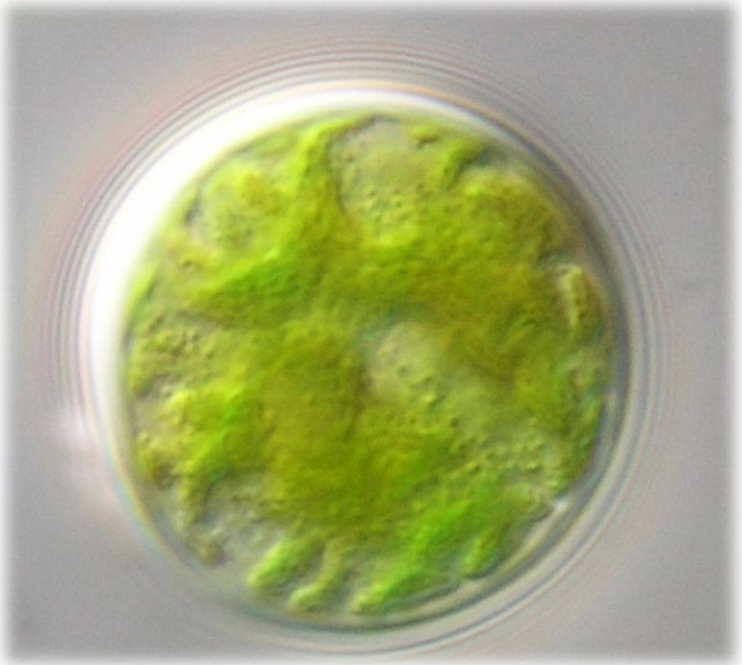
Svět paradoxů a záhad:
Partnerský život řasových symbiontů



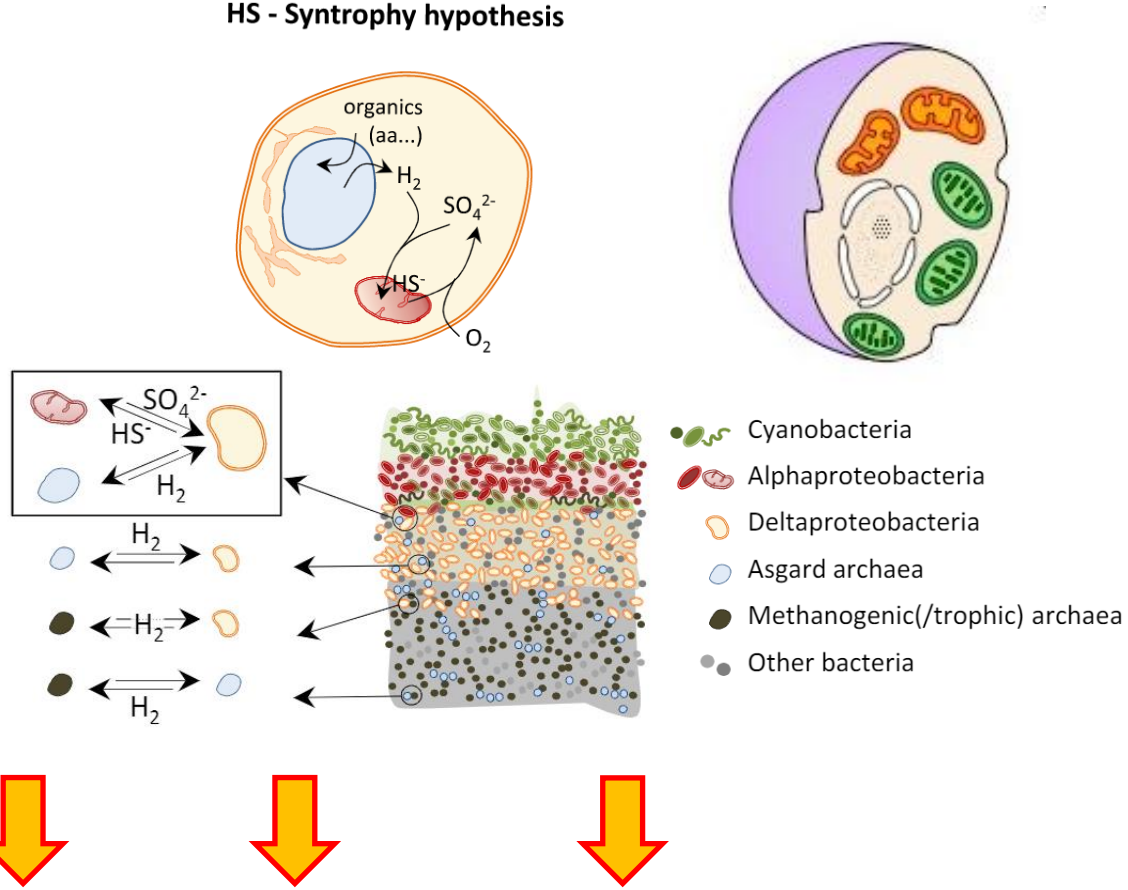
Pavel Škaloud

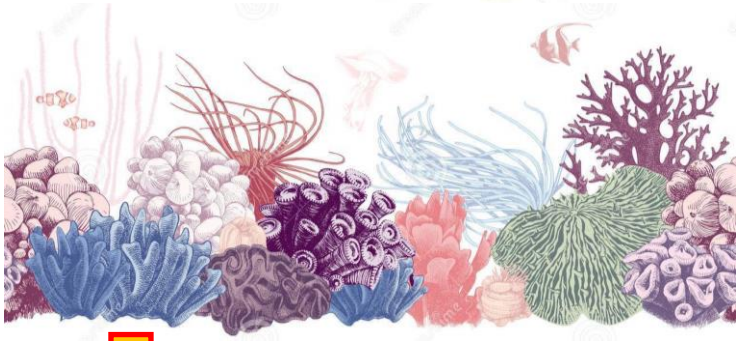
FACULTY OF SCIENCE
Charles University

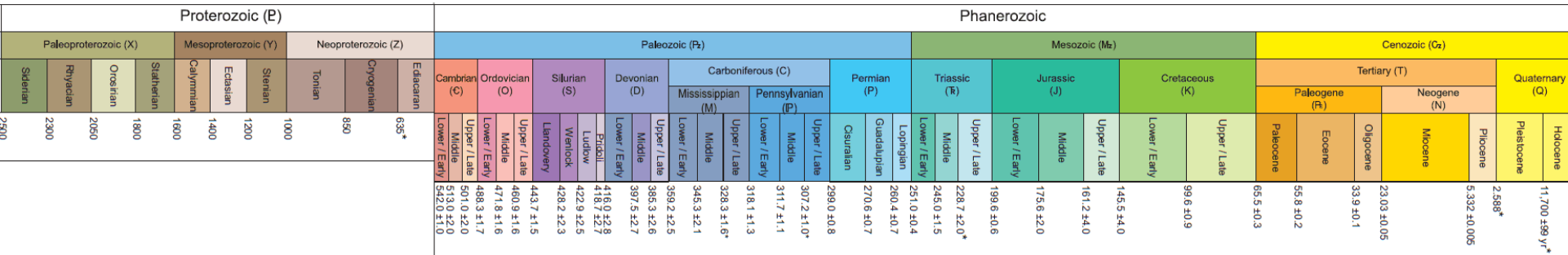
Algal speciation & evolution lab

Symbiosis

- Central driver for evolution across the entire tree of life

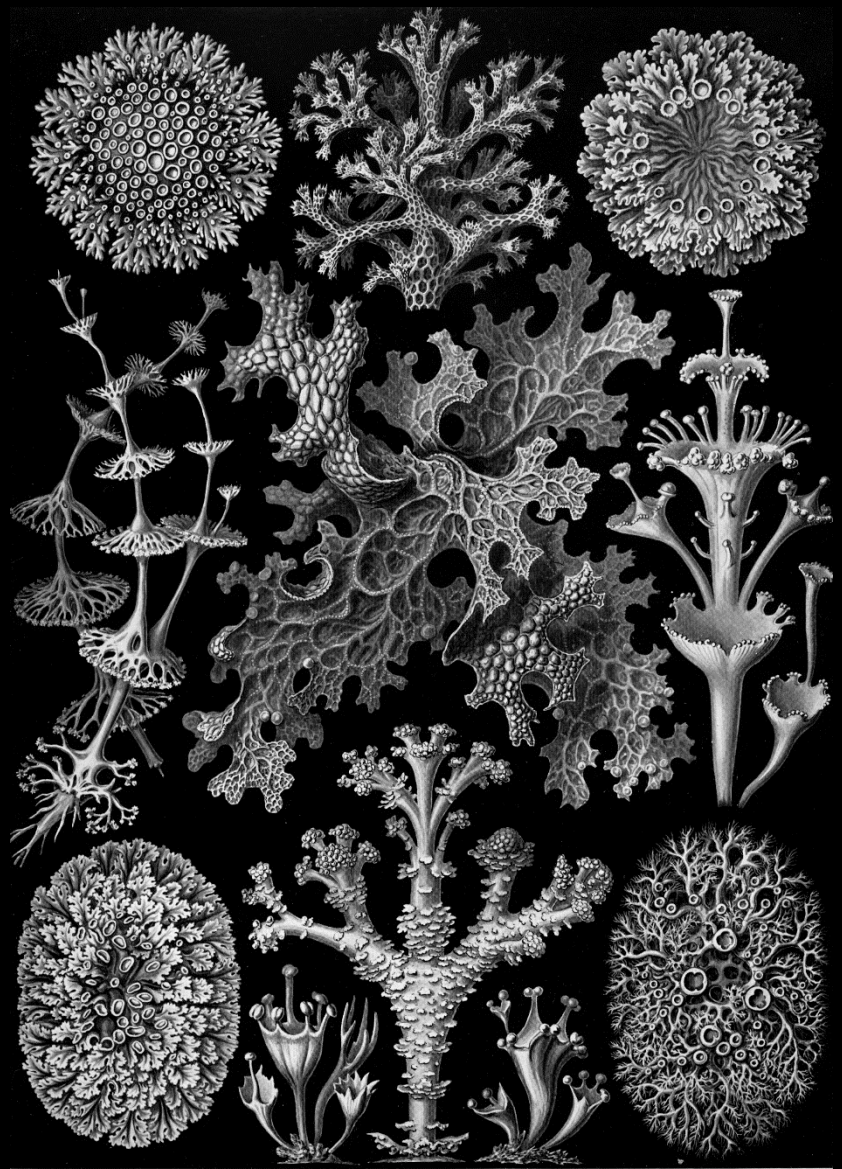


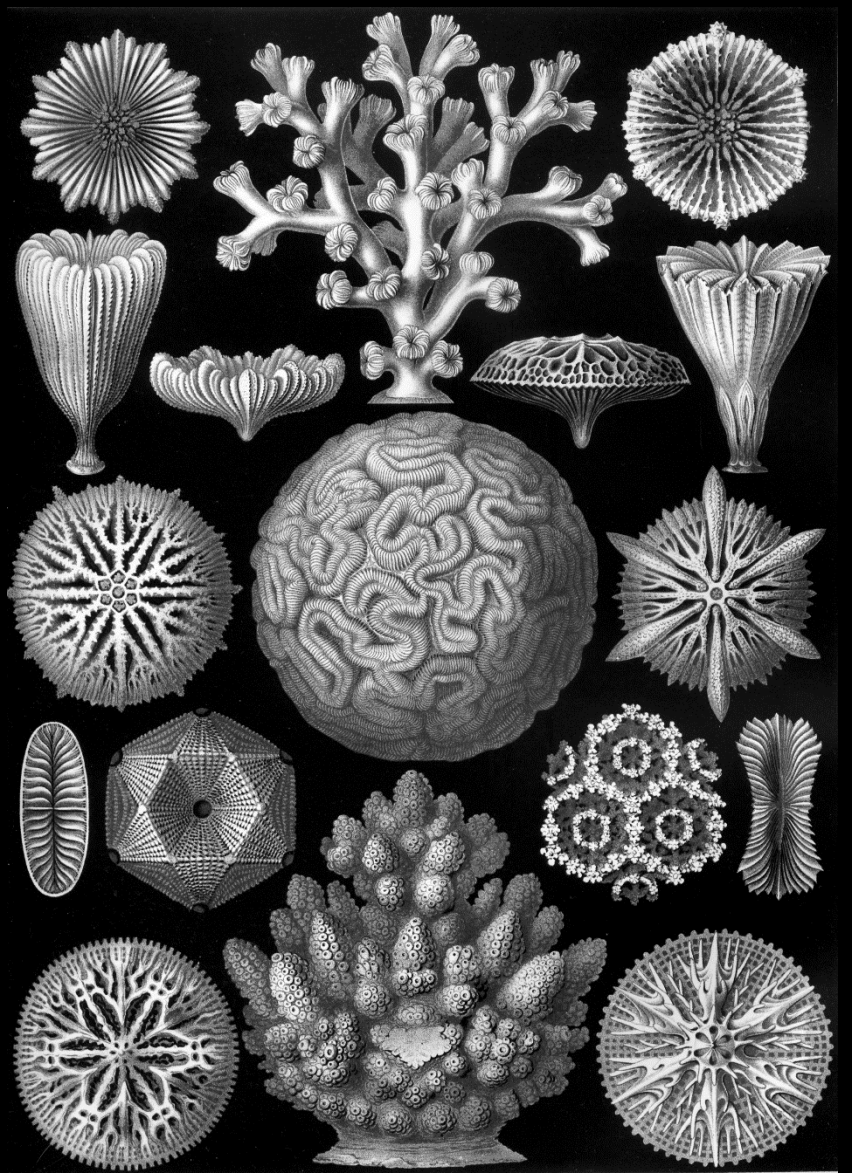




Phototrophic symbioses

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

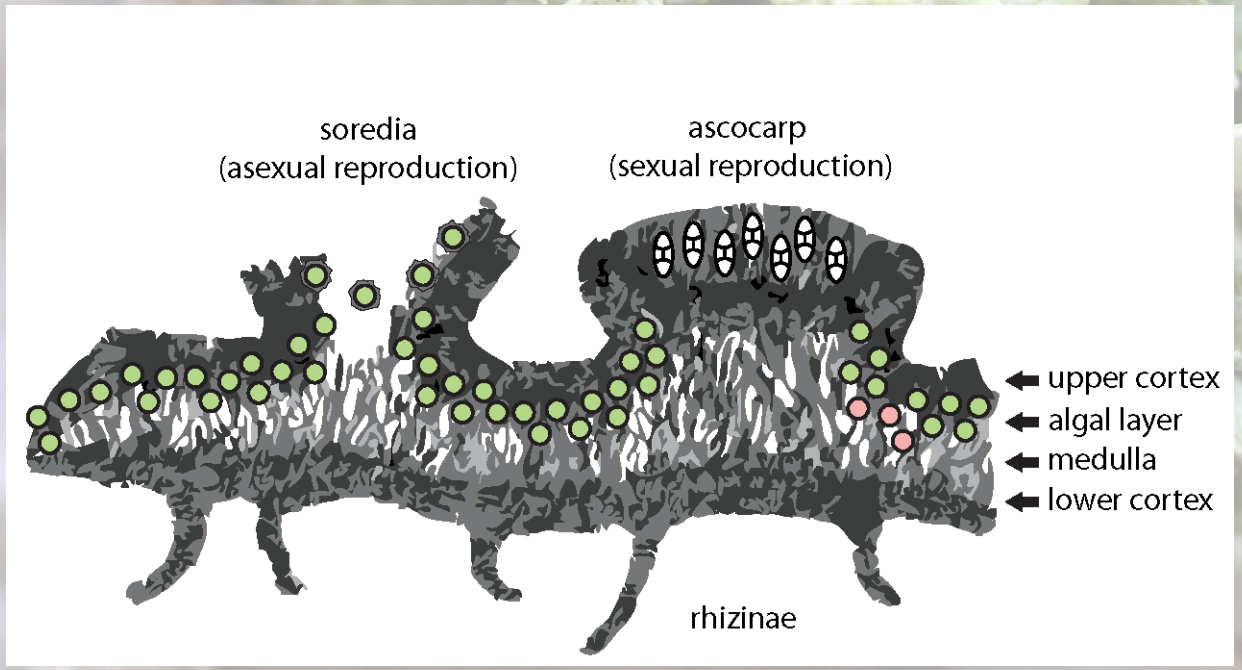


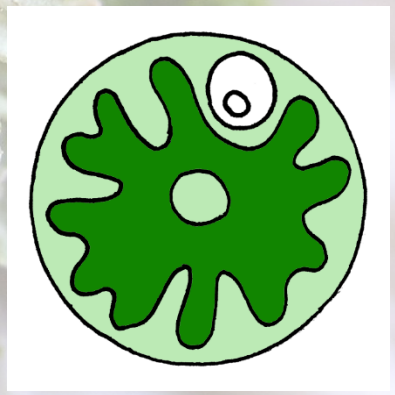


Haeckel (1904)

Phototrophic symbioses

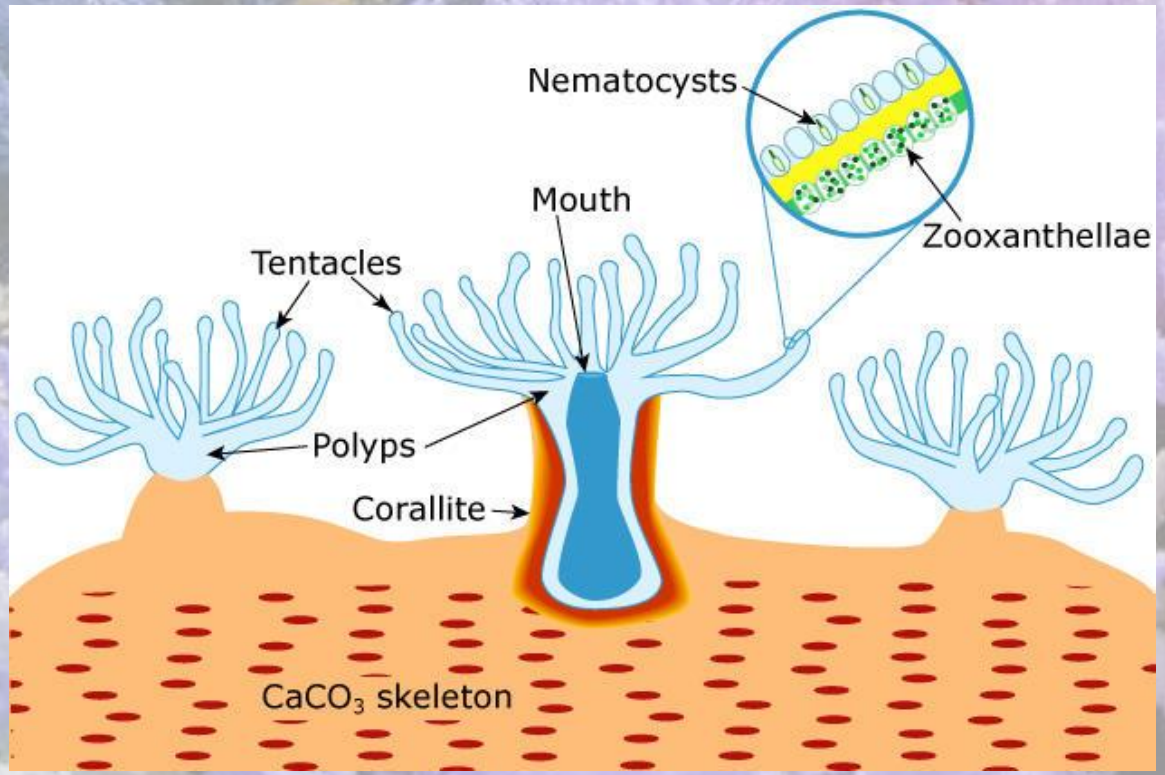
- Lichens
  - Dominate 8% of the Earth's land surface
  - Impacting global fluxes of carbon and nutrients
  - Soil stabilization and development





