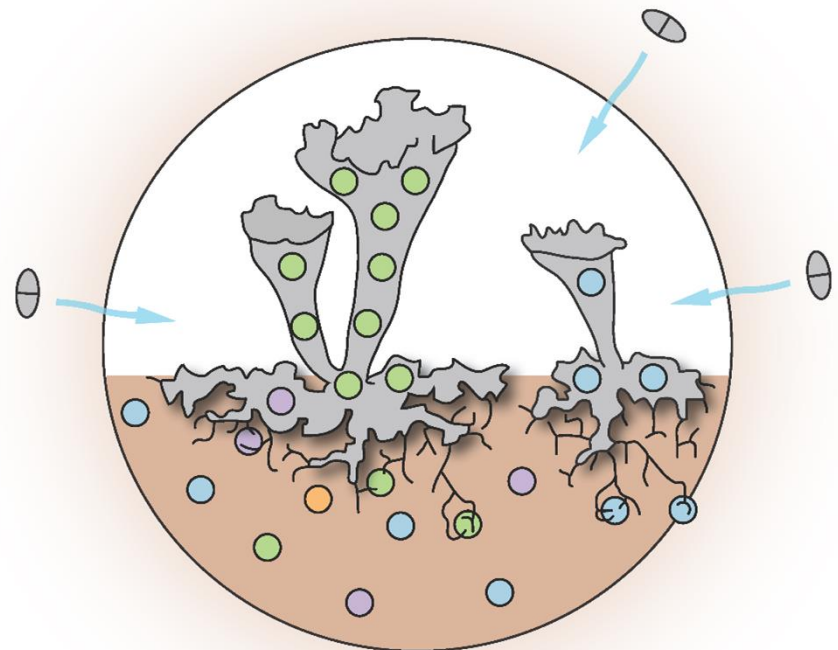
Paradox I.

Contrasting diversity of differently dispersed symbionts?

- Hosts that maternally transfer symbionts to their offspring (**vertical dispersal**) might be expected to contain less diverse symbionts than hosts which are required to obtain them environmentally (**horizontal dispersal**).



vertical dispersal

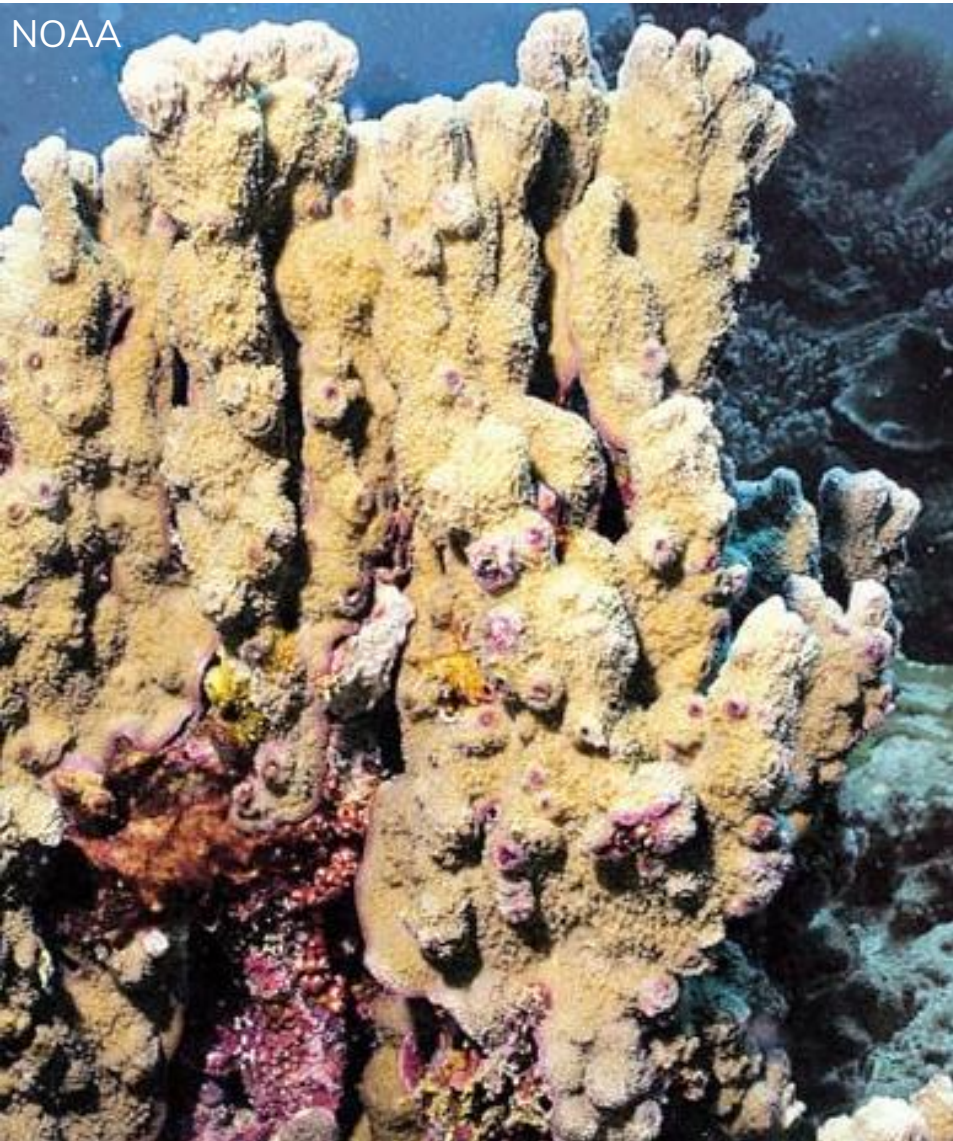


horizontal dispersal

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

NOAA



Montipora - vertical dispersal

van Oppen (2004): Mar. Biol.

NOAA



Acropora - horizontal dispersal

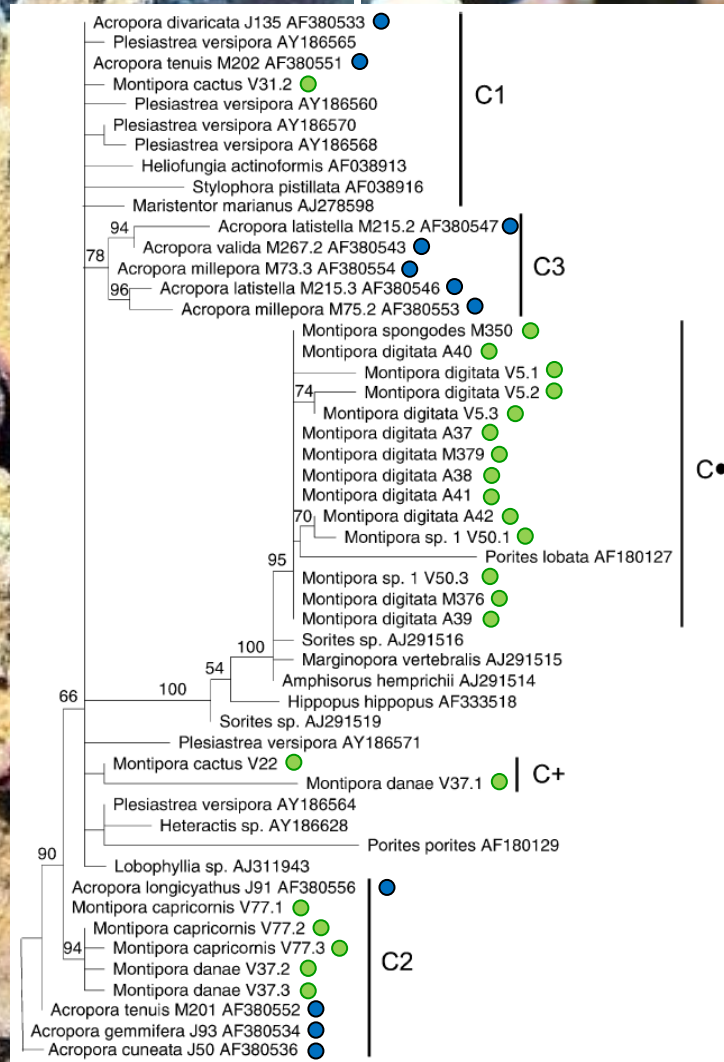
Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

NOAA

van Oppen (2004): Mar. Biol.