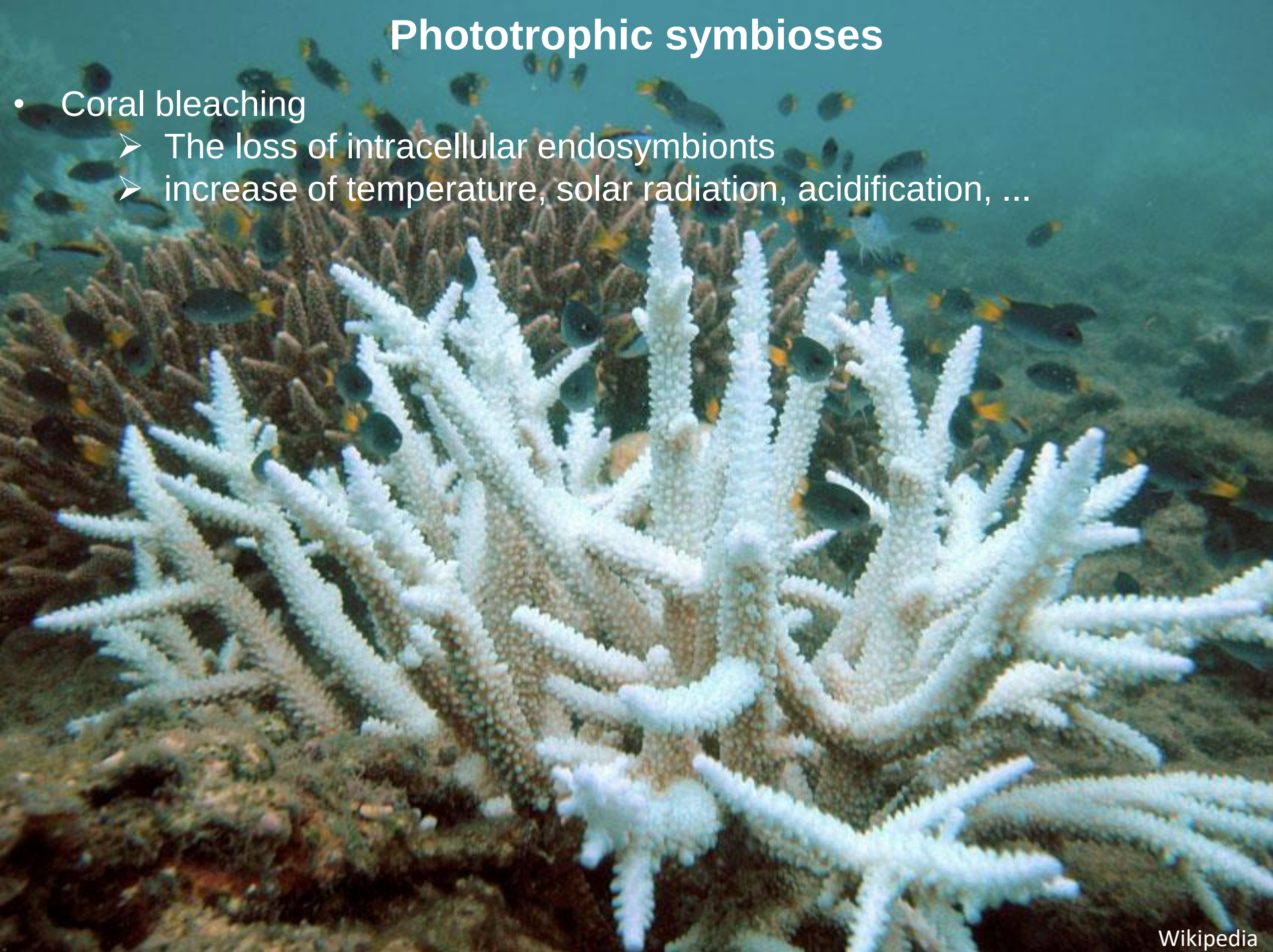
Phototrophic symbioses

- Corals
  - Cover 0.17% of the ocean surface
  - Coral reefs harbour the highest biodiversity of any ecosystem globally, even more than tropical rainforests



Phototrophic symbioses

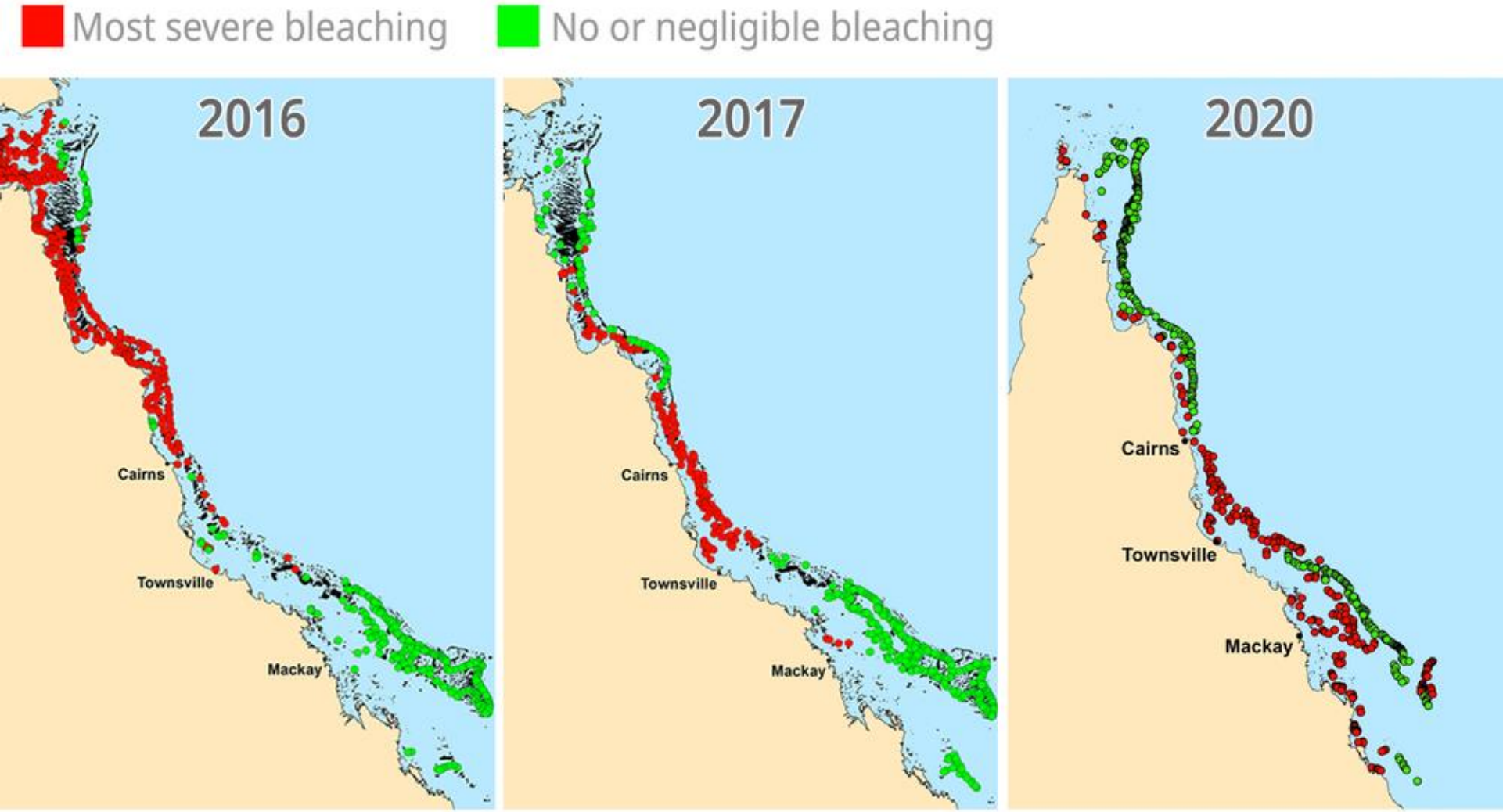
- Coral bleaching
  - The loss of intracellular endosymbionts
  - increase of temperature, solar radiation, acidification, ...



Wikipedia

Phototrophic symbioses

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



Source: ARC Centre of Excellence for Coral Reef Studies

Phototrophic symbioses

- Decrease of lichens in Arctic ecosystems
  - ➢ Dramatic decline in reindeer populations in recent years

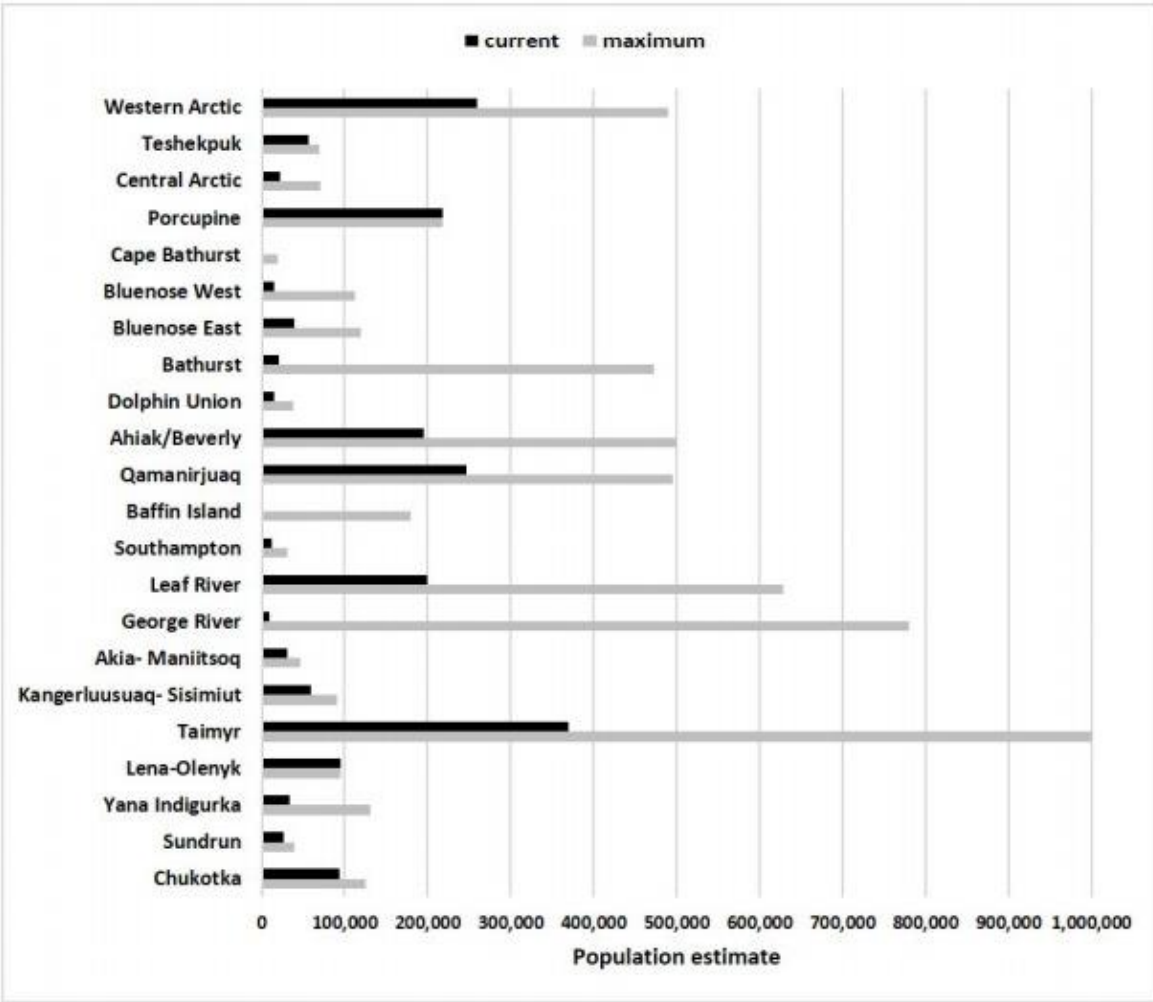
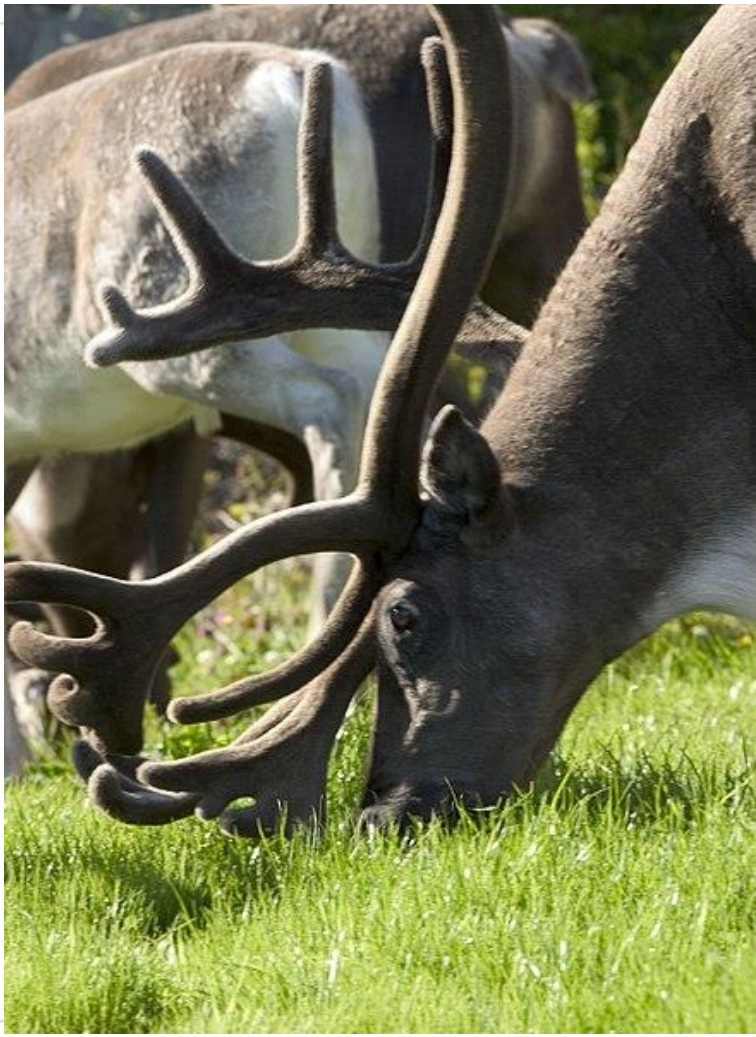


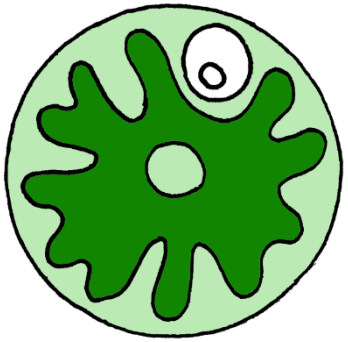
Figure 2. The current and peak estimates for migratory tundra wild reindeer/caribou herds for the 22 herds with at least three censuses. Data from CARMA's population database and covers population estimates from 1970-2017. Herds are ordered from west to east, starting in western Alaska.