NOAA

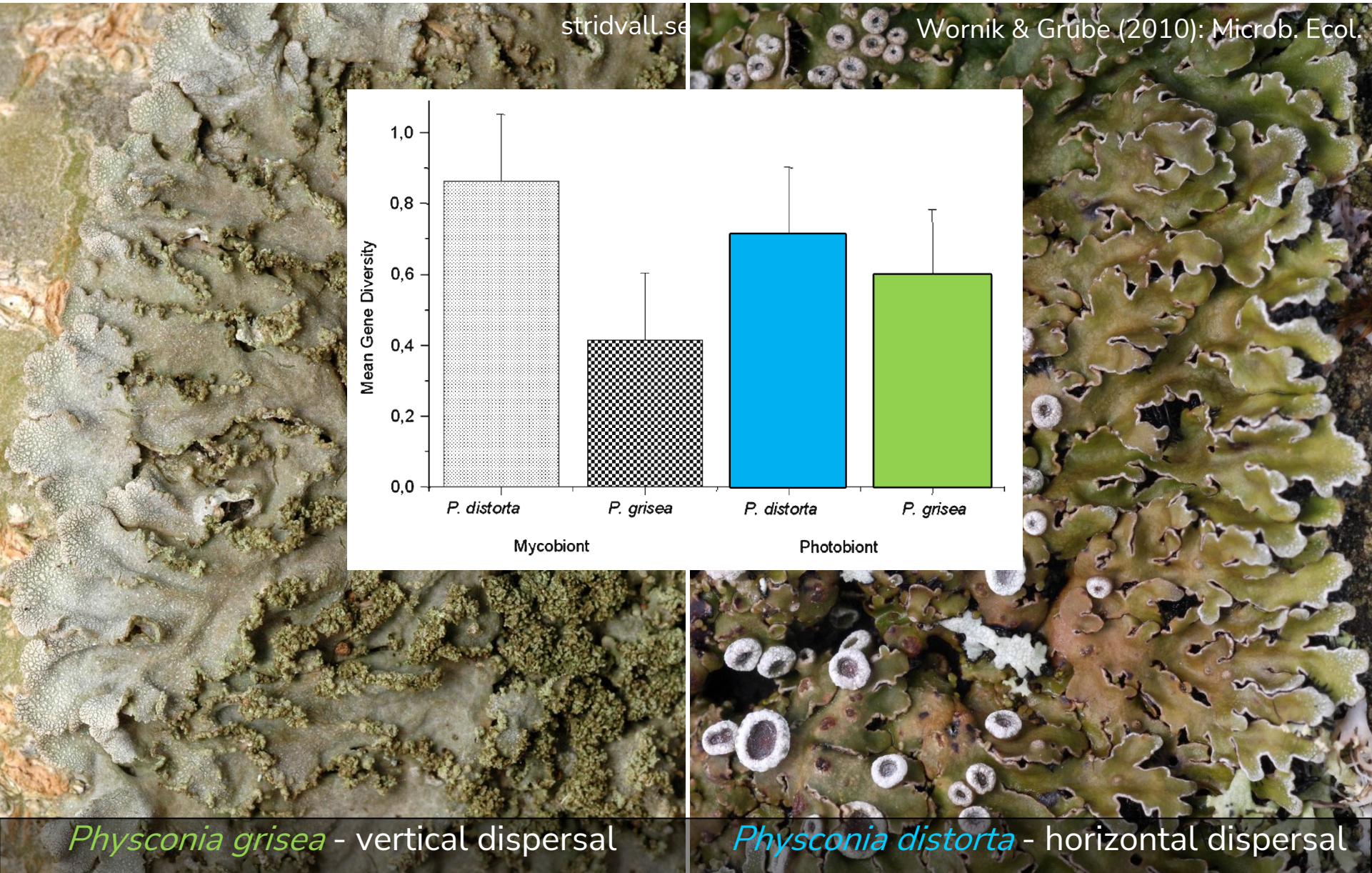


Montipora - vertical dispersal

Acropora - horizontal dispersal

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity



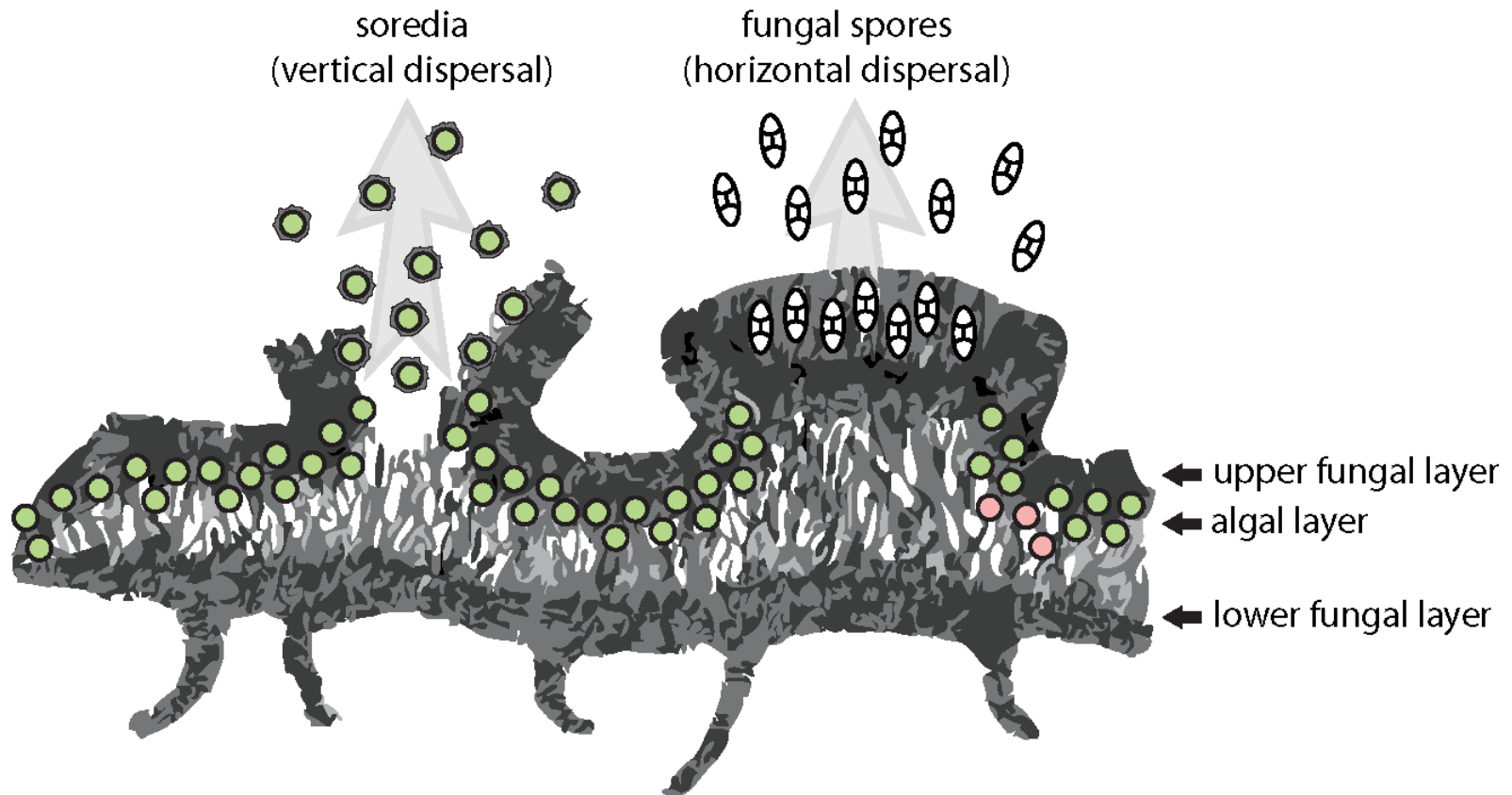
Physconia grisea - vertical dispersal

Physconia distorta - horizontal dispersal

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

- Why do hosts maintain vertical dispersal of symbionts?
 - Need to convince the symbiont to travel with the host
 - Need to form specialized structures
 - The propagules are heavy, produced in less quantities in comparison with sexual offspring



Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

- Why do hosts maintain vertical dispersal of symbionts?
 - To win the battle against other symbionts in a local space



Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity



Ohmura et al. (2006): Bryologist



Parmotrema tinctorum - vertical dispersal

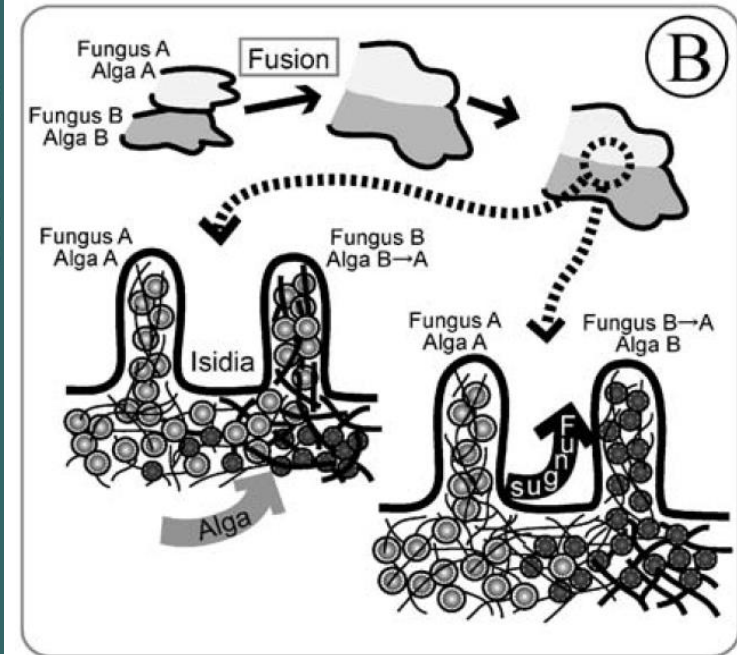
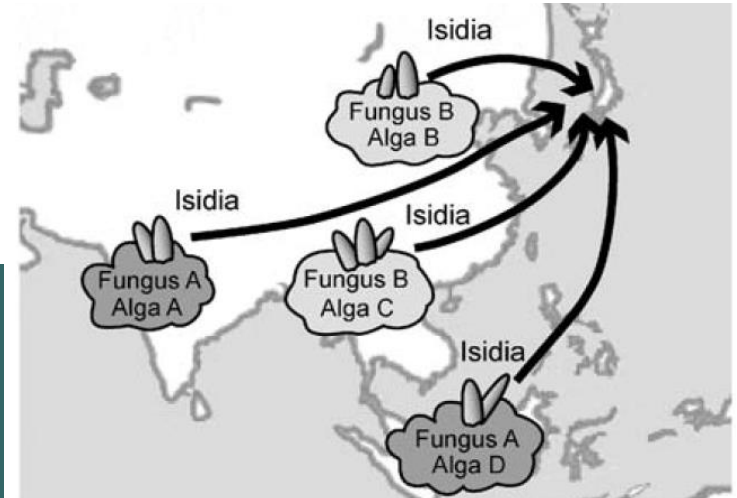
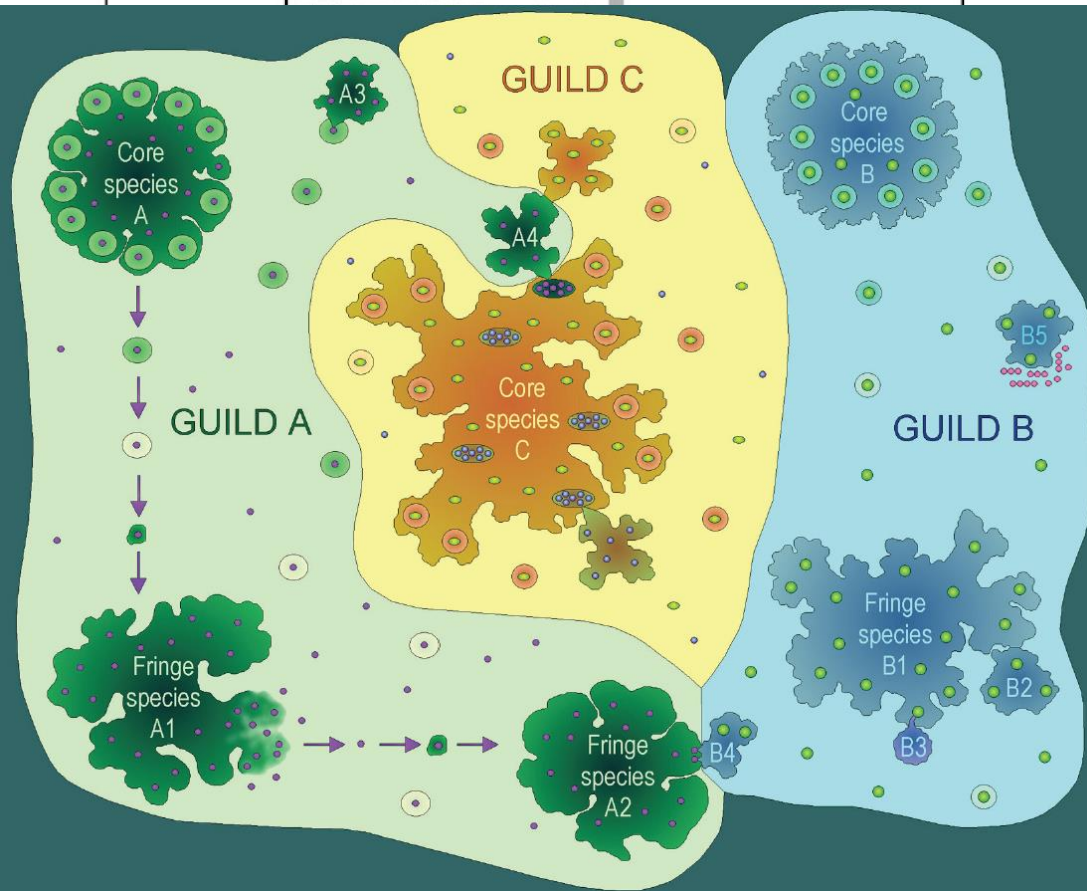
tropicallichens.net