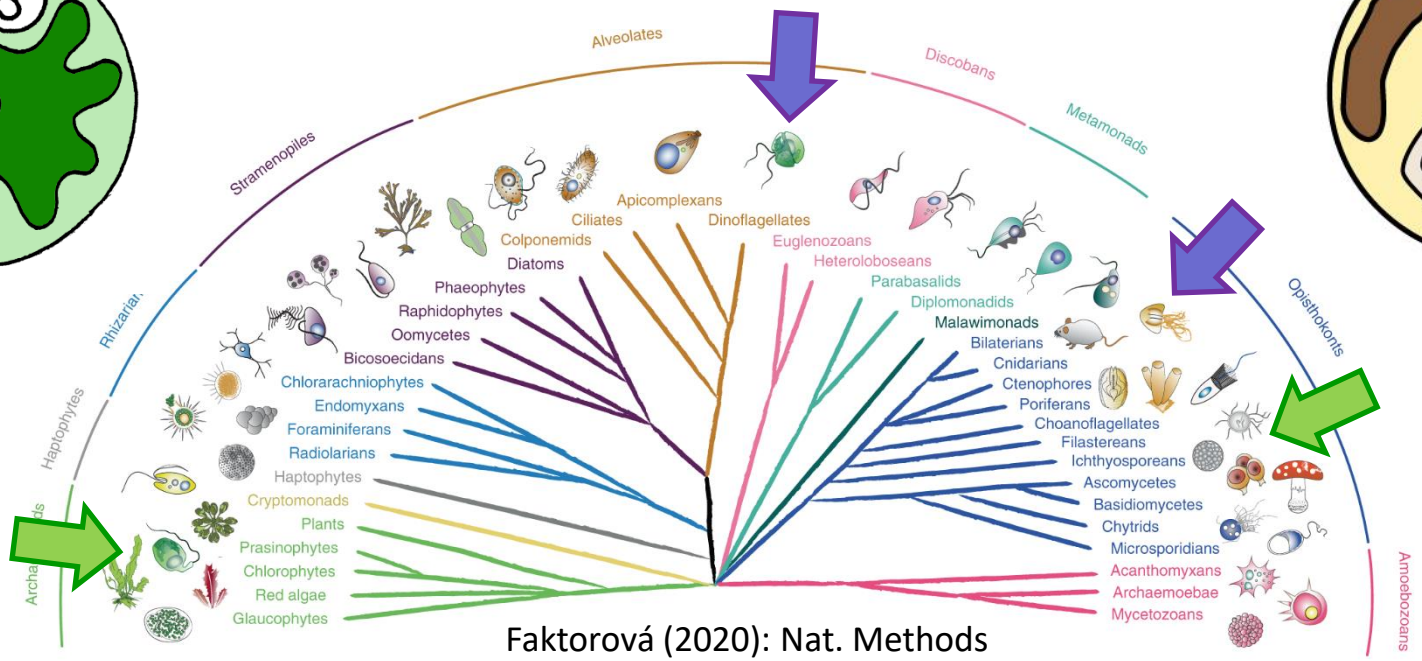


Arctic Report Card/NOAA

https://www.statnews.com/2016/12/09/suicide-sweden-sami-mental-health/

Phototrophic symbioses



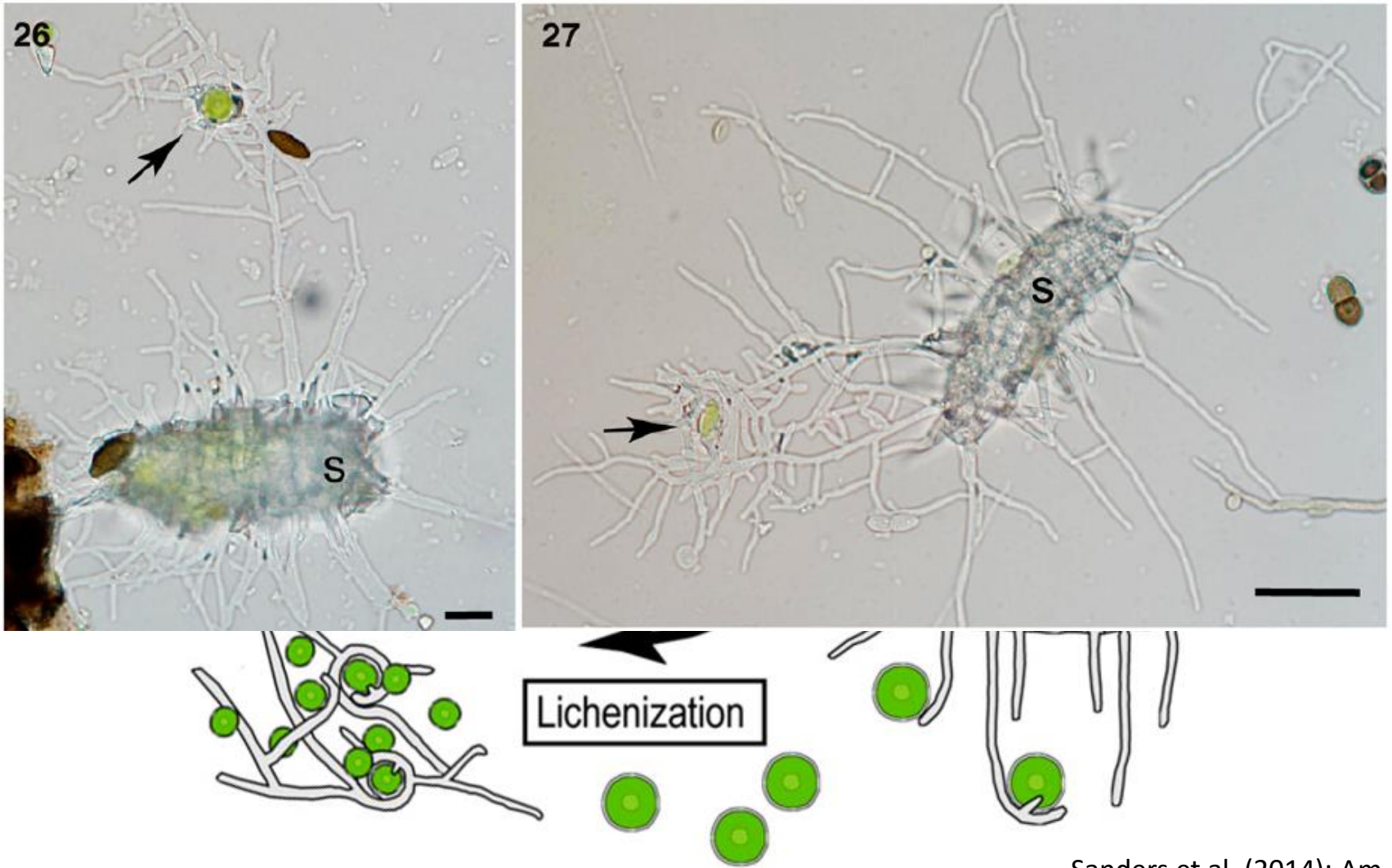


Faktorová (2020): Nat. Methods

nytimes.com

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



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

Horizontal transmission

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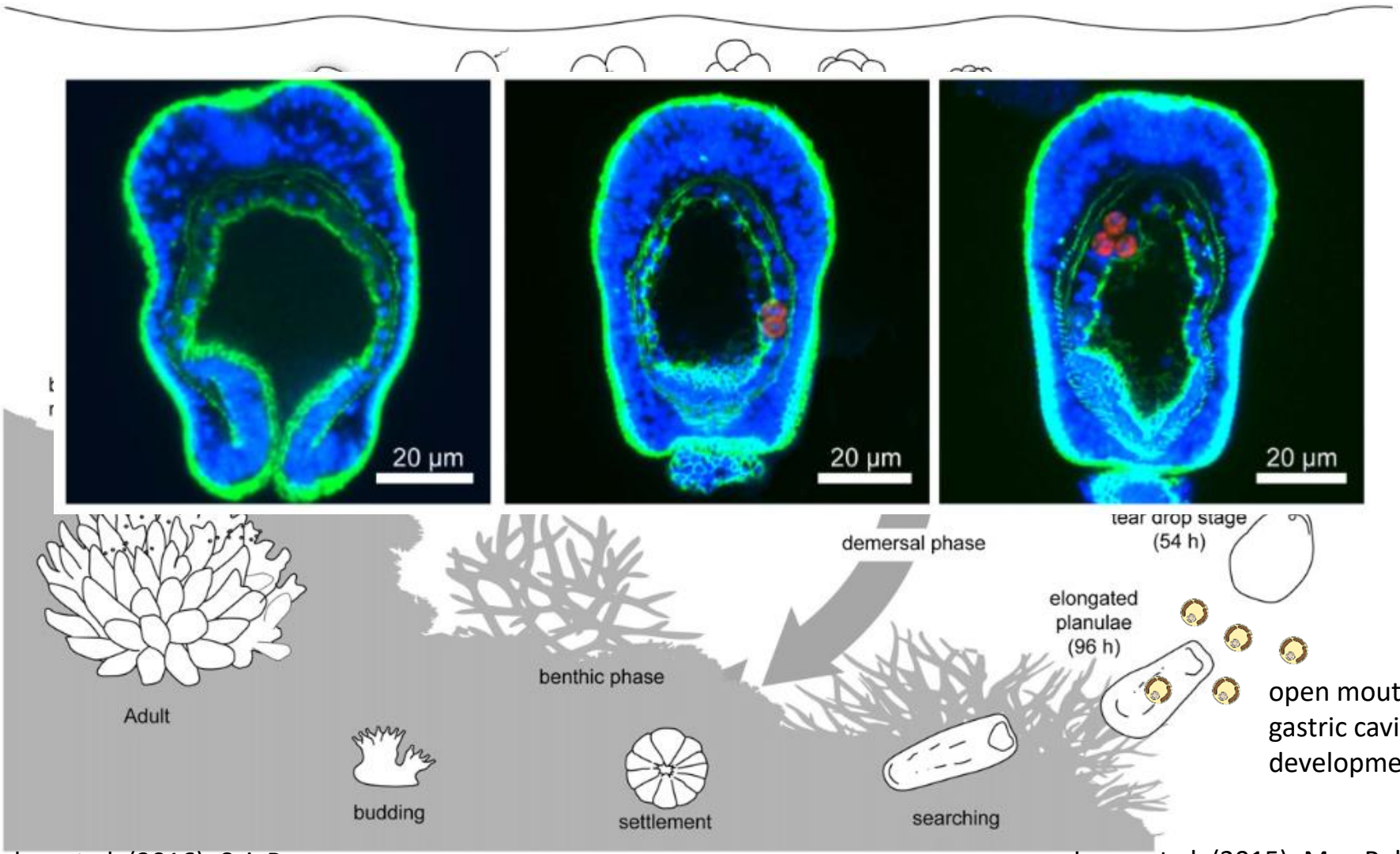


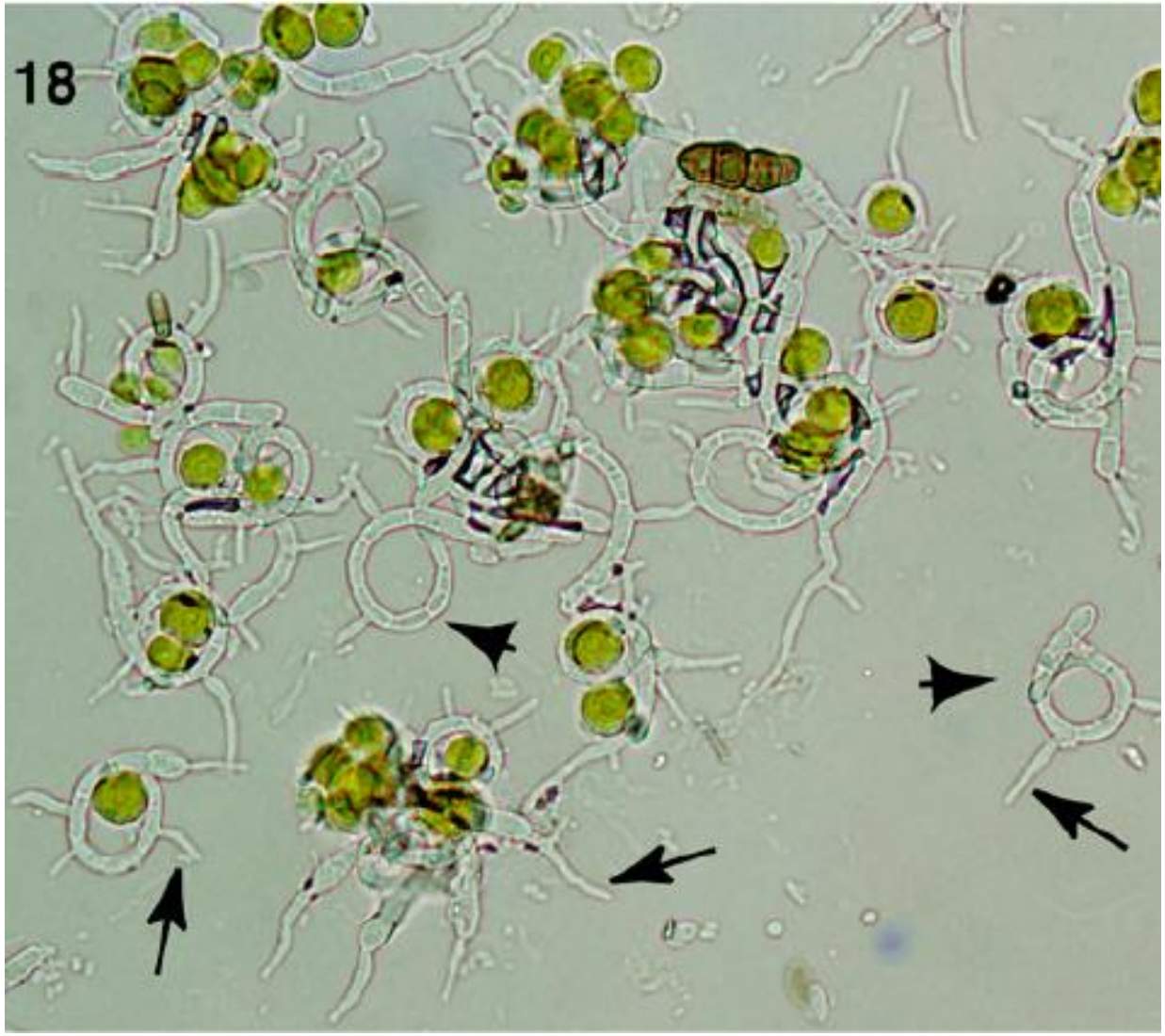
open mouth, gastric cavity development

Bucher et al. (2016): Sci. Rep.

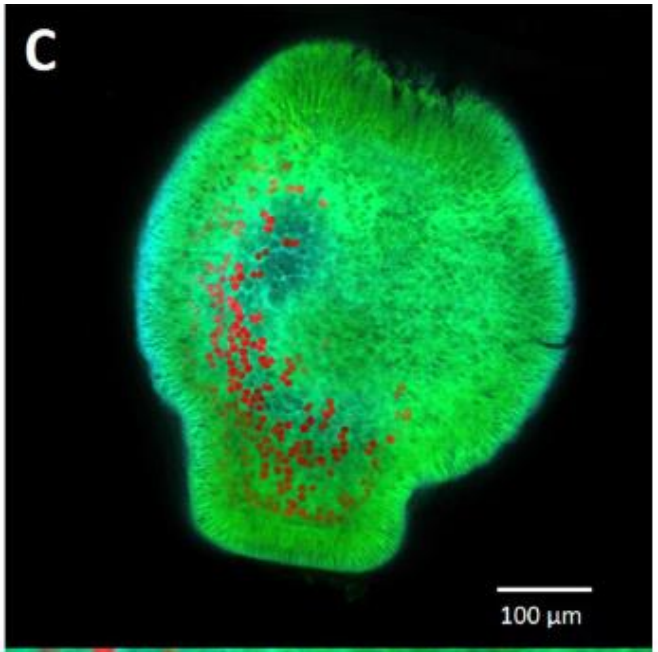
Jones et al. (2015): Mar. Poll. Bul.

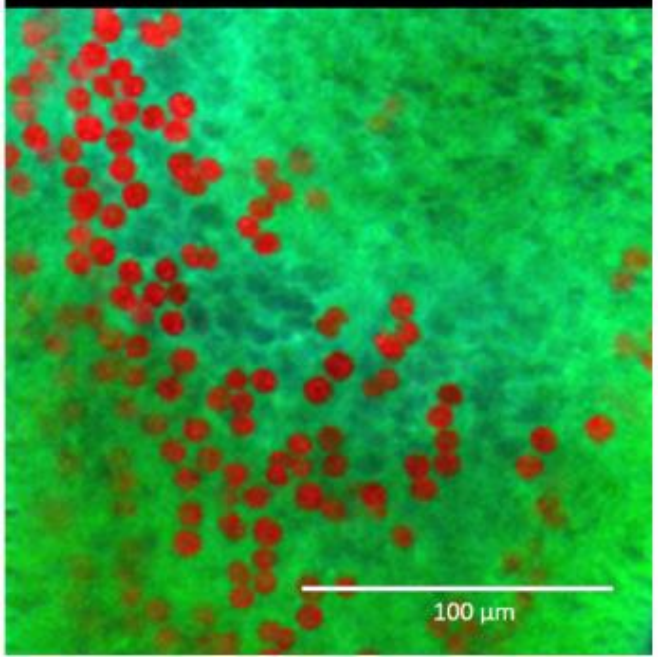
Vertical transmission

- Co-dispersal of both symbionts



Sanders (2014): Am. J. Bot.

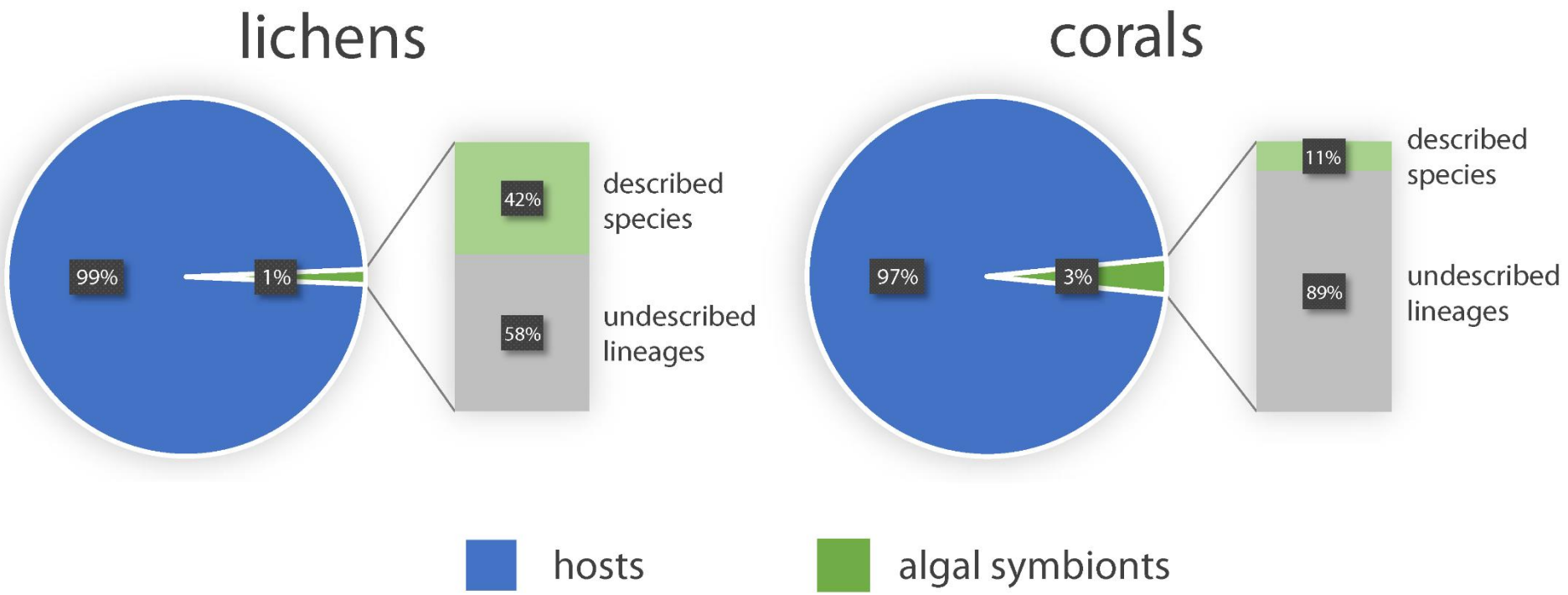




Chakravarti et al. (2019): Front. Microbiol.