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

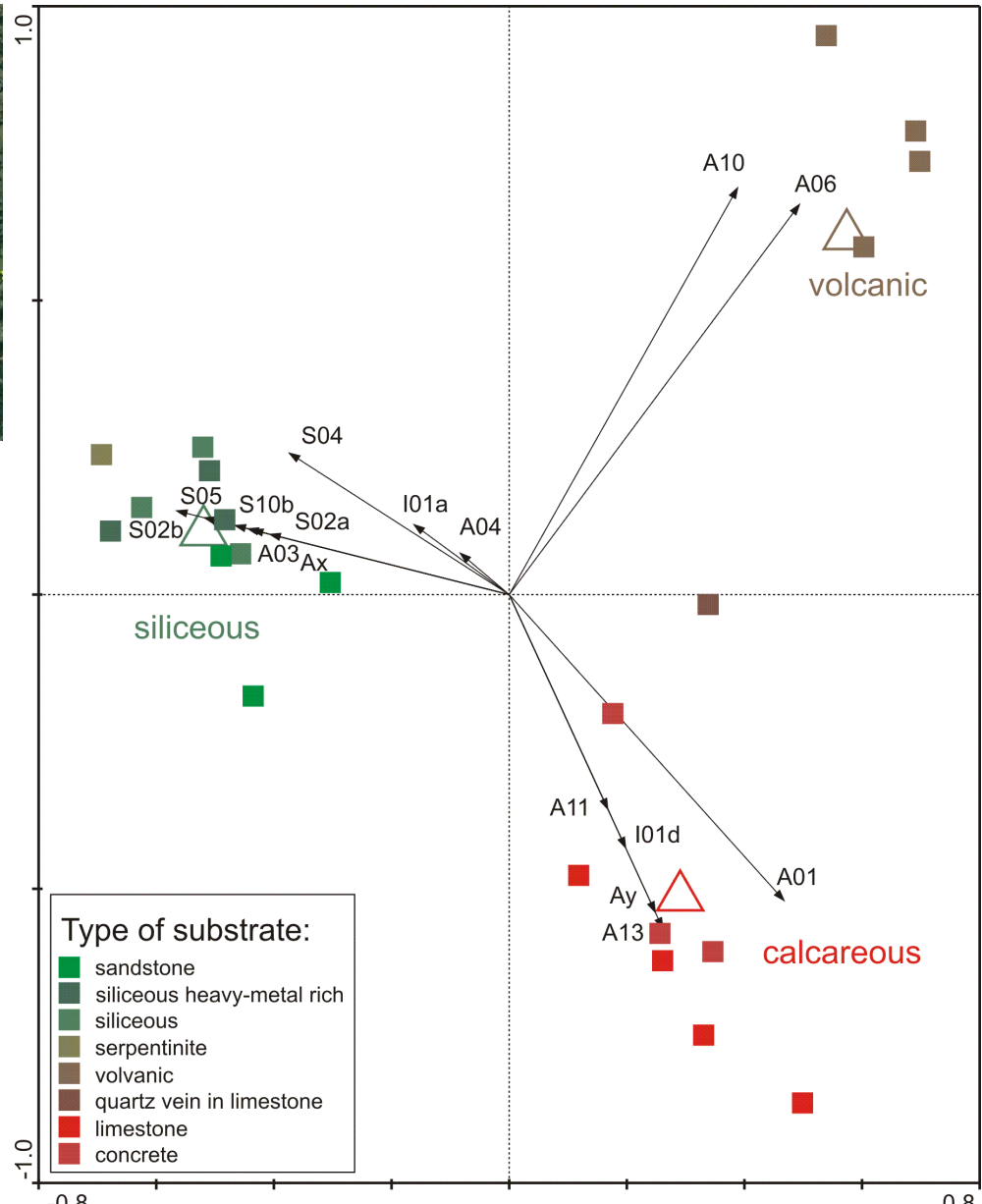
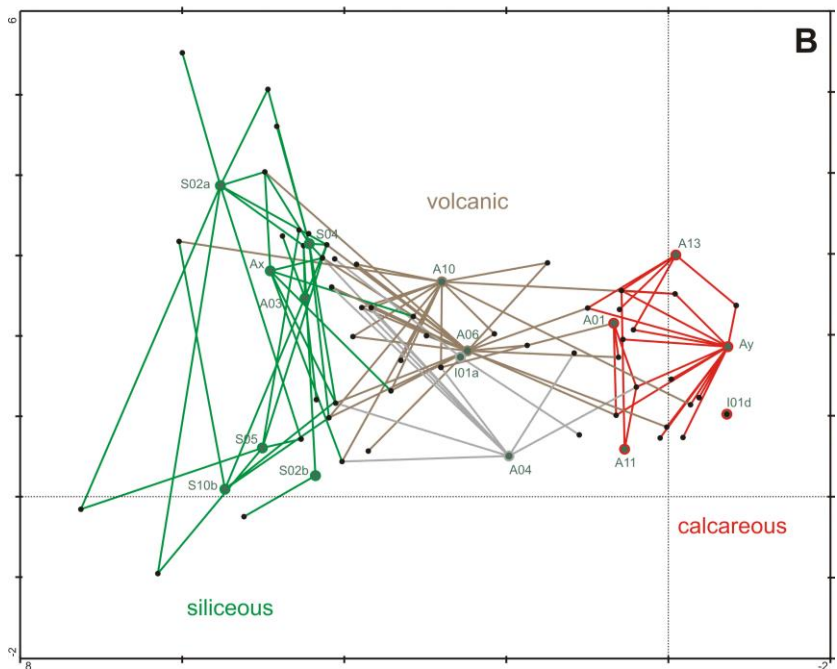
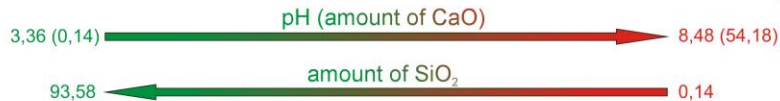
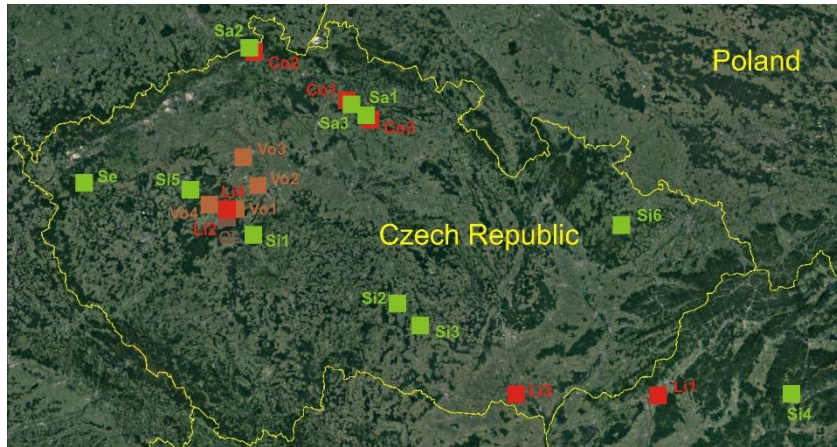
- Exceptionally high diversity of symbionts for a vertically-dispersed lichen (23 genotypes)
- Long dispersal? Fungal fusion?

<i>Ohmura 5357C*</i>	A	11
<i>Ohmura 5361A*</i>	B	1
<i>Ohmura 5410</i>	C	2
<i>Ohmura 5372*</i>	D	3



Paradox I.

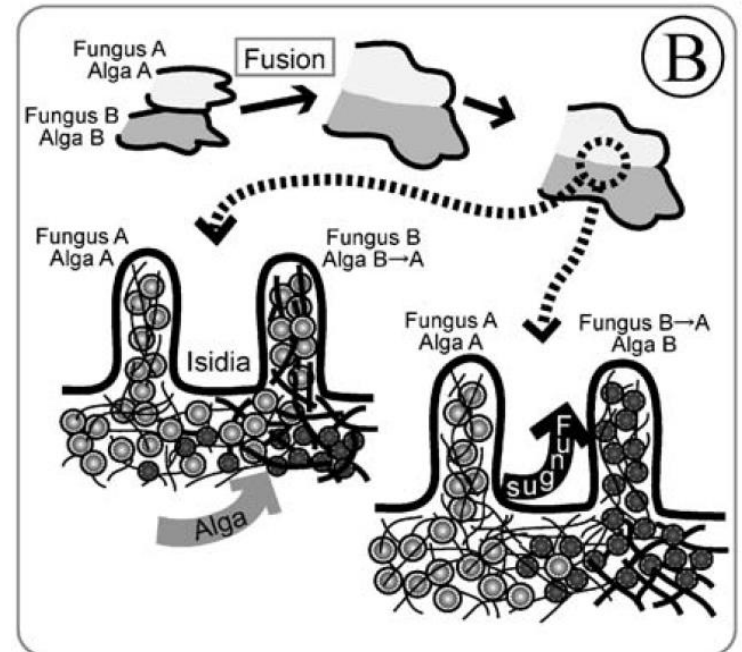
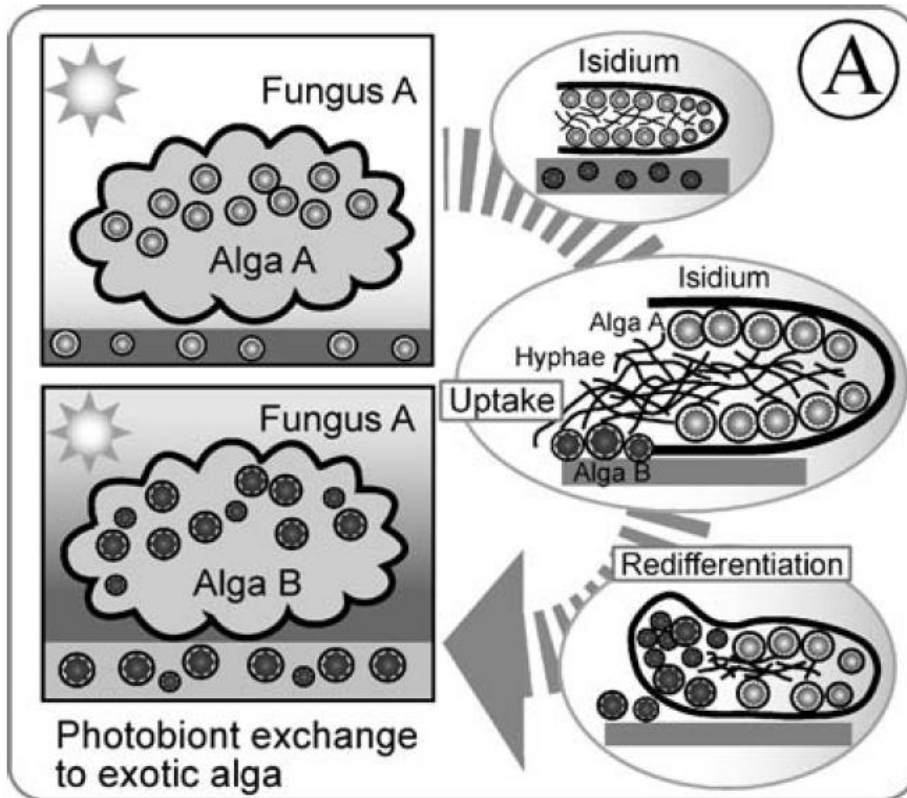
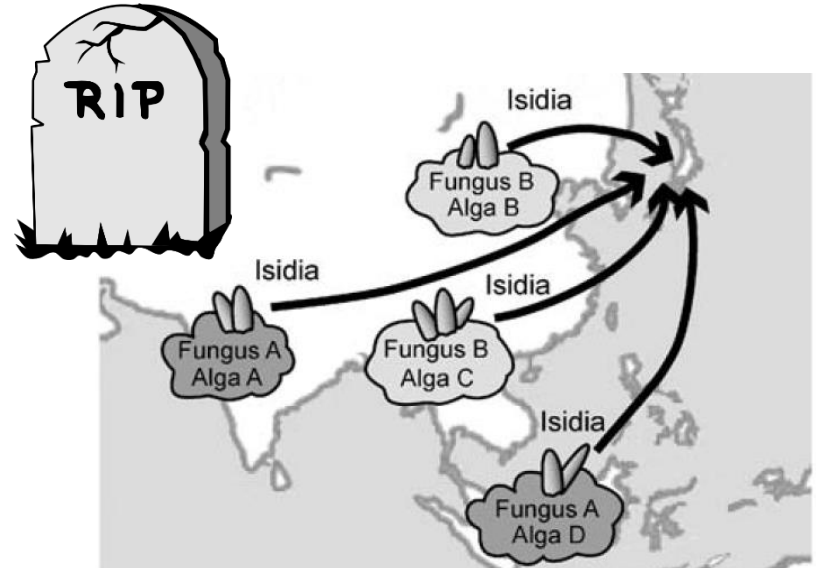
The mode of symbiont dispersal does not affect symbiont diversity



Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

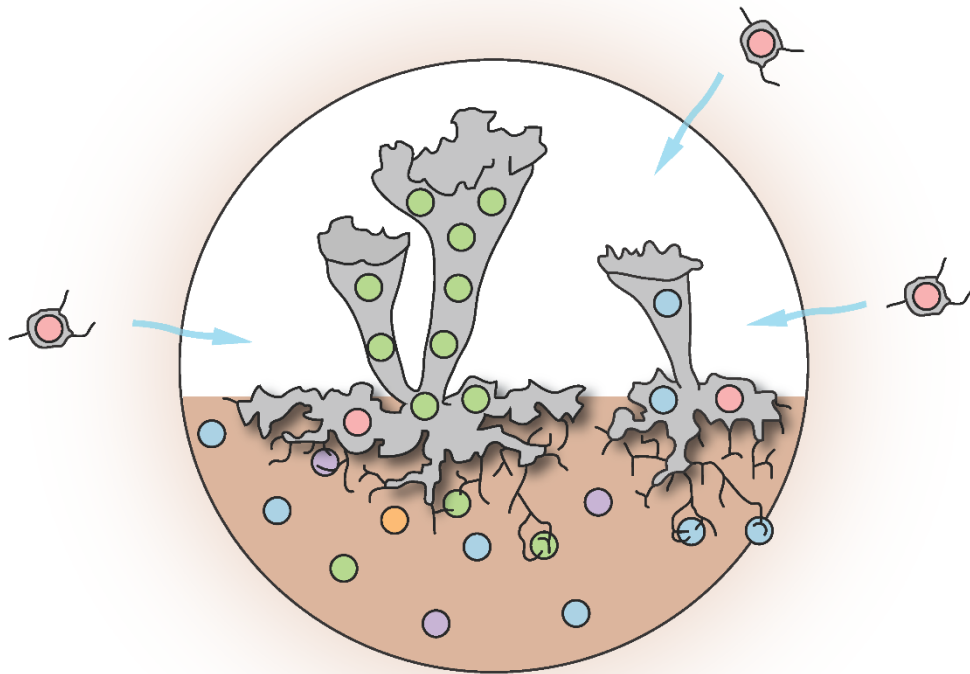
- No long dispersal
- No fungal fusion
- **Symbiont switch to locally-adapted alga!**



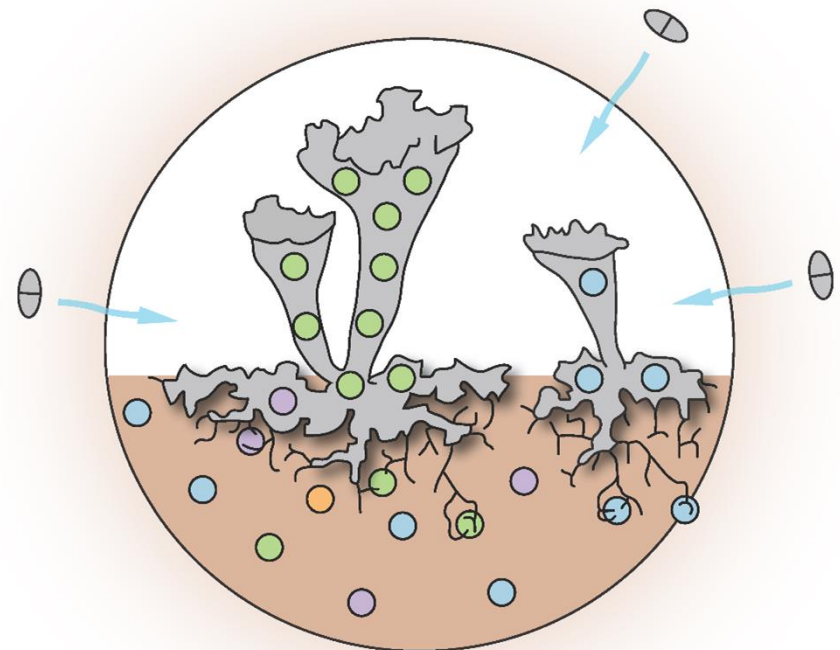
Paradox II.

Symbiont switch to locally-adapted alga?

- Hosts are selecting their algal symbionts from a regional pool of free-living algae, preferring well adapted local genotypes



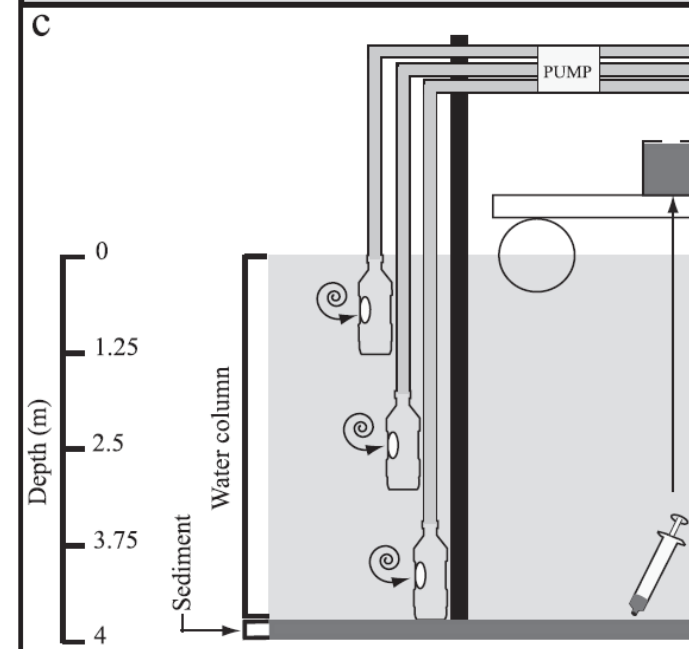
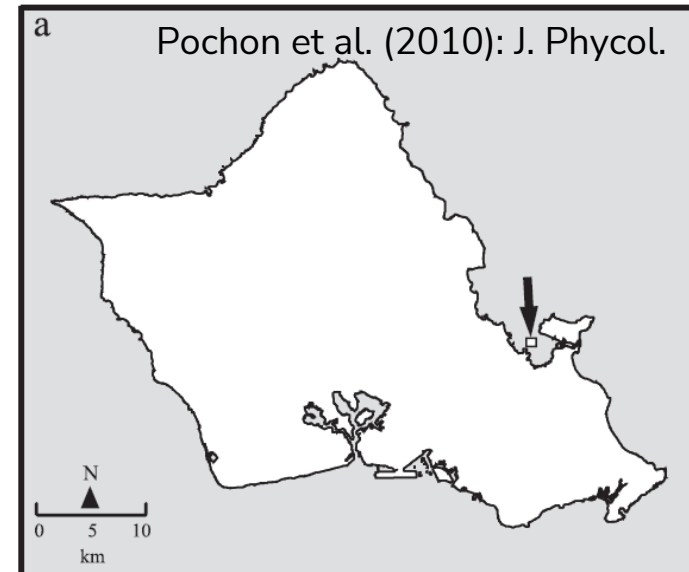
vertical dispersal



horizontal dispersal

Paradox II.

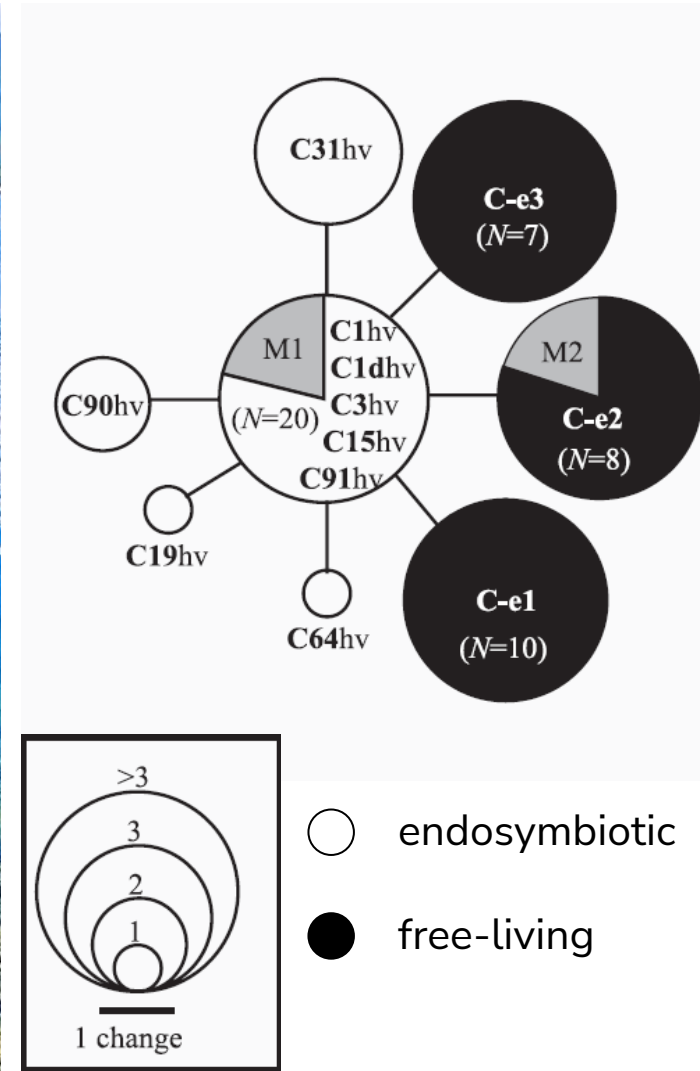
Host symbionts are physically absent in the environment



Paradox II.