Enormous disparity in species richness

- Lichens:
  - ~ 17,000 host species
  - ~ 233 algal symbiotic lineages
- Corals:
  - ~ 6,000 host species
  - ~ 200 algal symbiotic lineages



High specialization of symbionts

- Strong algal host specificity

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

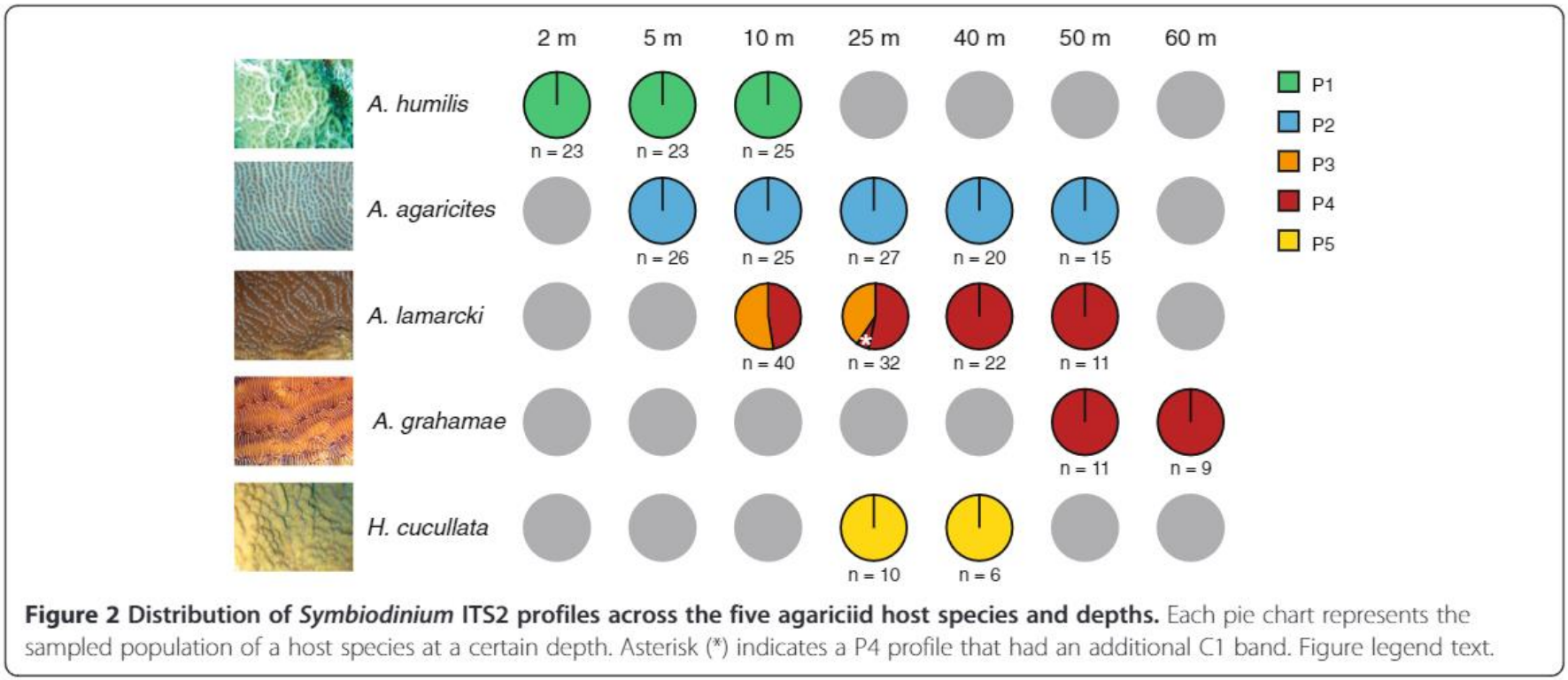
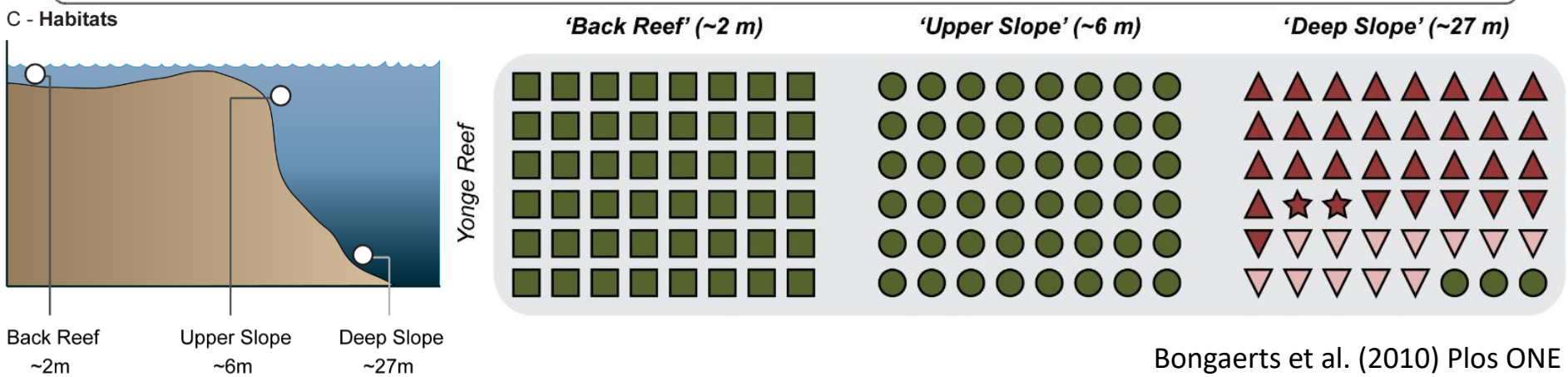


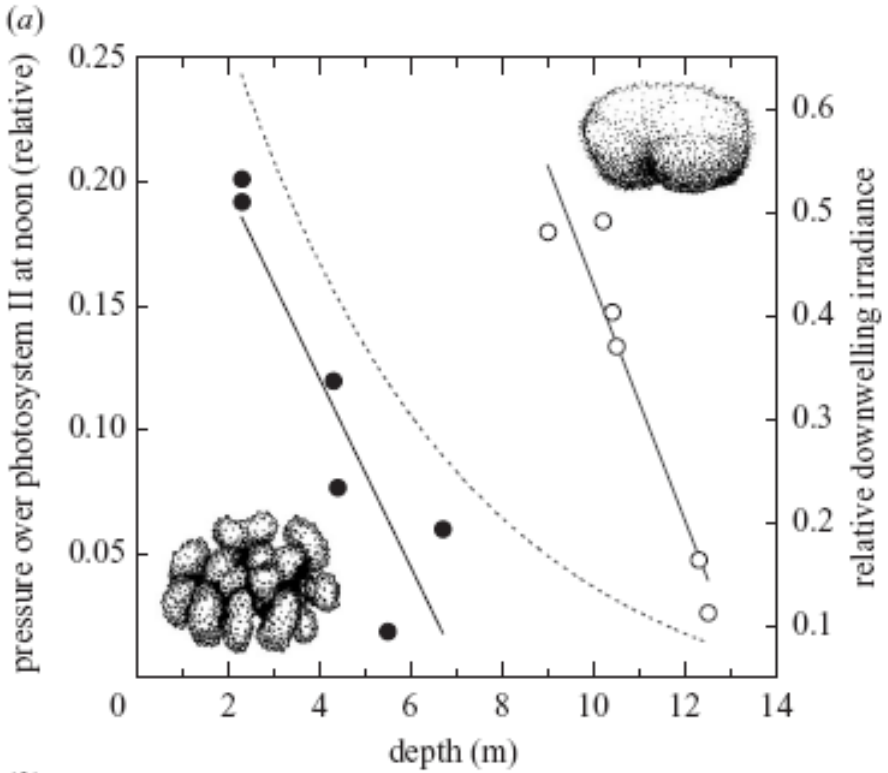
Figure 2 Distribution of *Symbiodinium* ITS2 profiles across the five agariciid host species and depths. Each pie chart represents the sampled population of a host species at a certain depth. Asterisk (*) indicates a P4 profile that had an additional C1 band. Figure legend text.

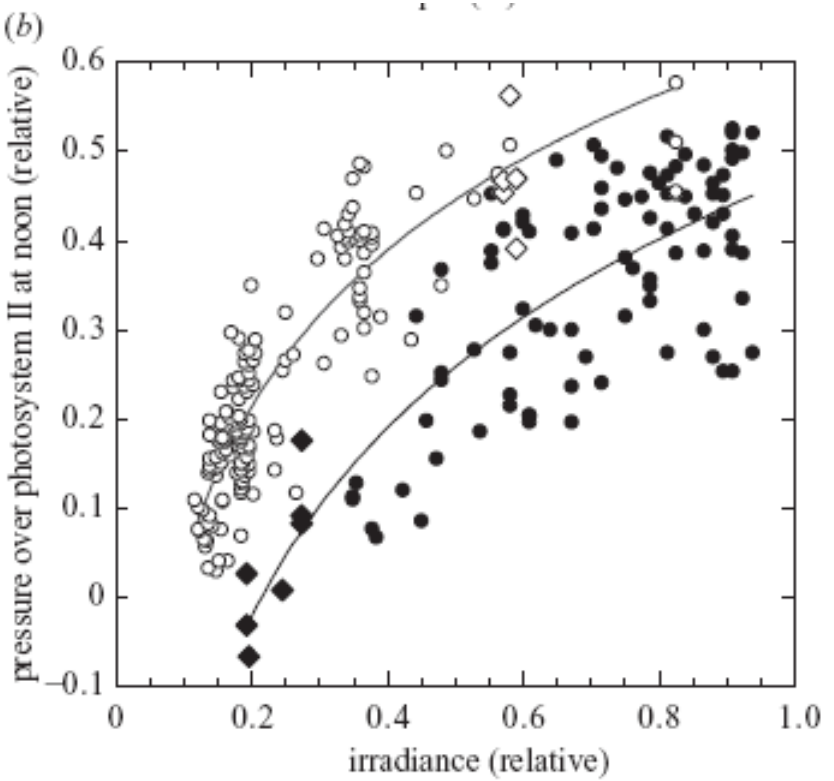


Bongaerts et al. (2010) Plos ONE

High specialization of symbionts

- Narrow ecological niches of algal symbionts





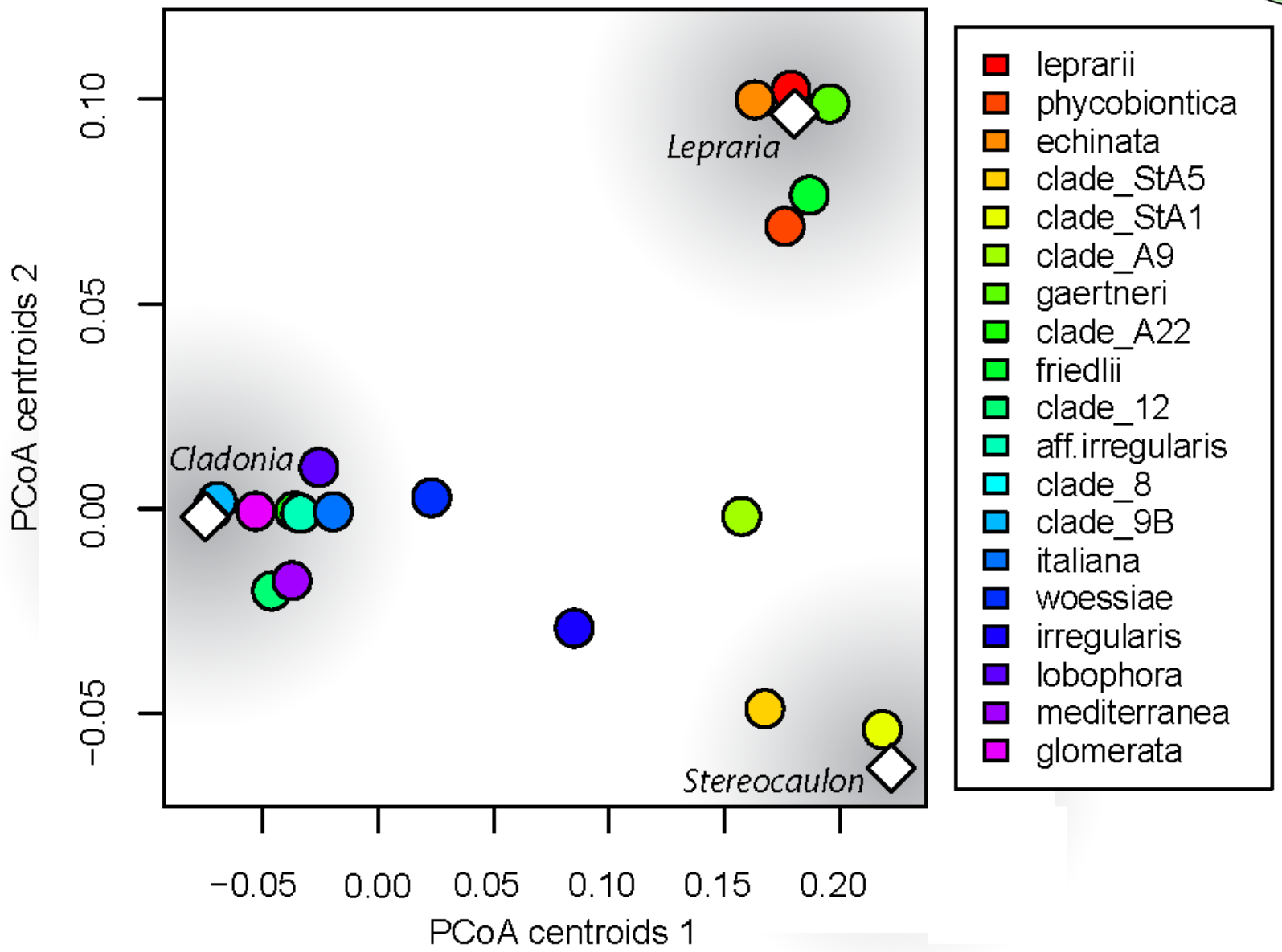
Pocillopora

Pavona

Iglesias-Prieto et al. (2004): Proc. R. Soc. Lond. B

High specialization of symbionts

- Strong algal host specificity



High specialization of symbionts

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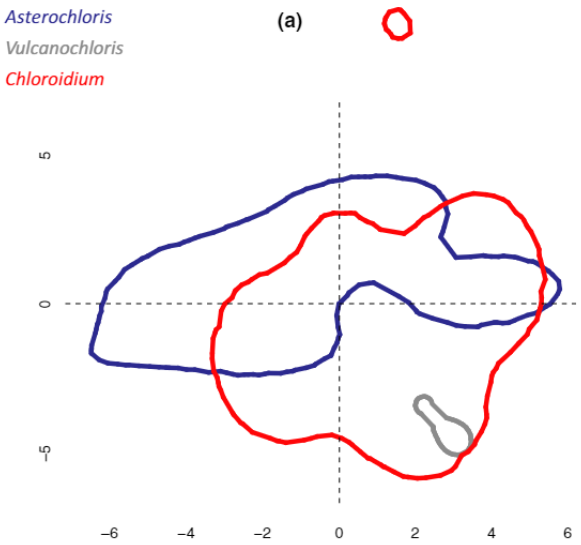
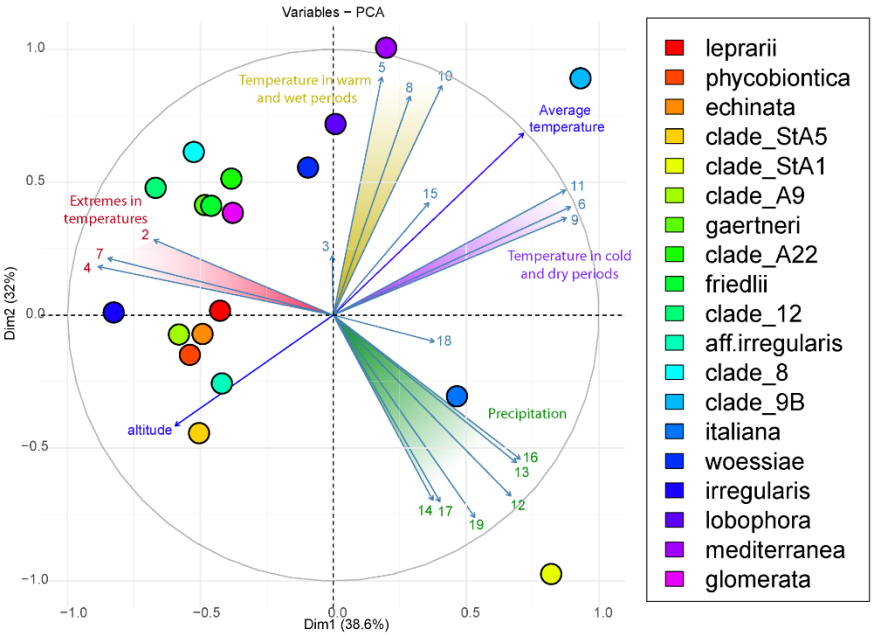
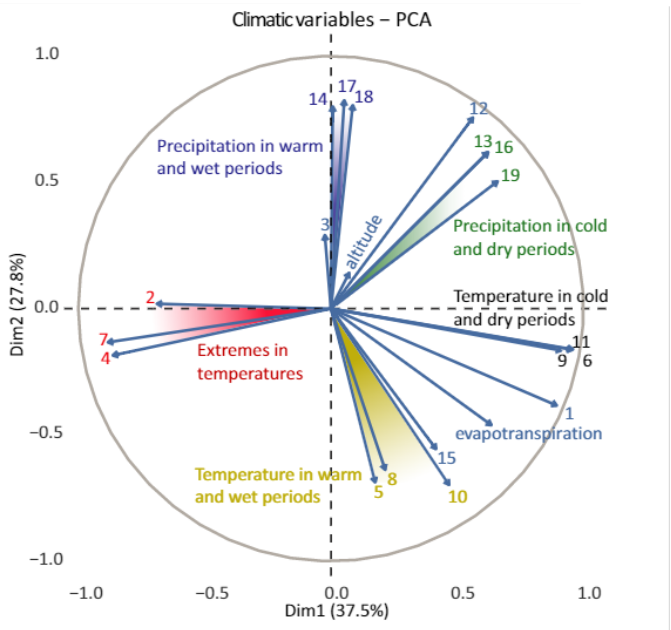
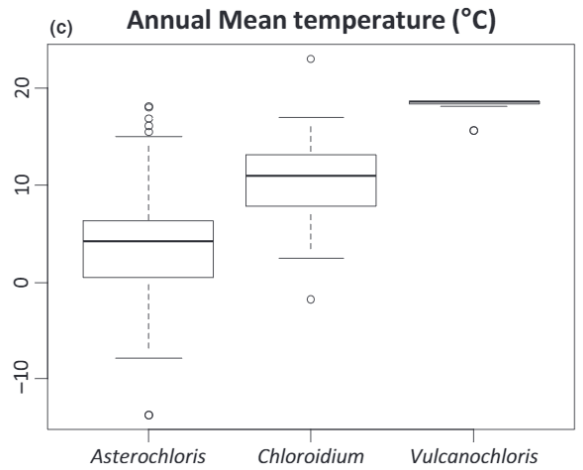


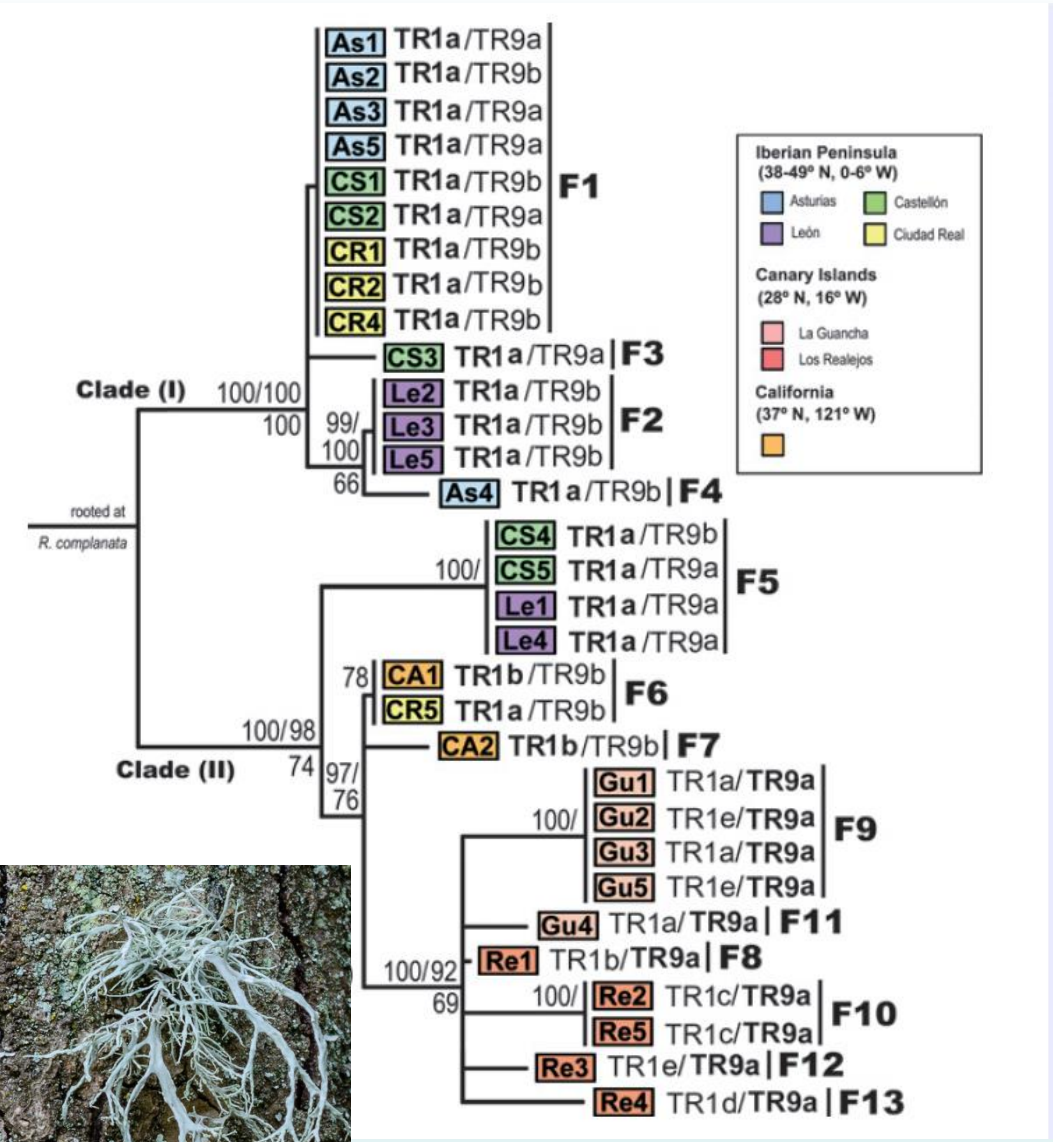




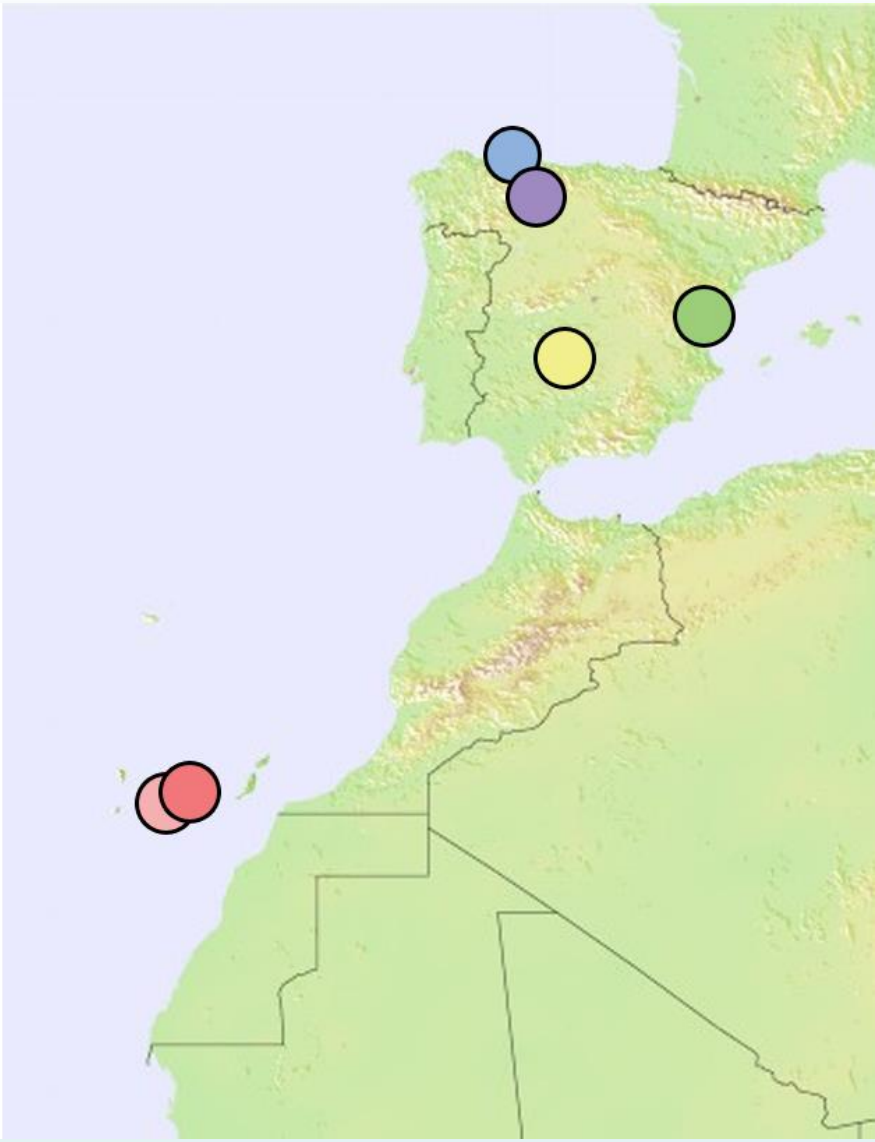


Vančurová et al. (2018): Mol. Ecol.

Multiple symbionts

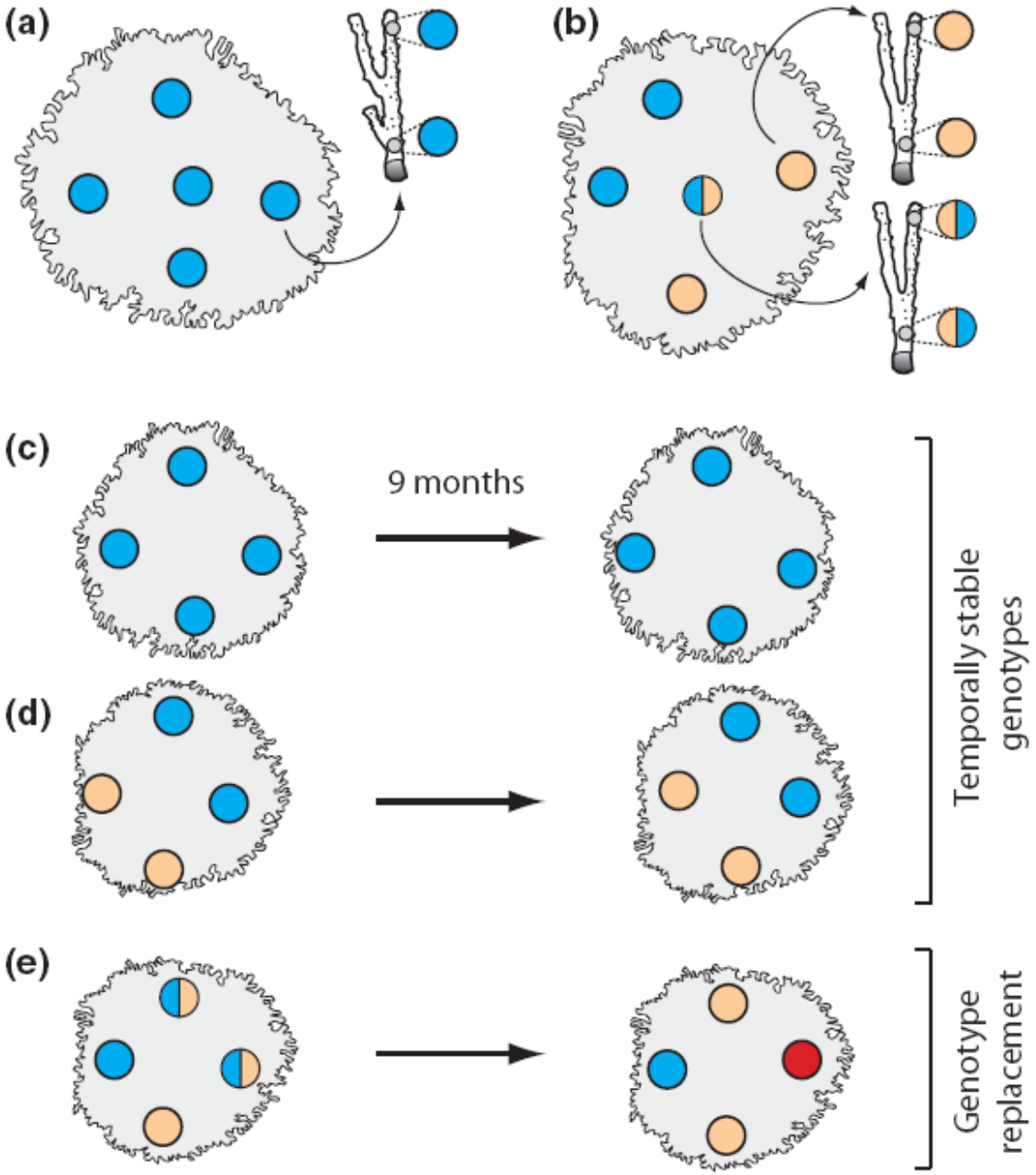


Ramalina farinacea



del Campo et al. (2012): FEMS Microbiol. Ecol.

Multiple symbionts

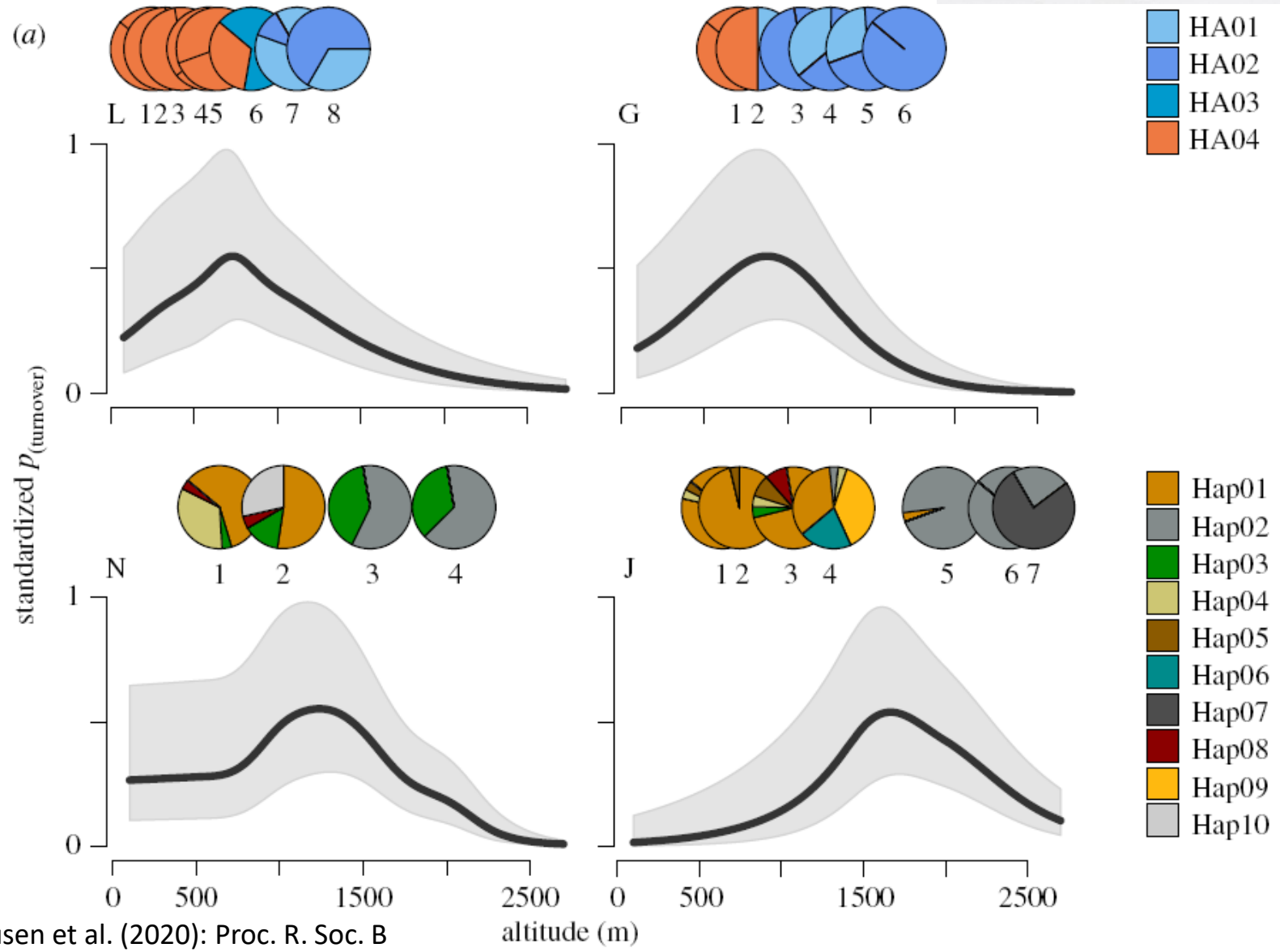


Pocillophora

Pettay et al. (2011): Mol. Ecol.