Host symbionts are physically absent in the environment

- No overlap between endosymbiotic and free-living communities of symbionts



Paradox II.

Host symbionts are physically absent in the environment

- Foraminifera endosymbiotic diatoms were extremely rare in the nearby habitat (<0.5%)

foraminifera.eu



Amphistegina

$\phi_{\max} = 1329 \mu\text{m}$

100 μm

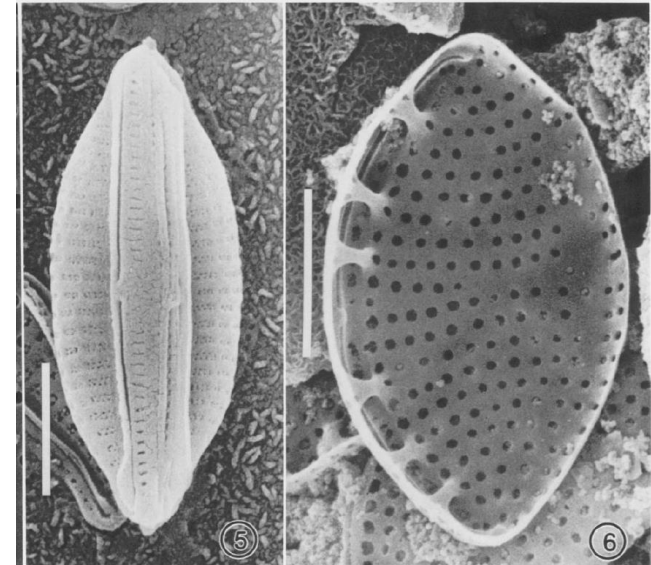
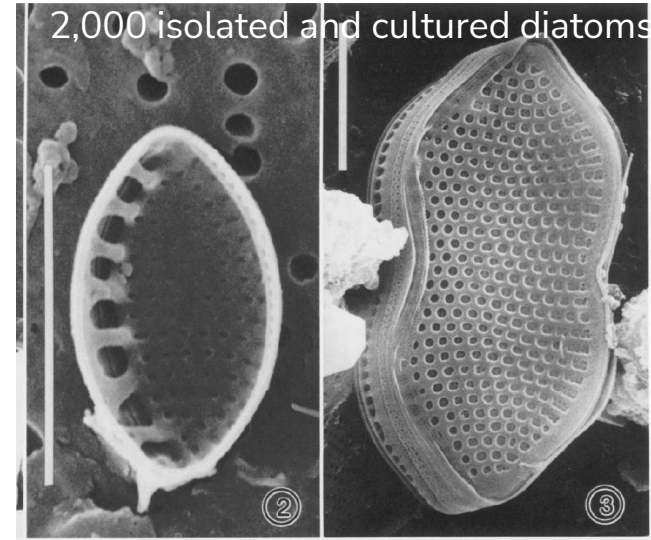
Borelis



Heterostegina

$\phi_{\max} = 750 \mu\text{m}$

Operculina



Lee et al. (1989): Micropaleontology

Paradox II.

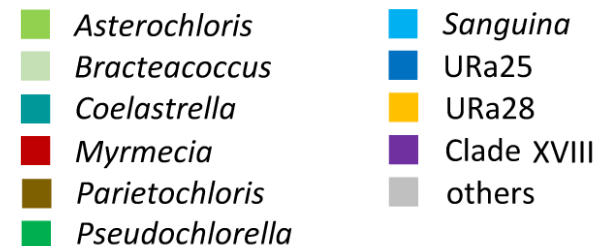
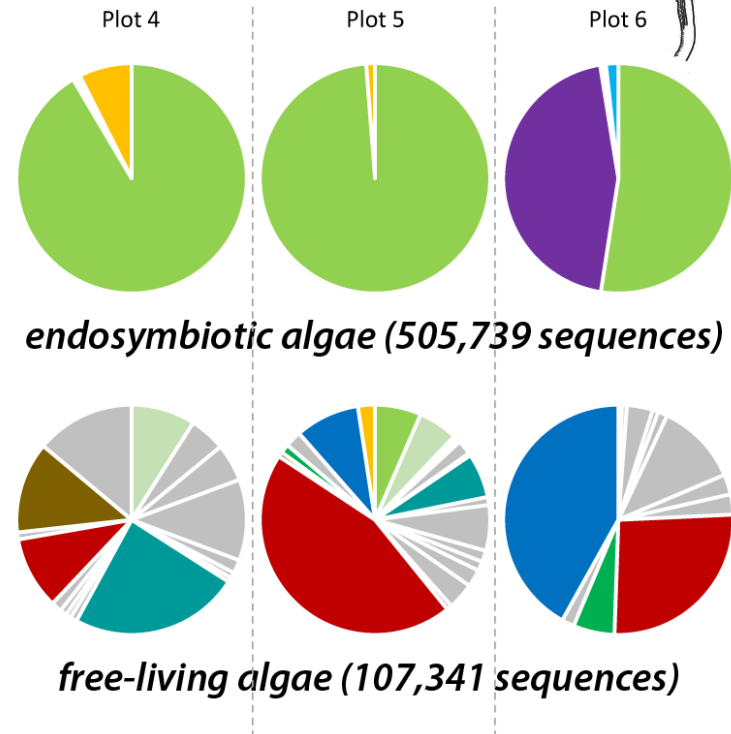
Host symbionts are physically absent in the environment

- Symbiosis dynamics on river gravel bars
- Selected plots - sequencing all endosymbiotic and free-living algae



Vančurová et al. (2020): Algal Res.

A. Roseg Valley, Switzerland *Stereocaulon*

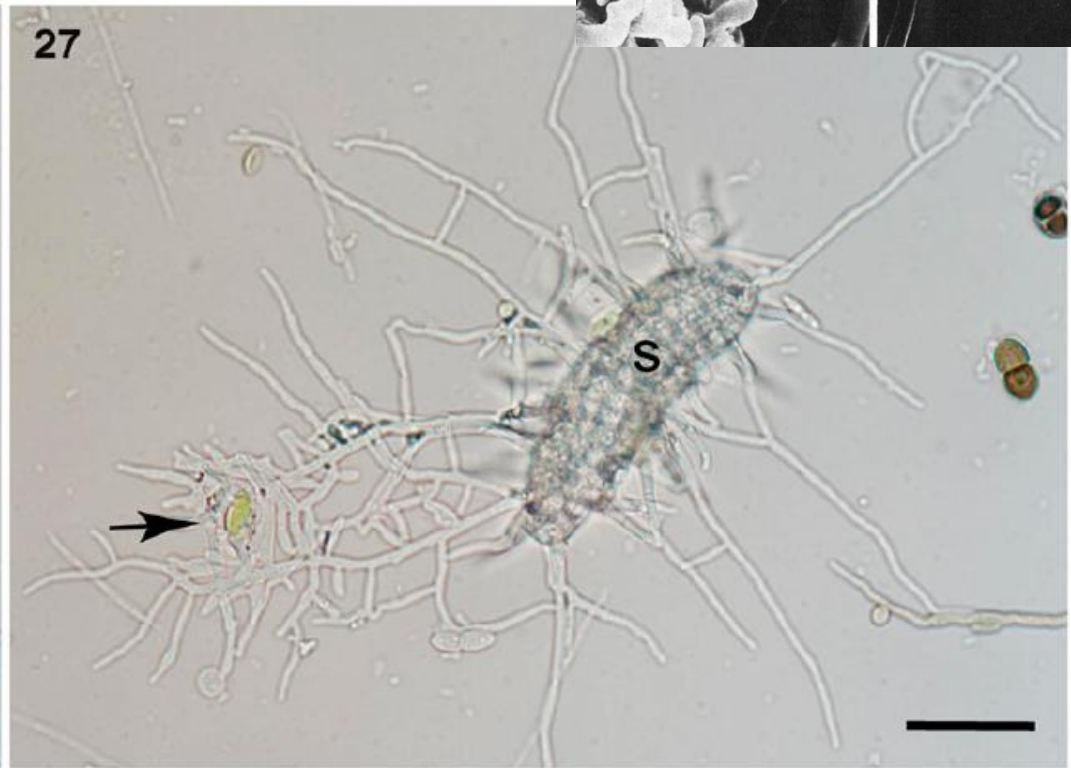
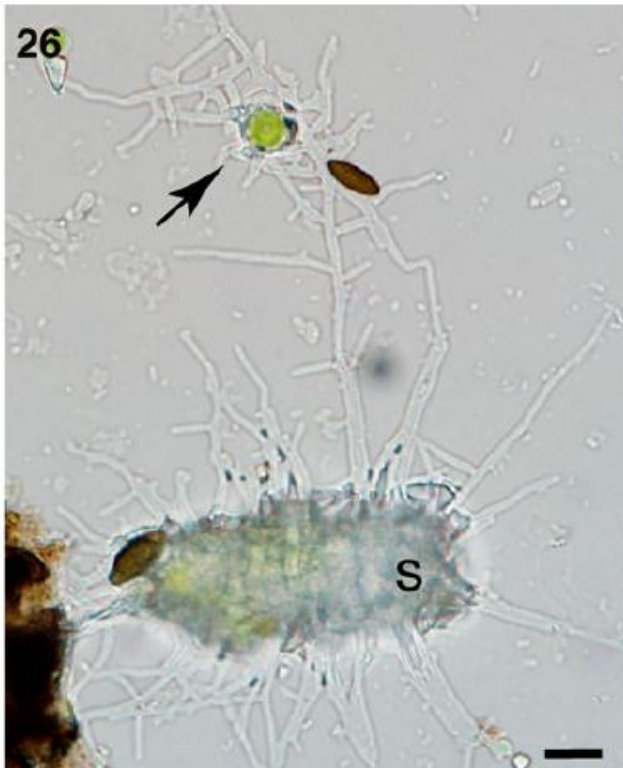
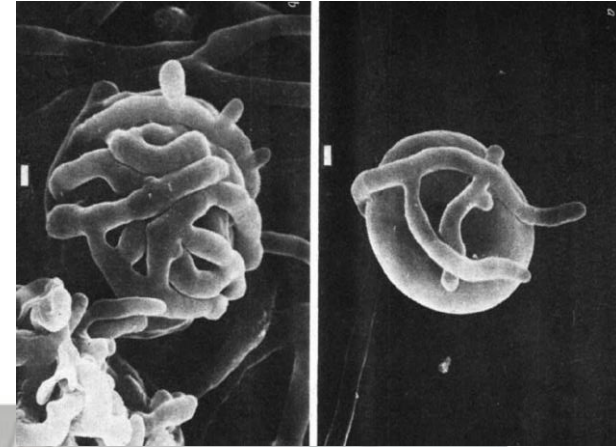


Paradox II.