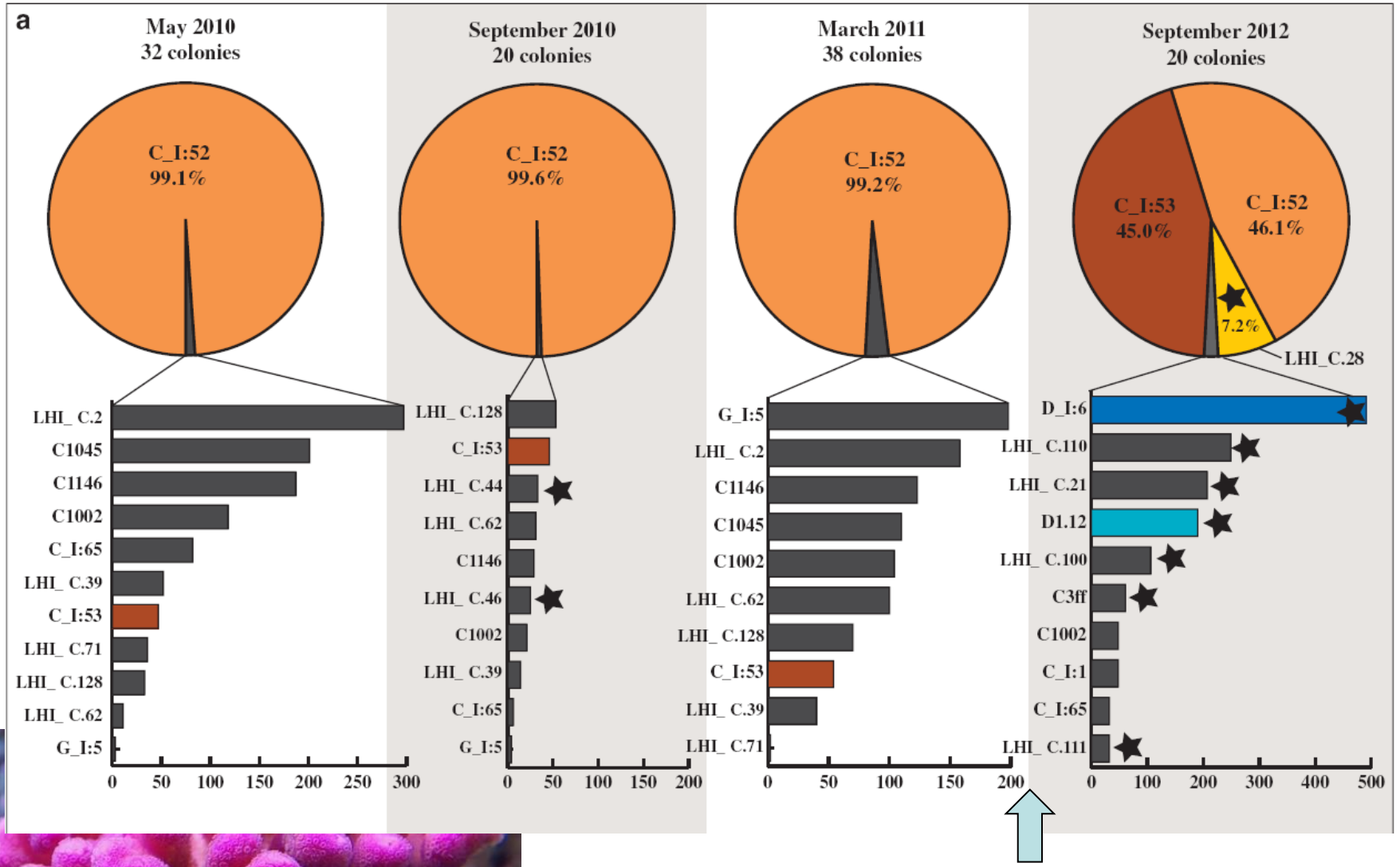
Symbiont switching

Lasallia

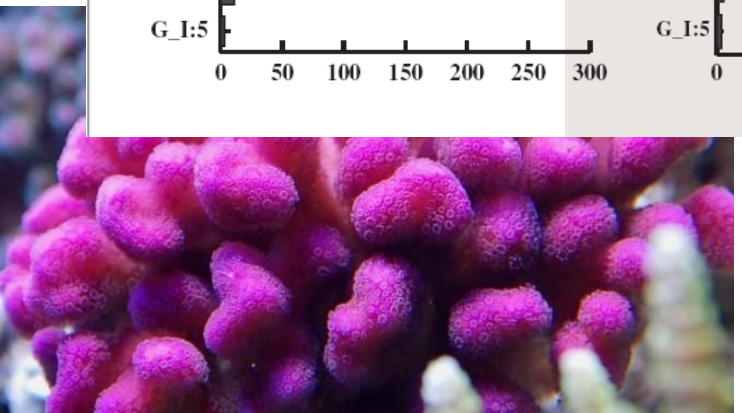


Rolshausen et al. (2020): Proc. R. Soc. B

Symbiont switching



bleaching event

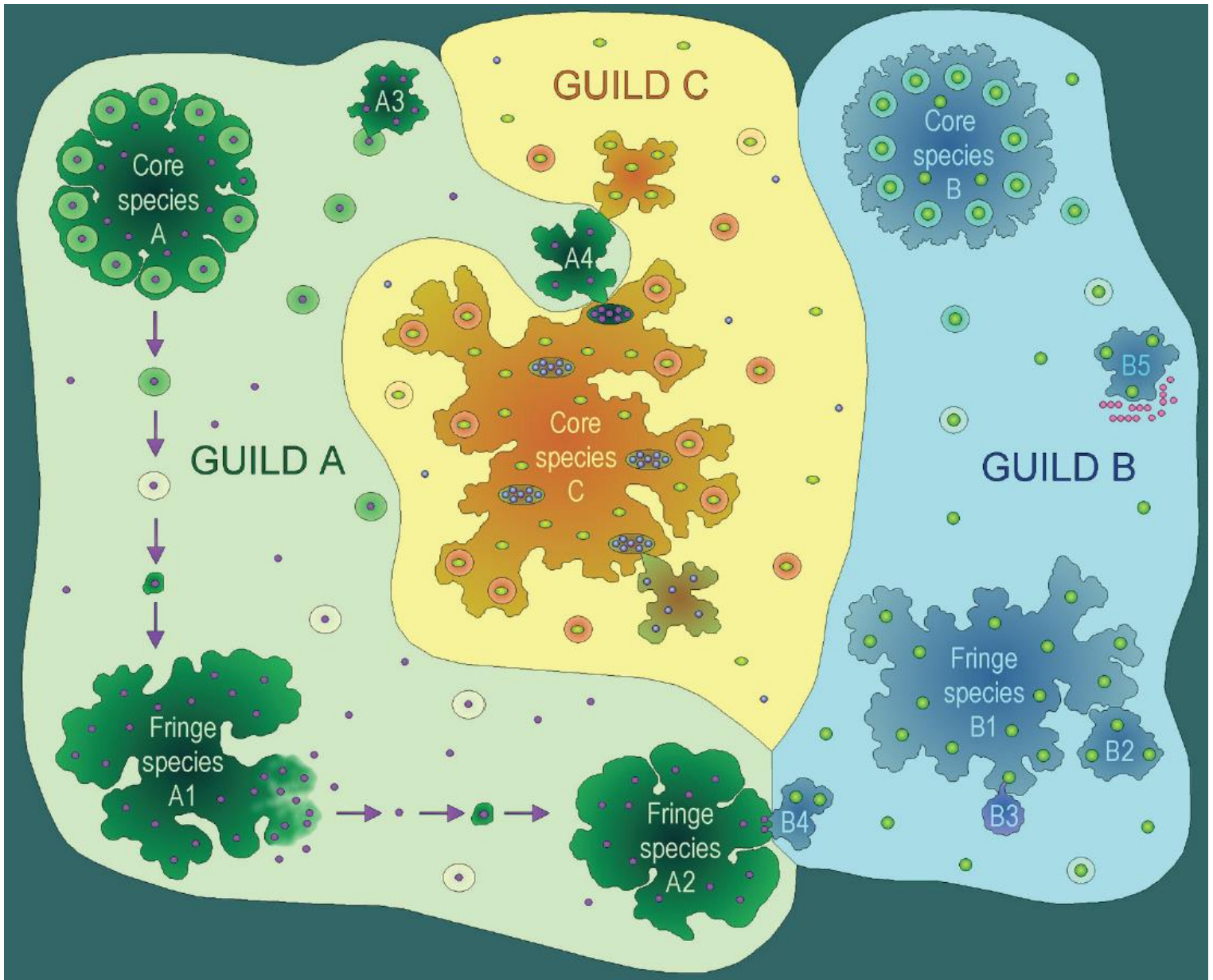


Stylophora pistillata

Boulotte et al. (2016): ISME J

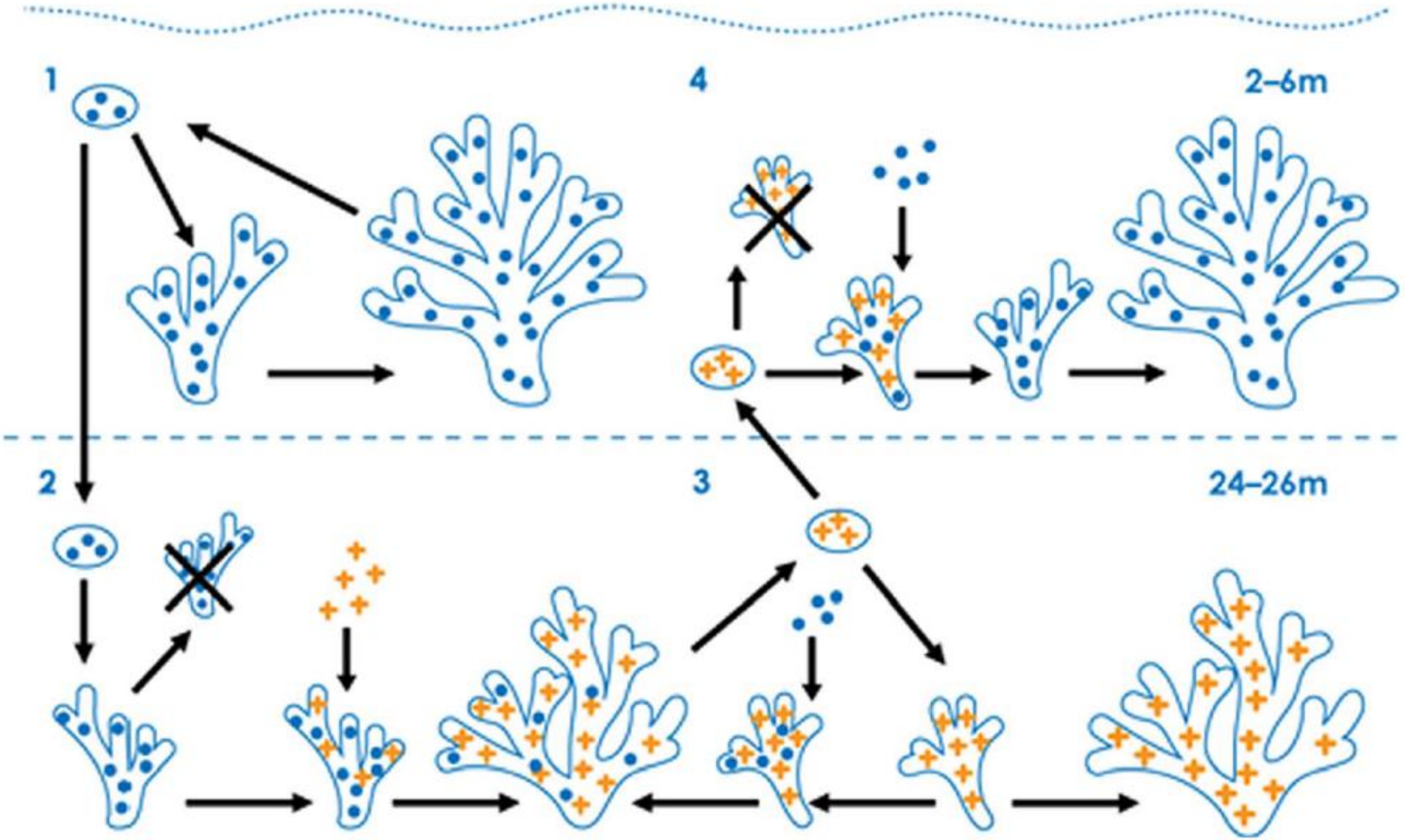
Habitat adapted symbiosis

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



Rikkinen (2013): MycoKeys

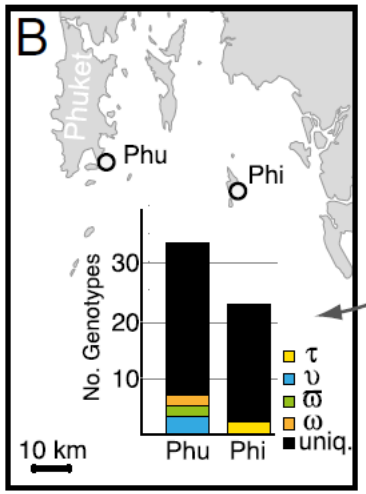
Habitat adapted symbiosis

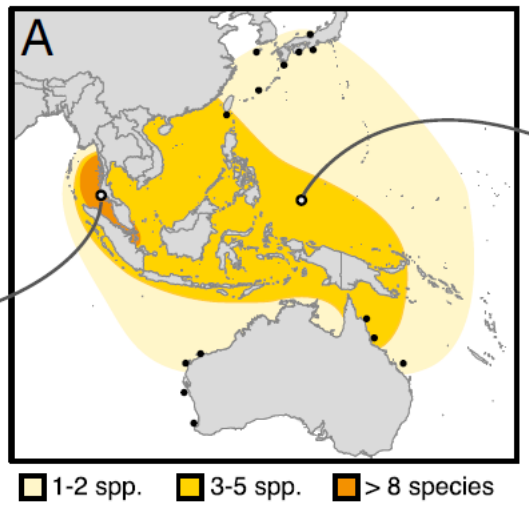


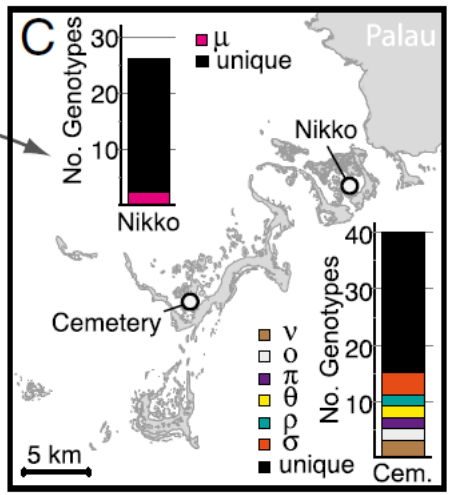
Byler et al. (2013): Plos ONE

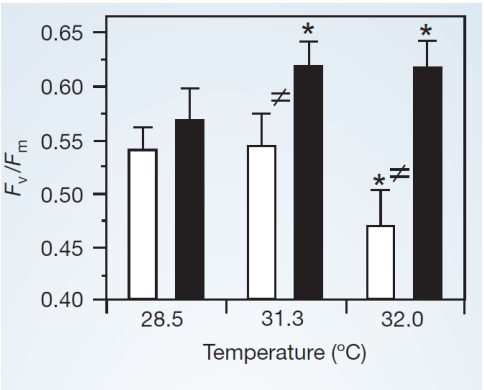
Habitat adapted symbiosis

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

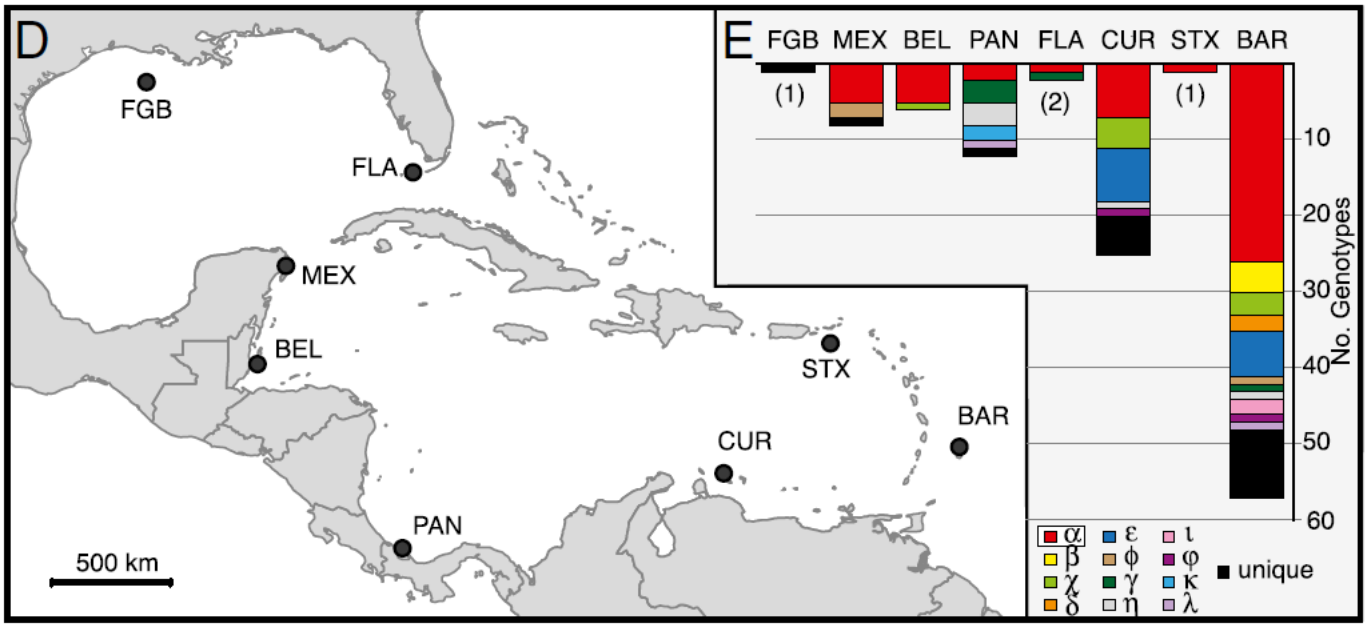








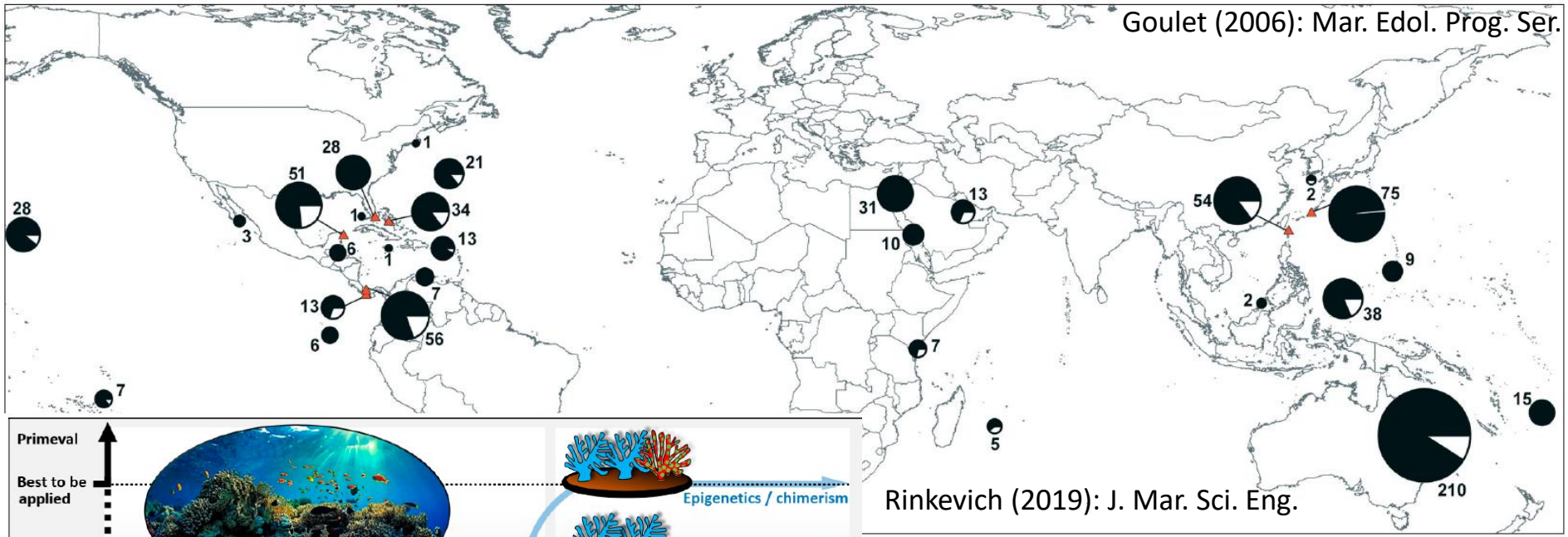
Rowan (2004): Nature