Host symbionts are physically absent in the environment

- How do hosts acquire their symbionts from environment?
 - Young lichen hosts are extremely unspecific towards their symbionts, their hyphae even encircle glass beads in the same manner as algal cells

Ahmadjian & Jacobs (1981): Nature

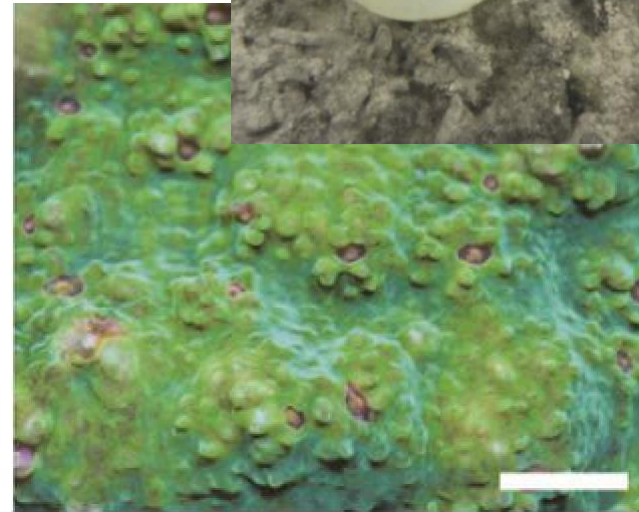
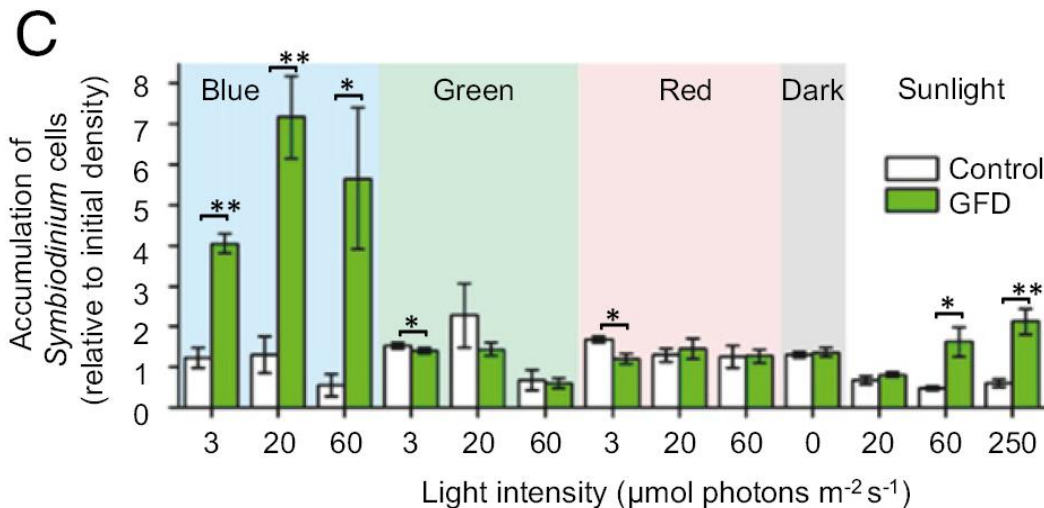
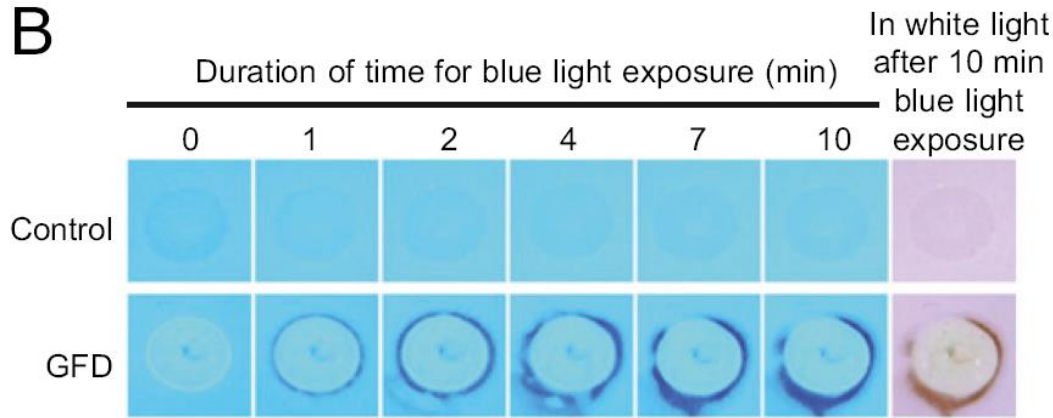


Sanders et al. (2014): Am. J. Bot.

Paradox II.

Host symbionts are physically absent in the environment

- How do hosts acquire their symbionts from environment?
 - Young corals may attract algal symbionts by emitting green fluorescence under daylight conditions (strong blue light), using GFP



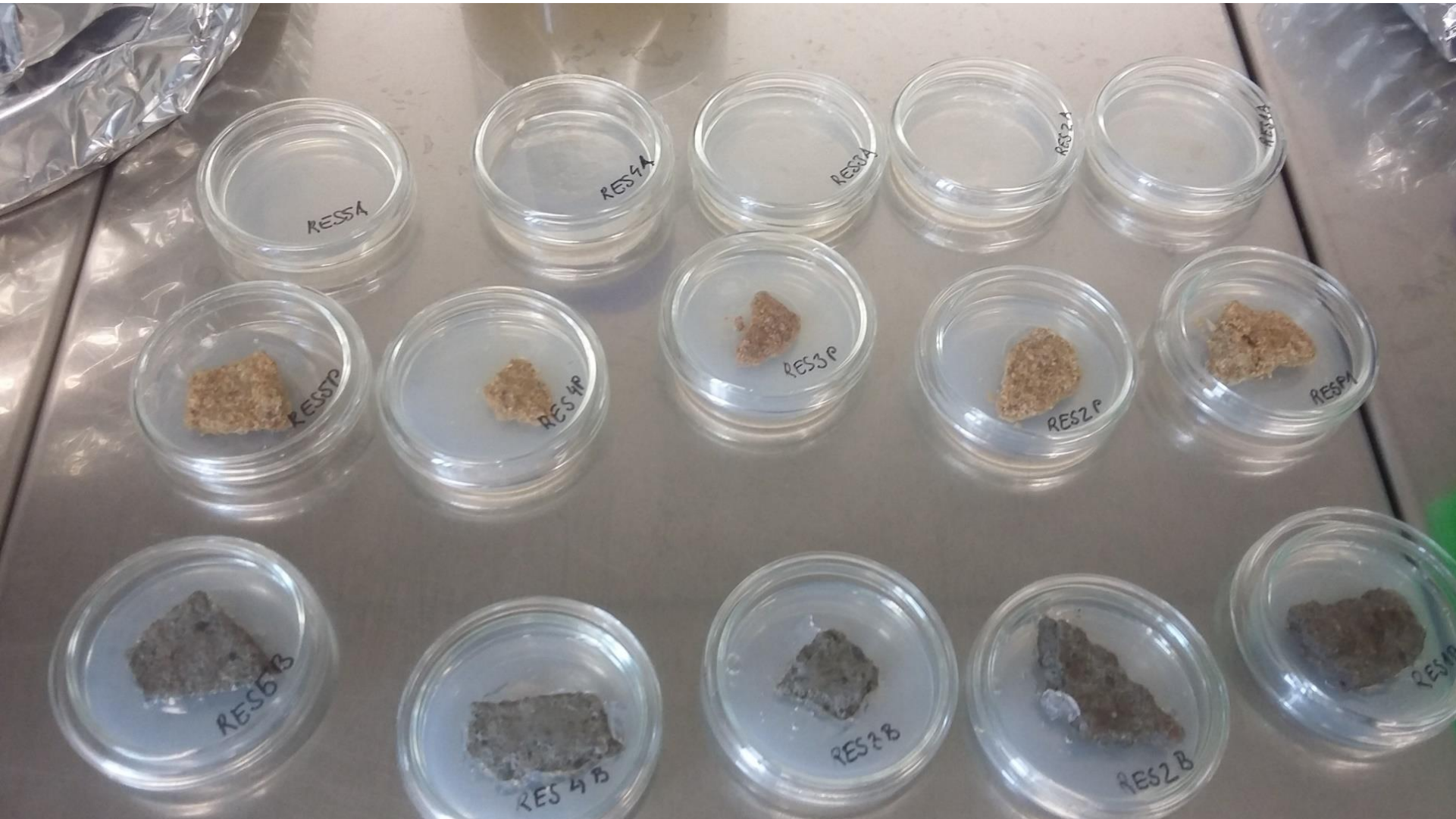
Paradoxes of lichen symbiosis

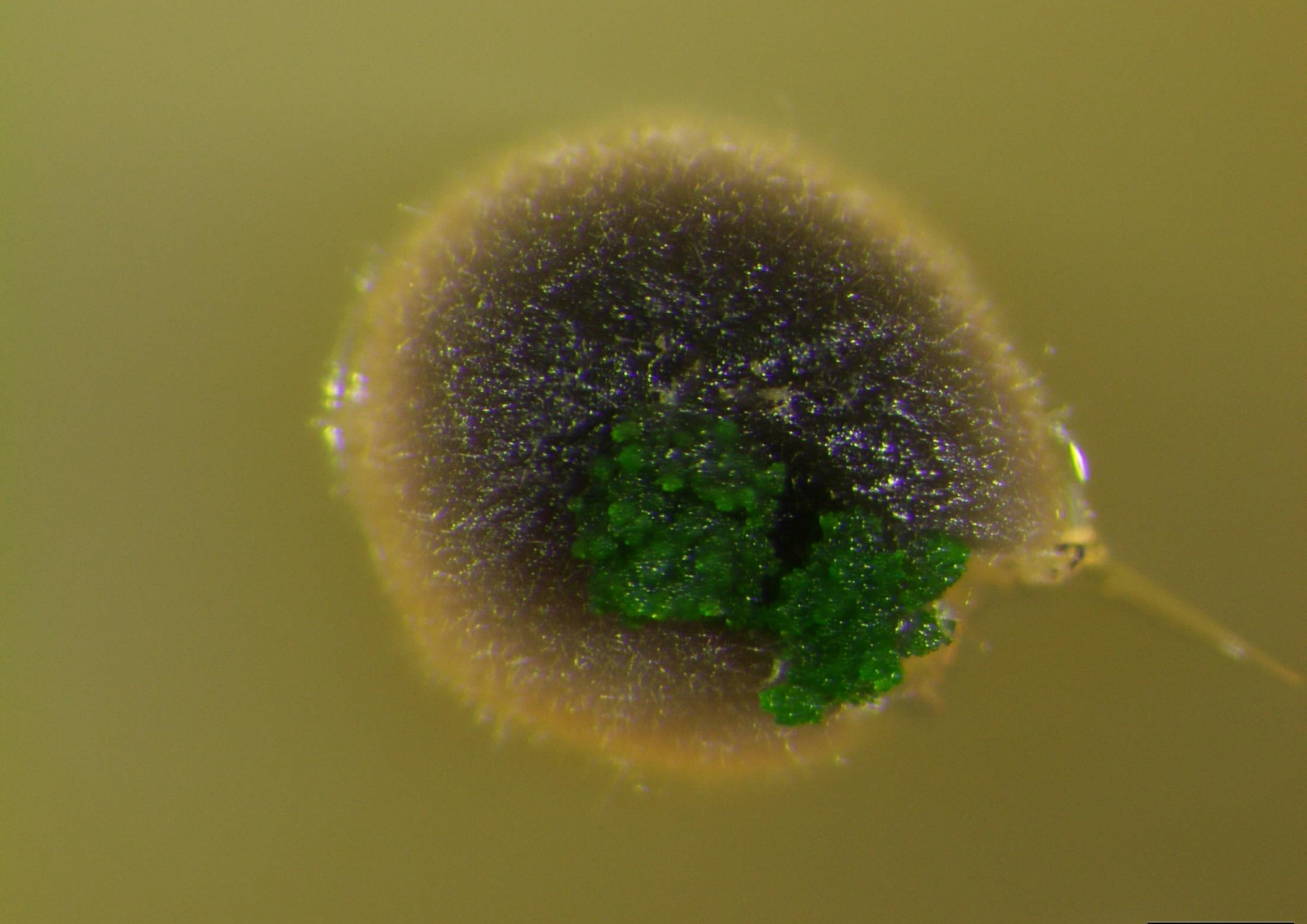


- Lichens have two types of dispersal propagules, one of them not being used for dispersal
- The fungal hosts are frequently forming symbiotic associations with algal partners, which are
 - physically absent in the environment
 - not co-dispersed with their host
 - absent in co-occurring vertically-dispersed lichens (so called core species)

Let's build a lichen!

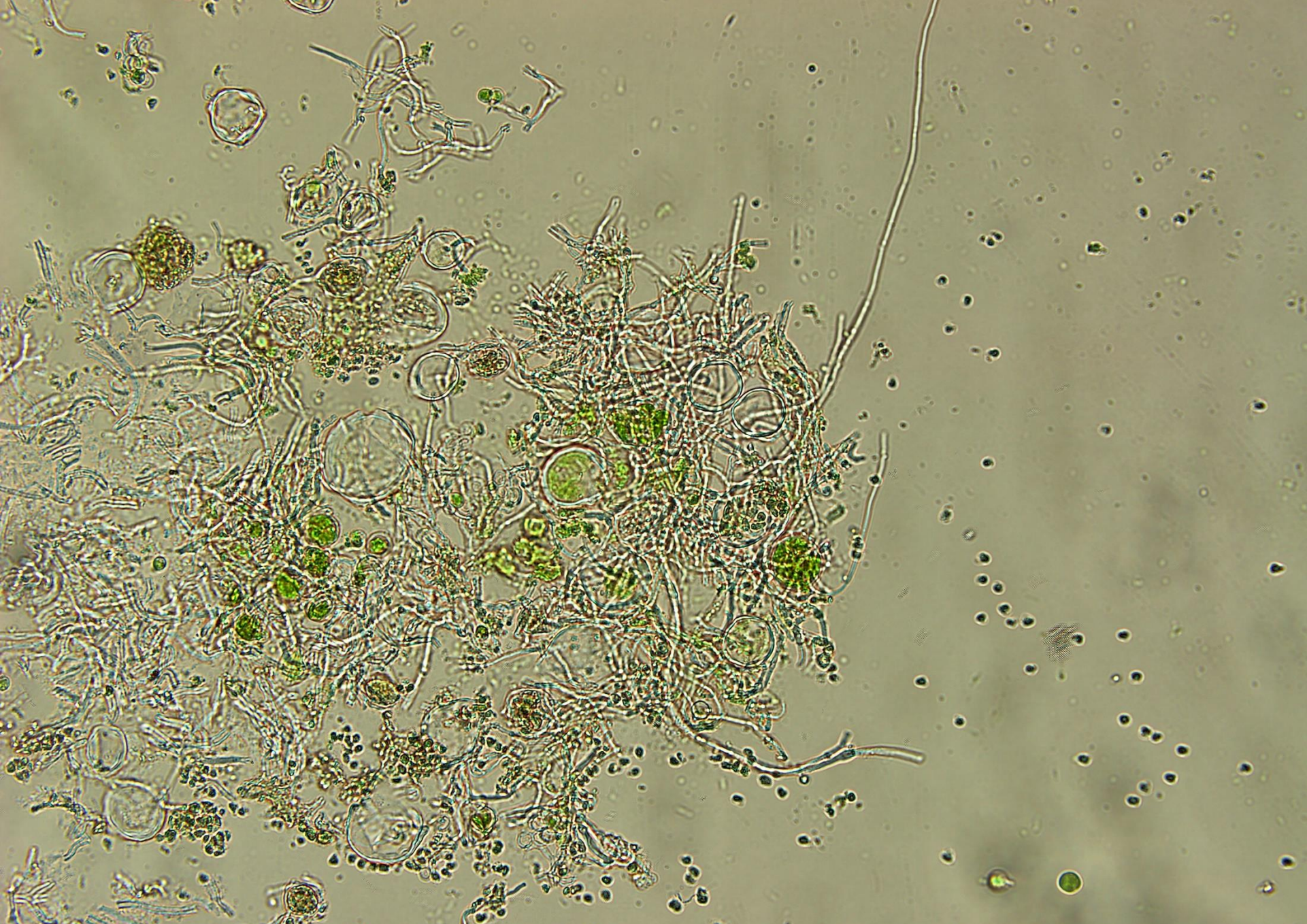
- Artificial lichen synthesis using pure fungal and algal cultures