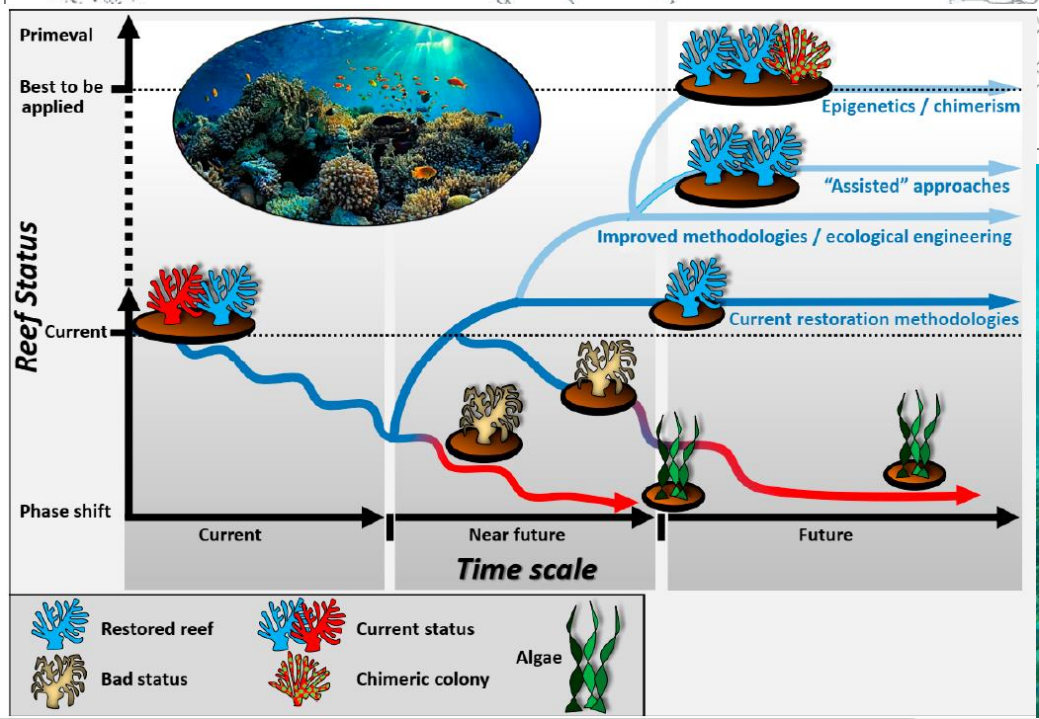


Pettay et al. (2015): PNAS

Habitat adapted symbiosis

- Only 23% of coral species host multiple symbions

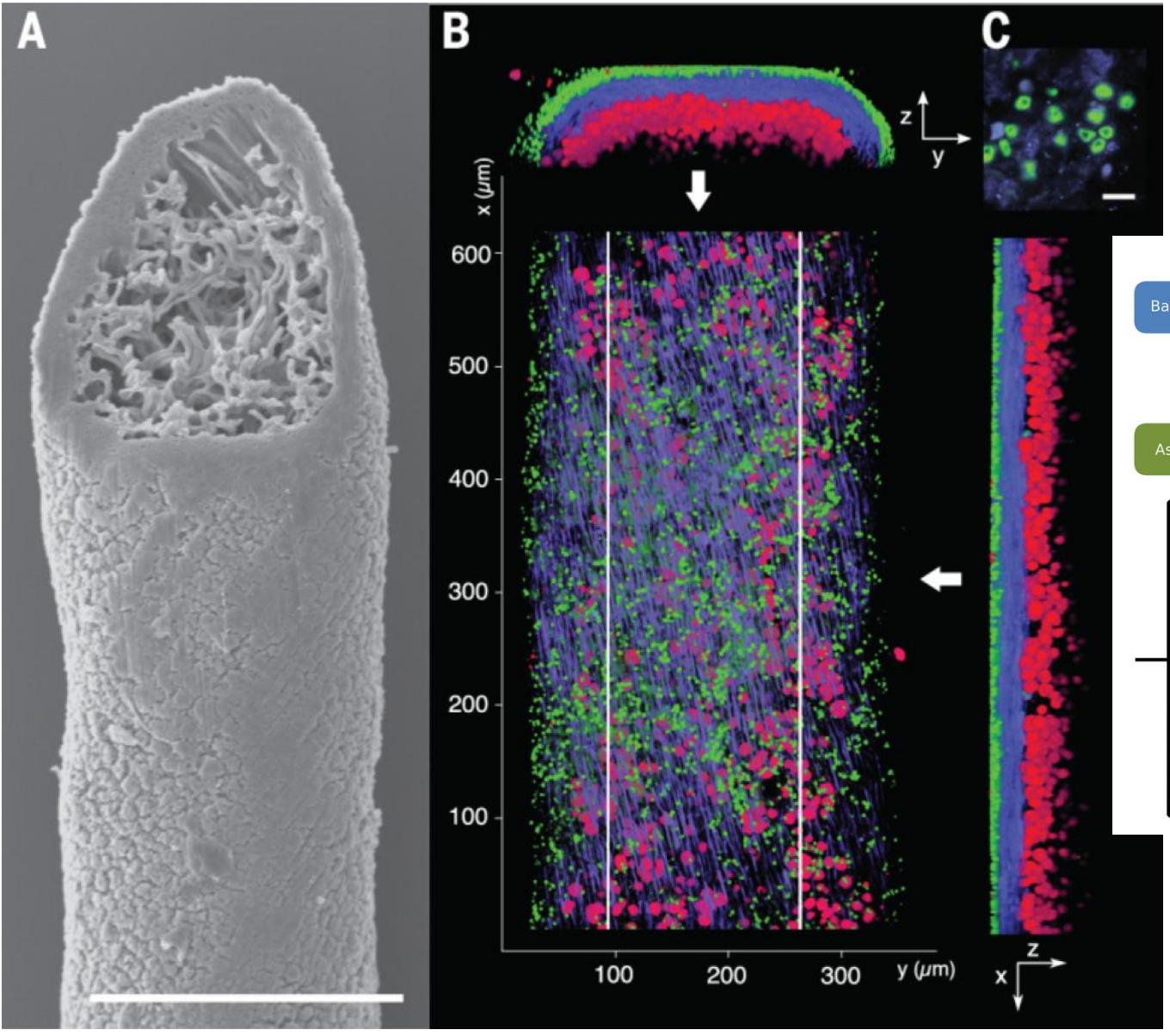


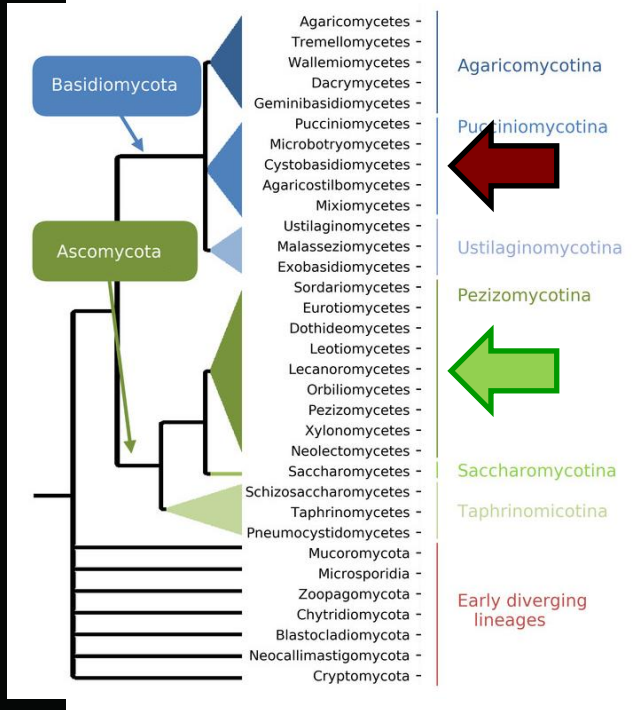



The University of Hong Kong

Revolution in symbiosis research

- Basidiomycete yeasts as a third partner in lichen symbiosis?

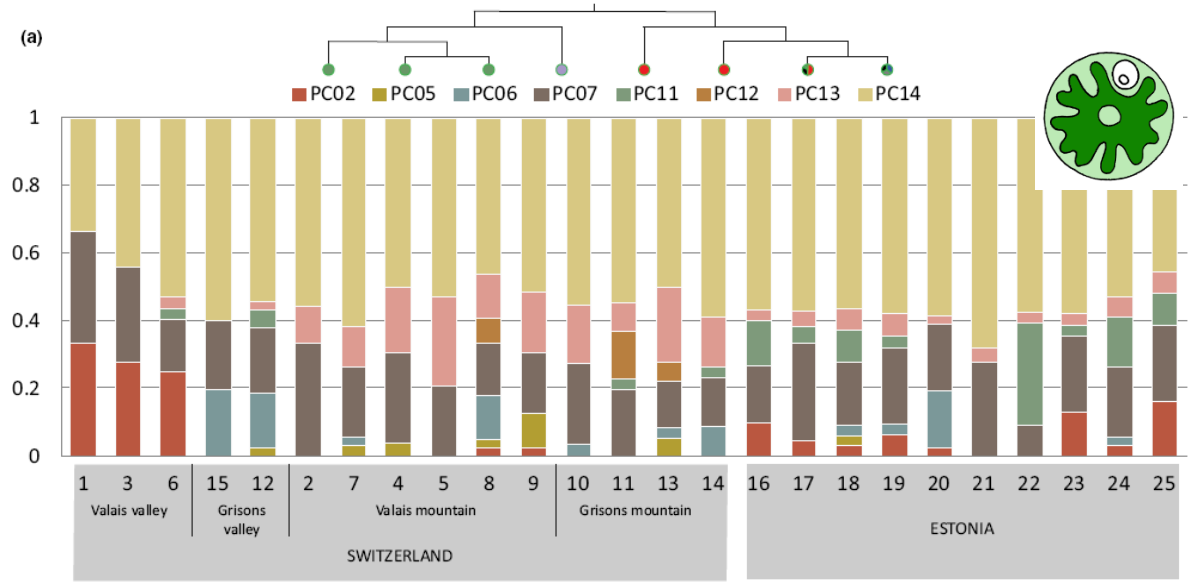


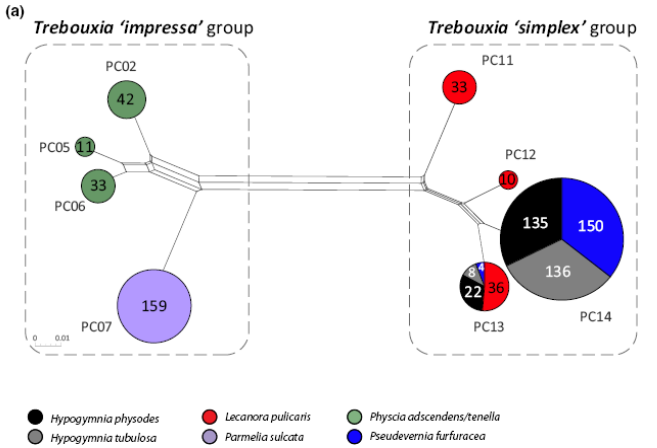


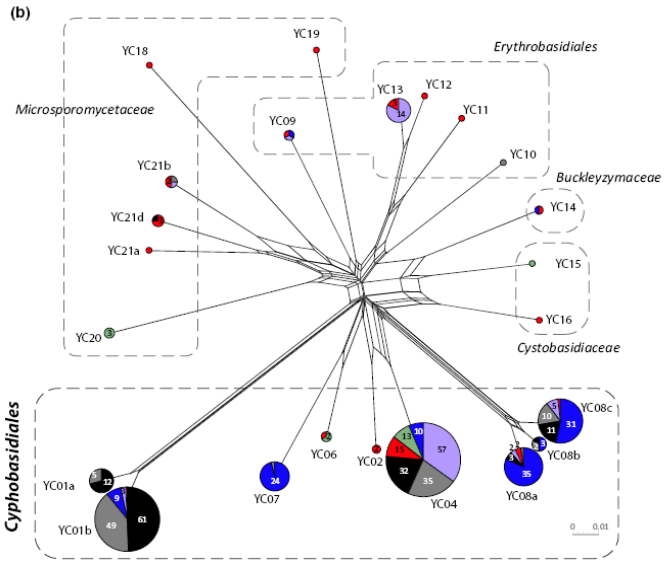
Spribille et al. (2016): Science

Revolution in symbiosis research

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



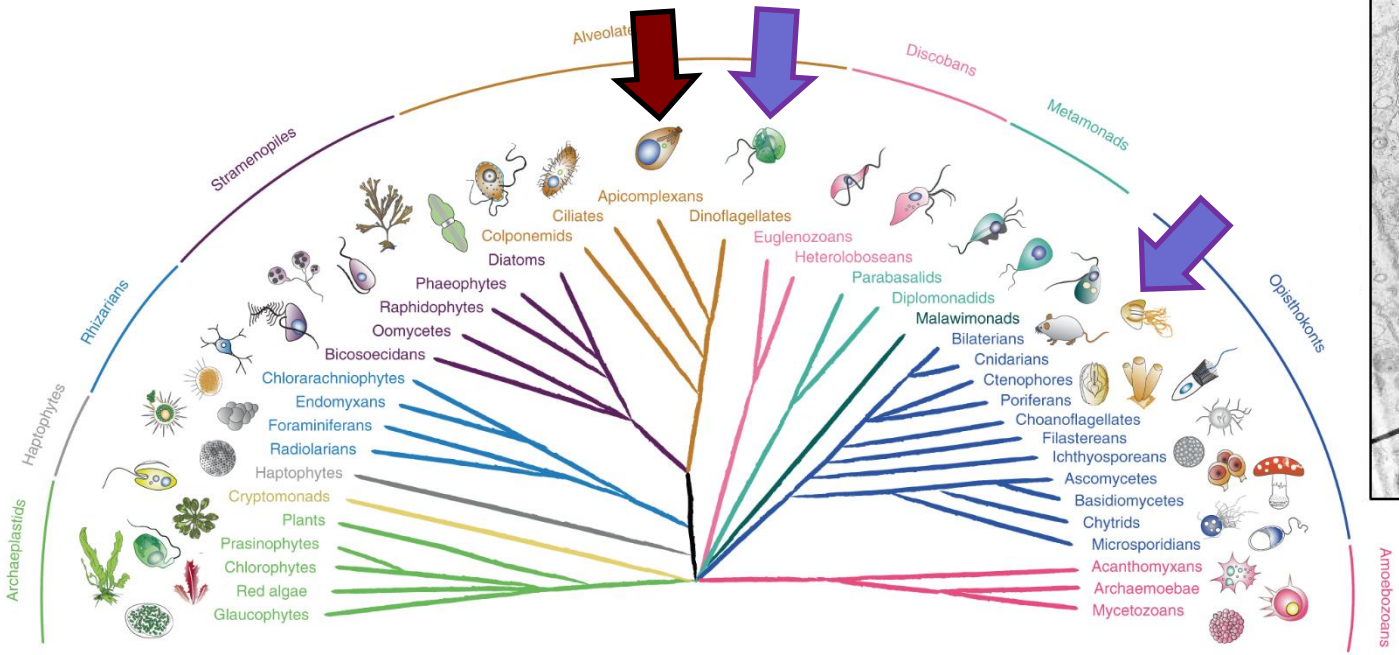


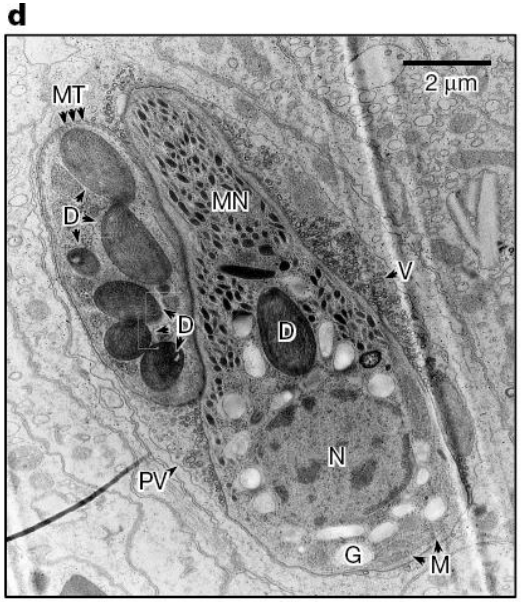


Mark et al. (2020): New Phytol.

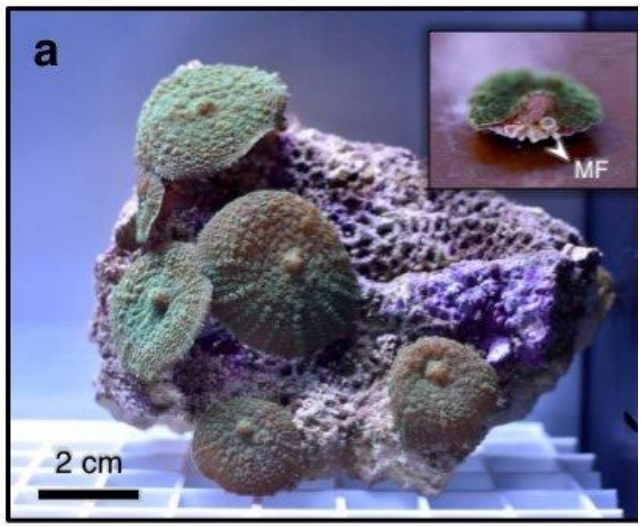
Revolution in symbiosis research

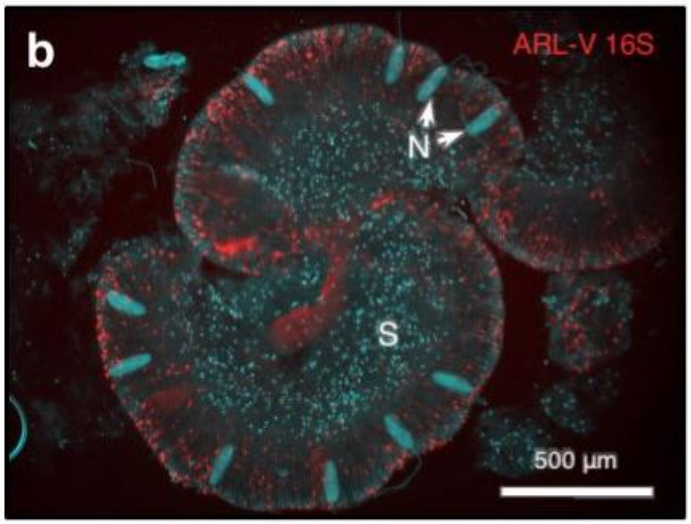
- Corallicolids – a third partner in coral symbiosis?