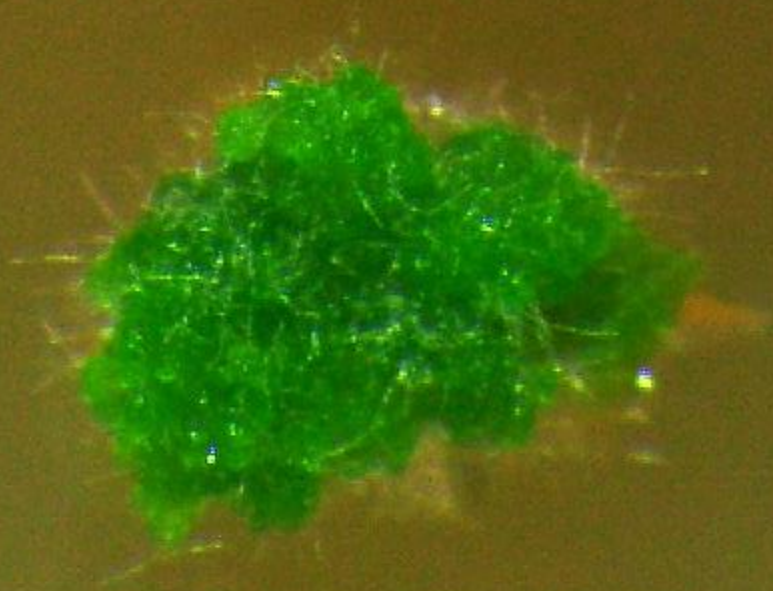


Fungal and algal pure cultures

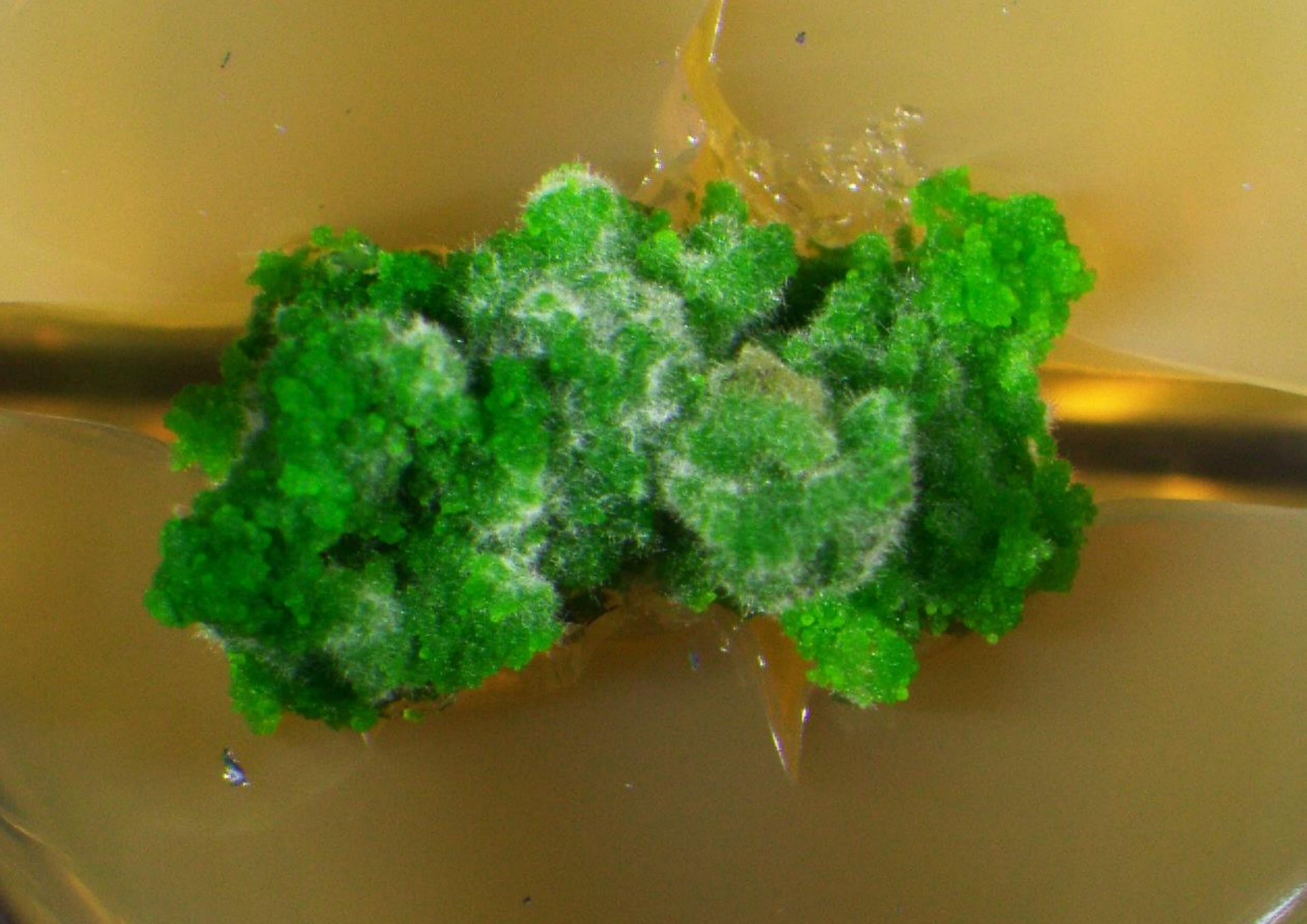
500 μm



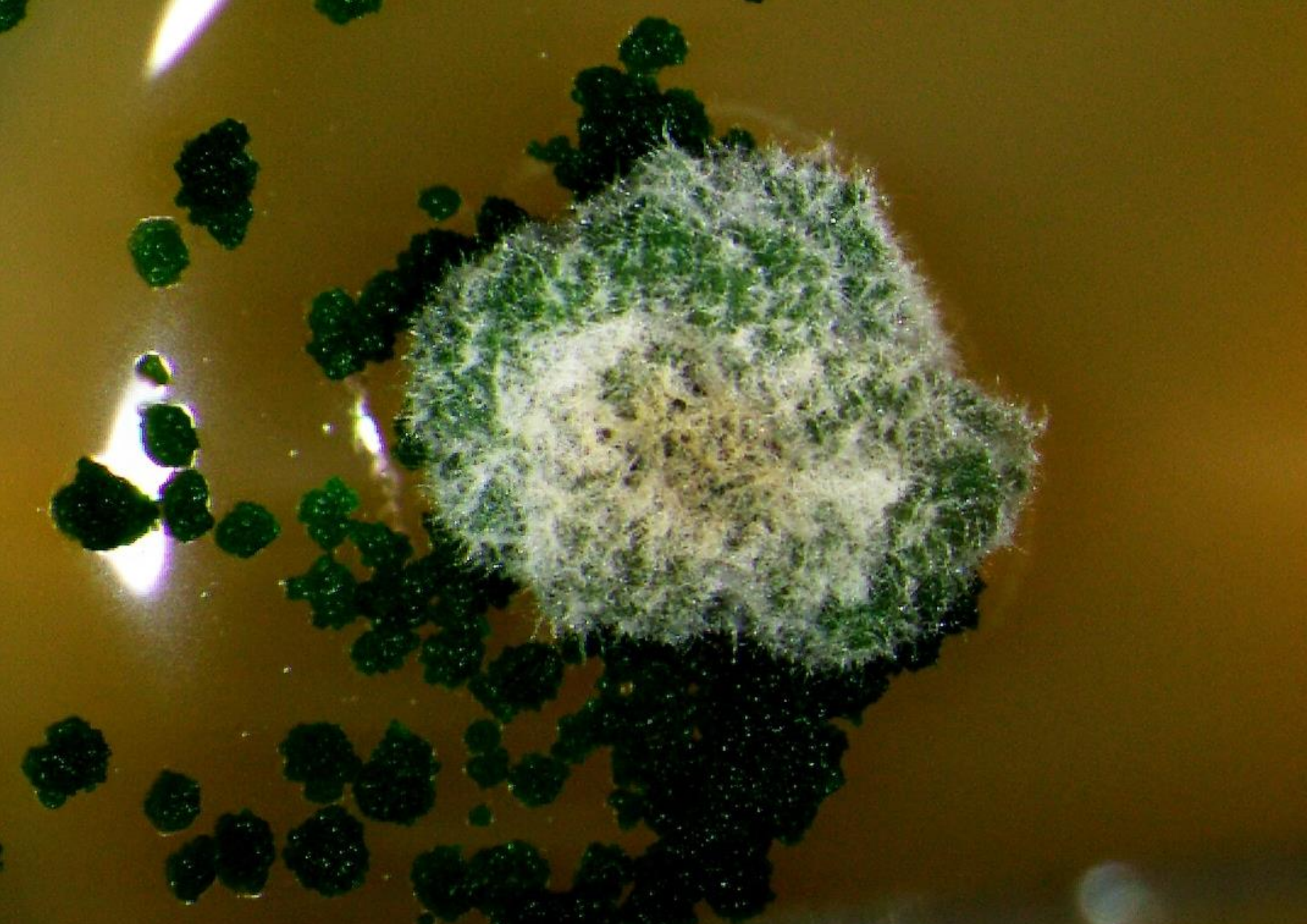
Fungus encircling algal cells



A mass of predominantly algal cells with a few interwoven fungal hyphae



Fungus starts to take over

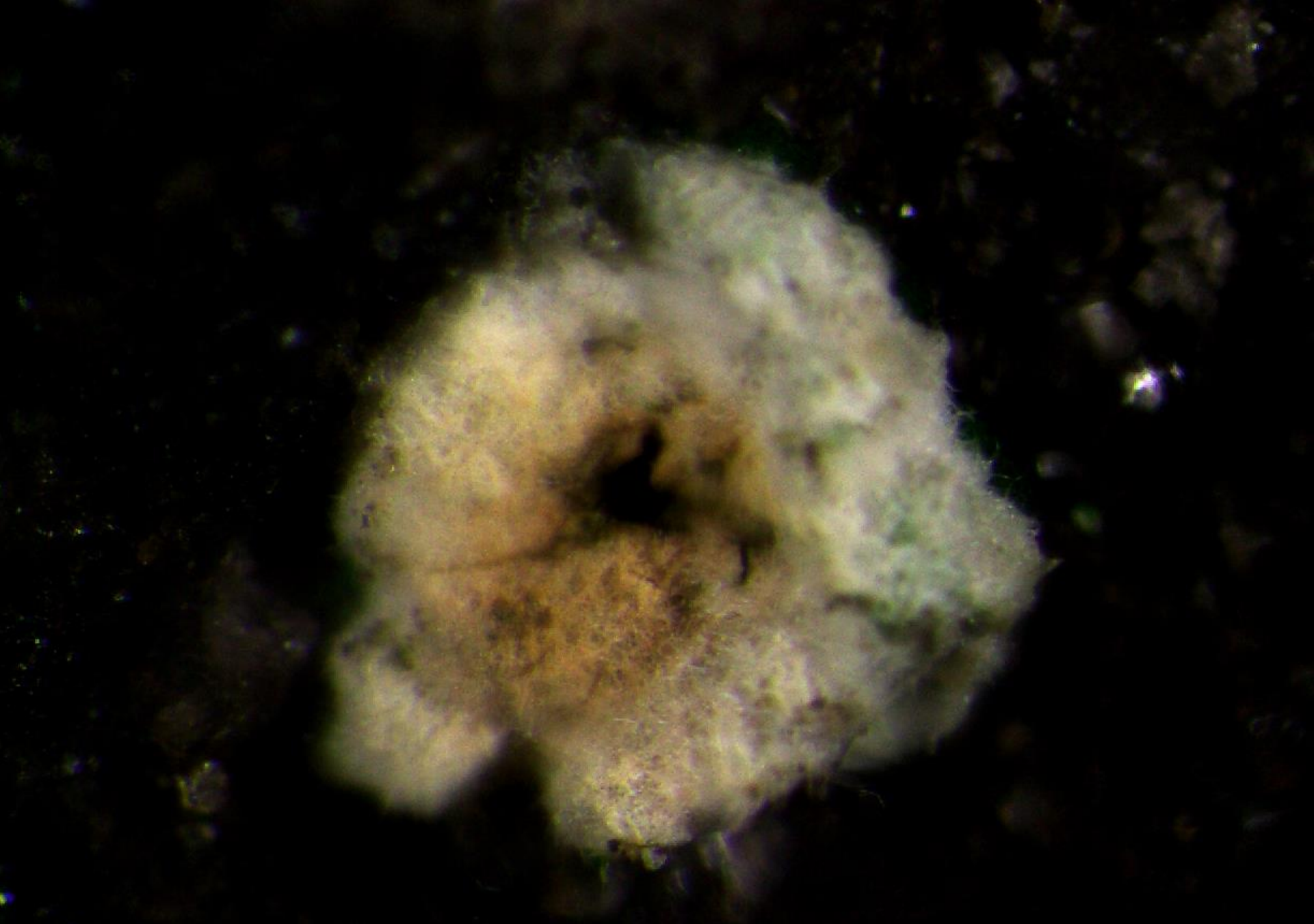


Fungus forms a superficial layer enclosing the algae inside

1 mm

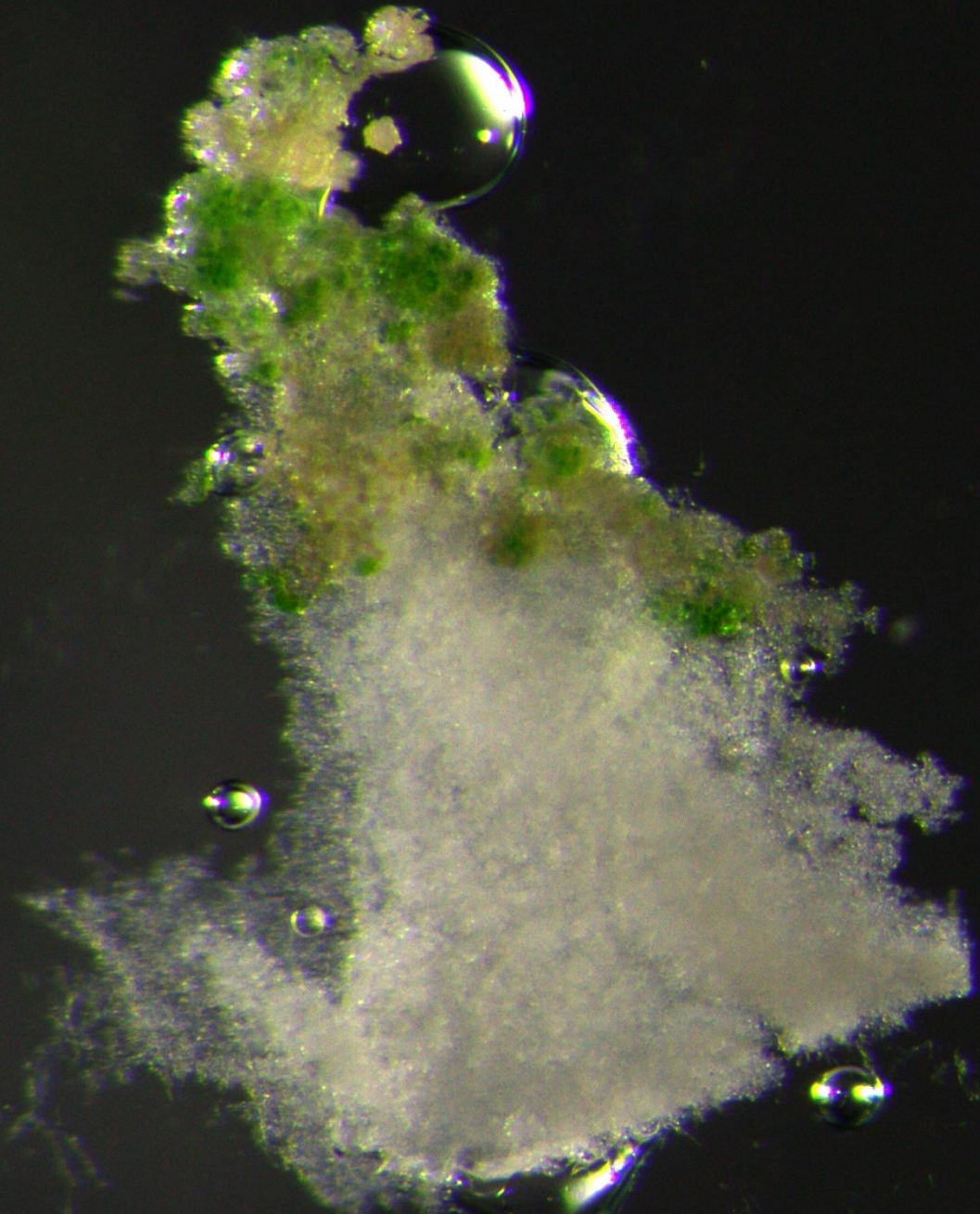


Transfer on the soil, development of rhizine-like structures



A young lichen – fungus completely enclosed the algae

500 μm



A young lichen (cross section) – fungal and algal layers are developed 100 μm



Ondřej
Peksa



Jana
Steinová



Lucie
Vančurová



Ivana
Černajová



Zuzana
Škvorová



Tereza
Gebouská



Helena
Bestová



Patricia
Moya

Thank you for your attention