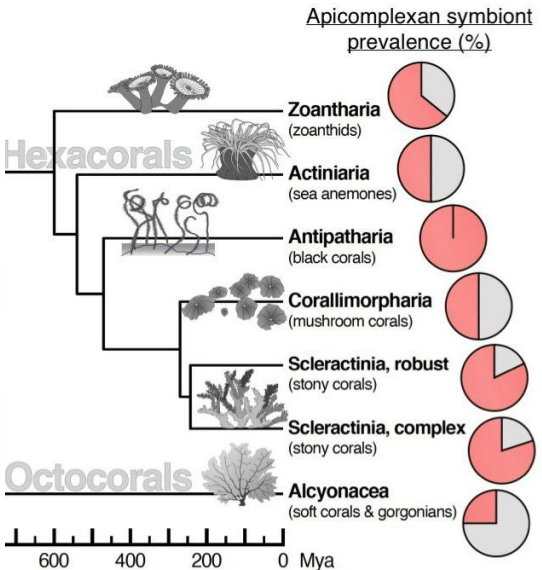




Kwong et al. (2019): Nature



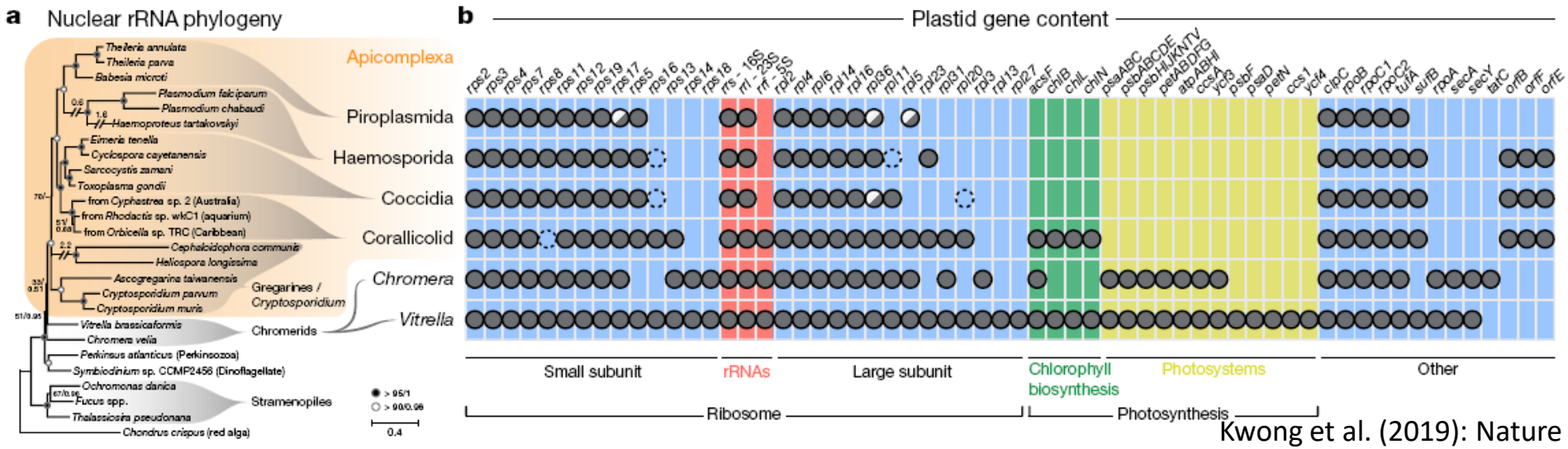




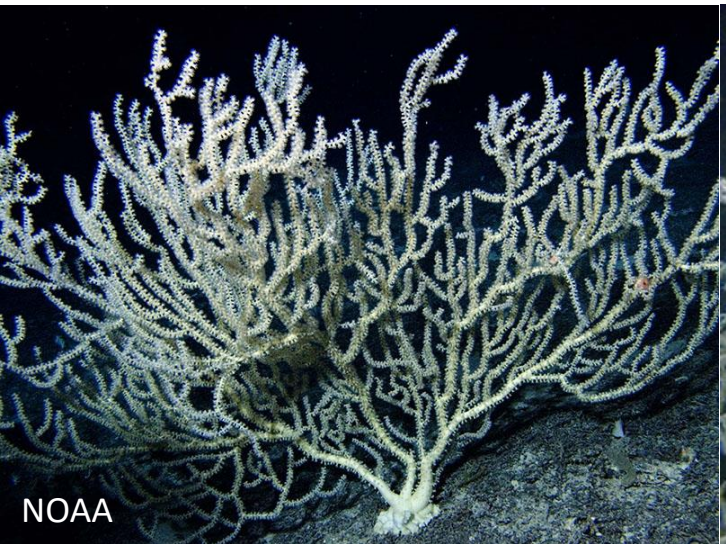
Revolution in symbiosis research

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

Vohsen et al. (2020): Microbiome



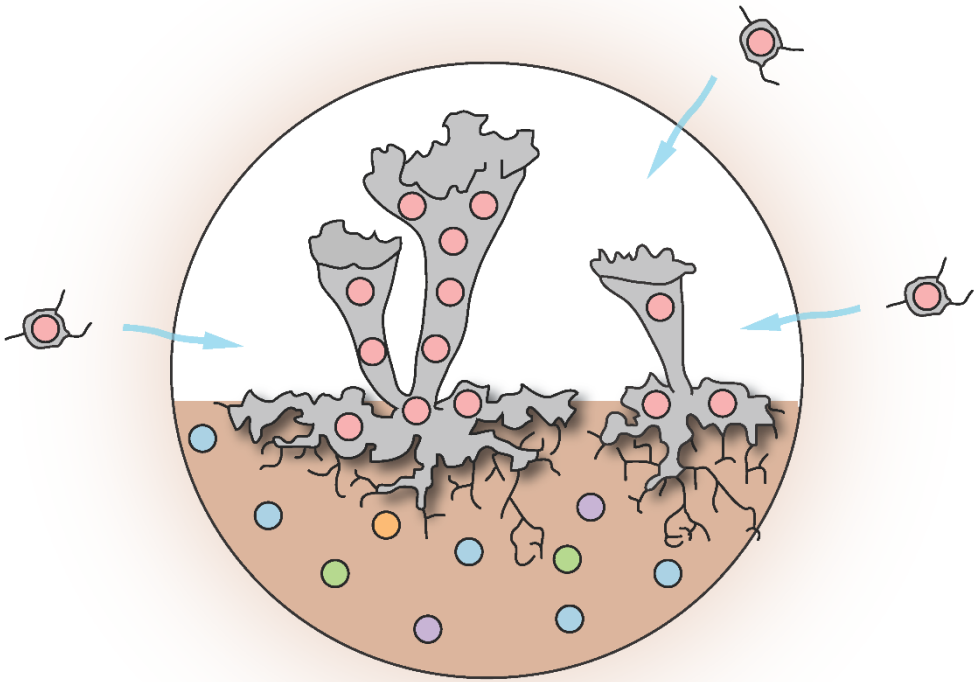
Kwong et al. (2019): Nature



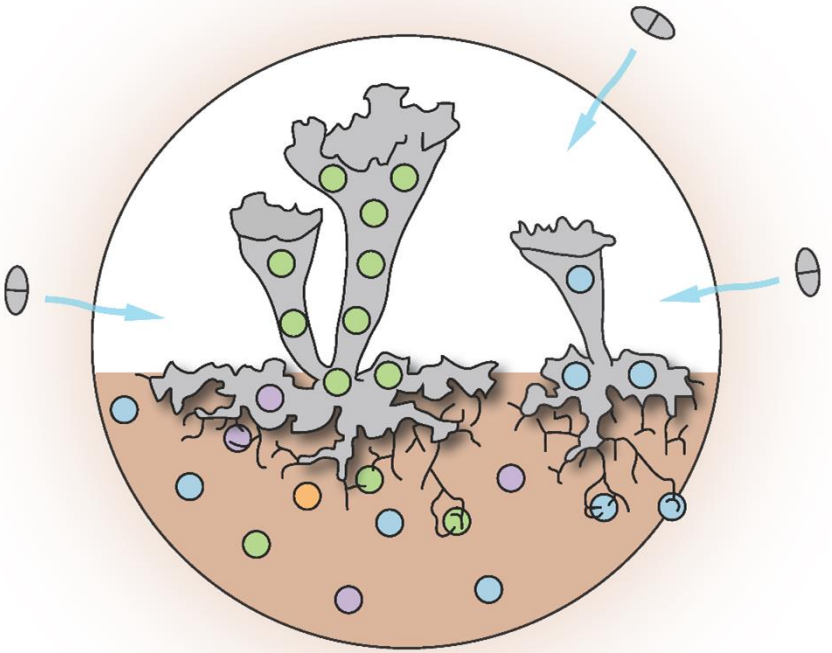
Paradox I.

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).



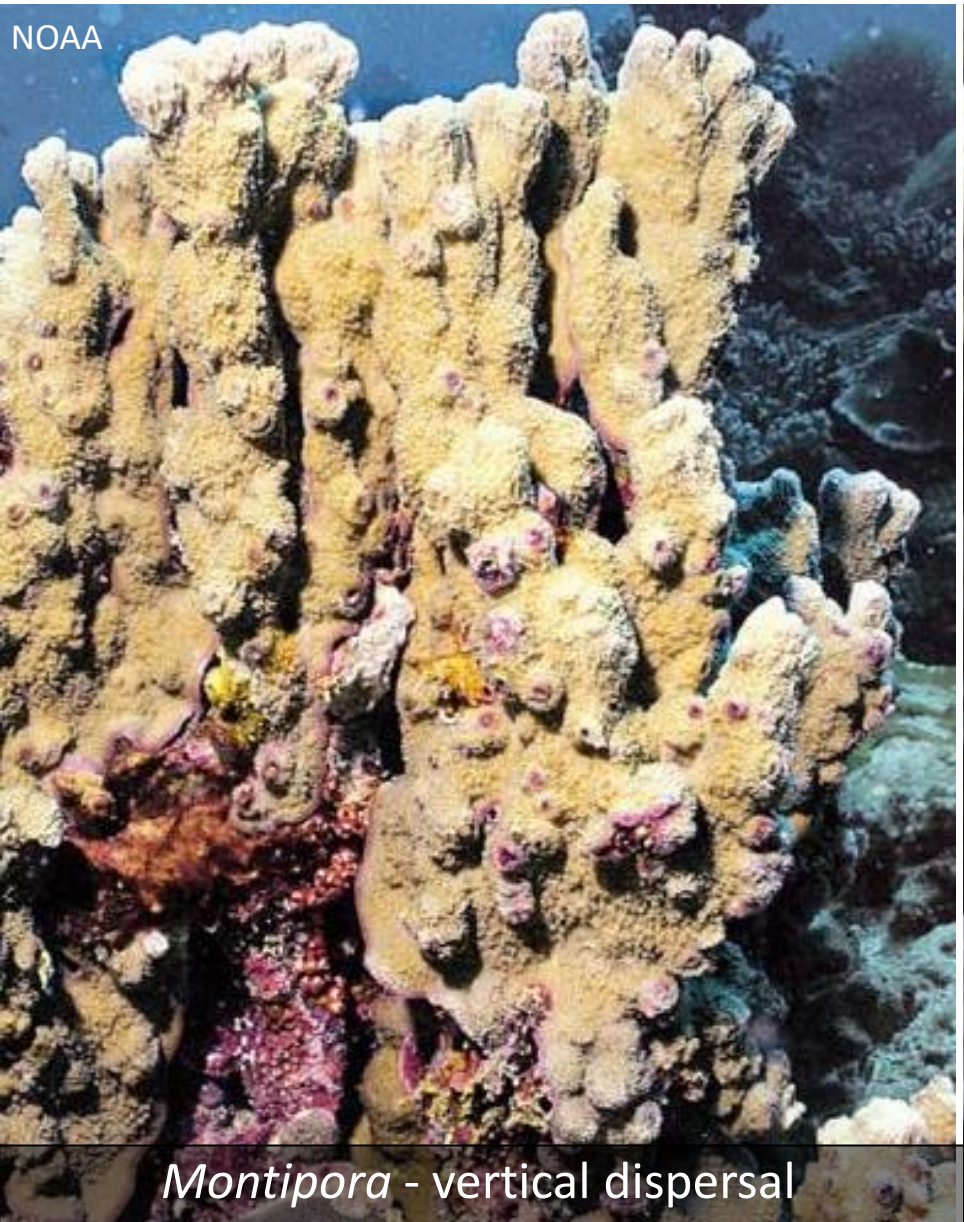
vertical dispersal



horizontal dispersal

Paradox I.

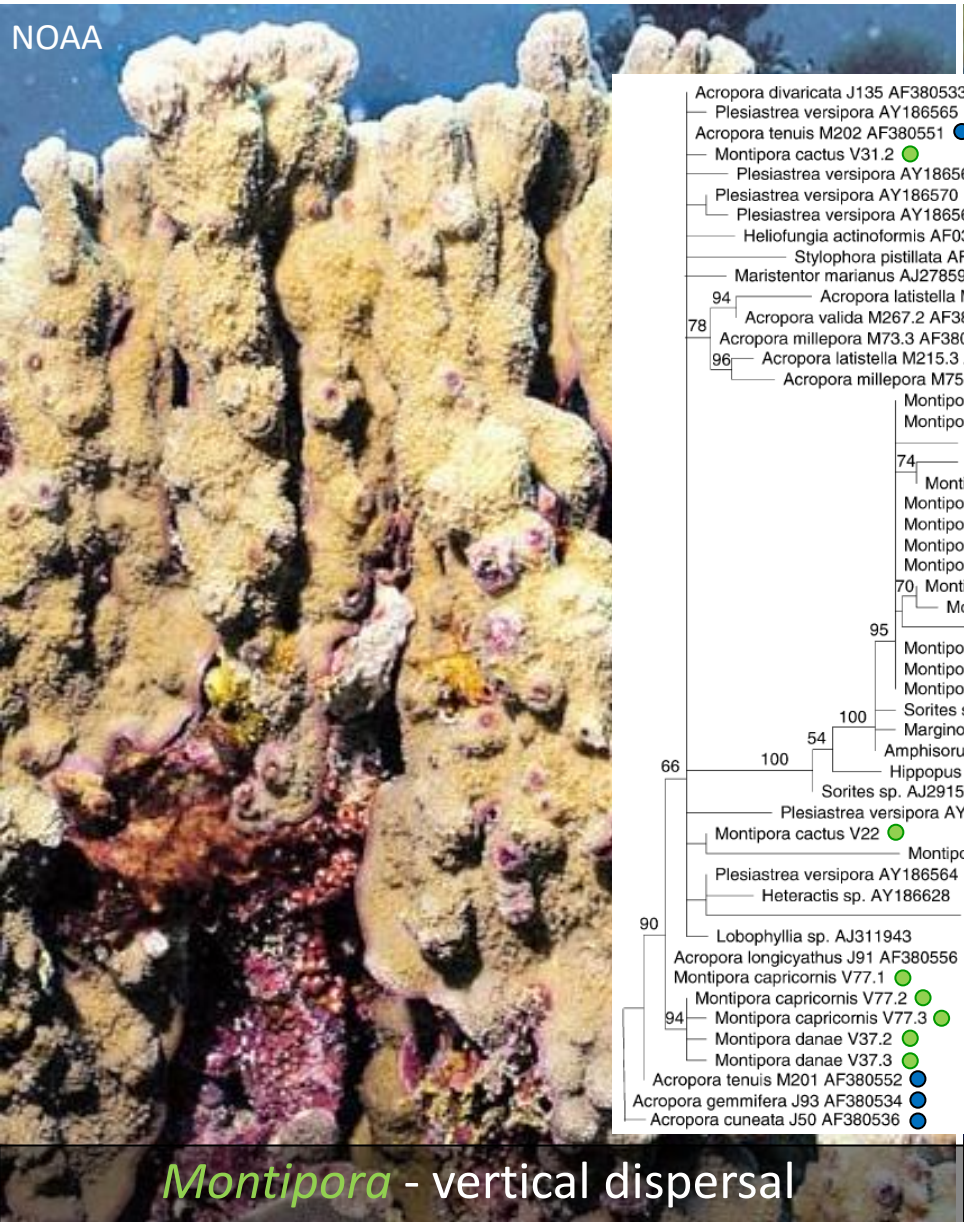
The mode of symbiont dispersal does not affect symbiont diversity



Paradox I.

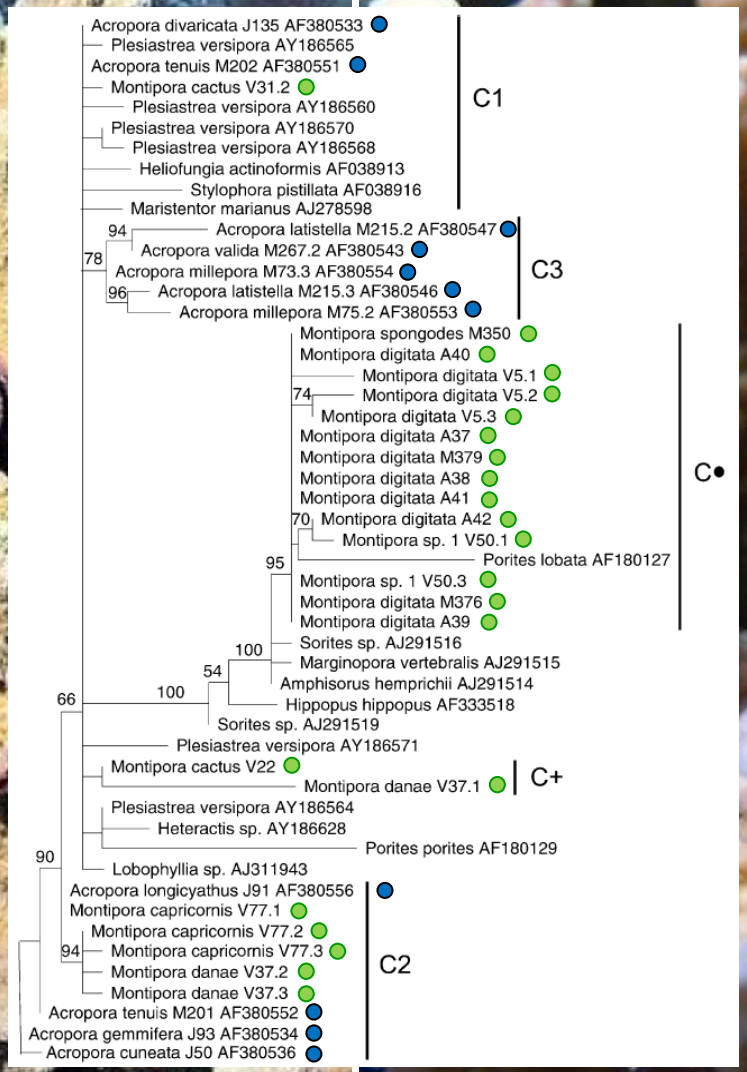
The mode of symbiont dispersal does not affect symbiont diversity

NOAA



Montipora - vertical dispersal

van Oppen (2004): Mar. Biol.



NOAA

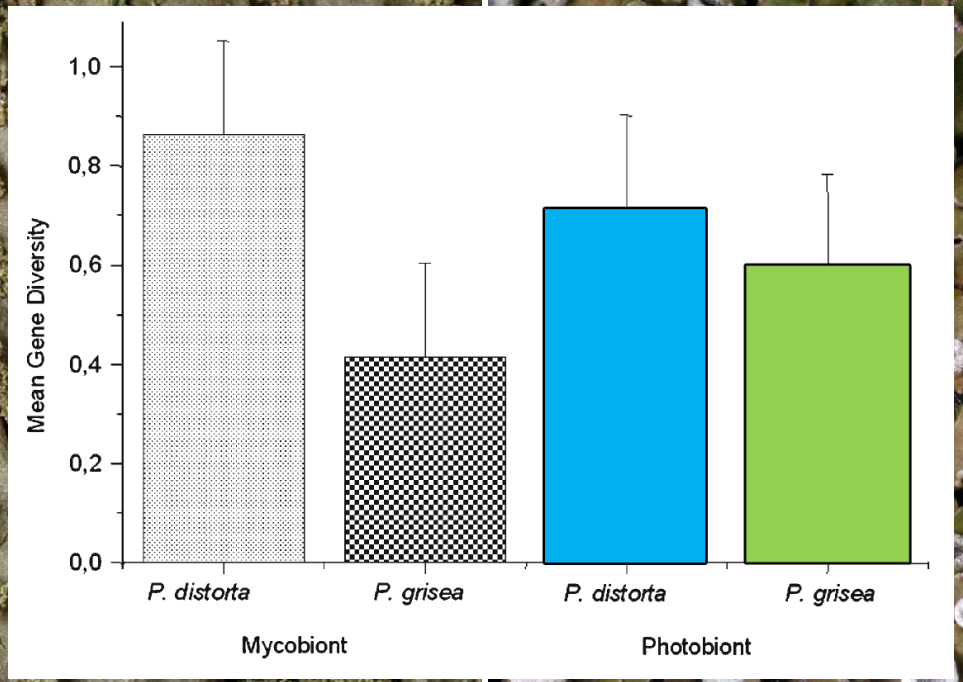
Acropora - horizontal dispersal

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

stridvall.se

Wornik & Grube (2010): Microb. Ecol.



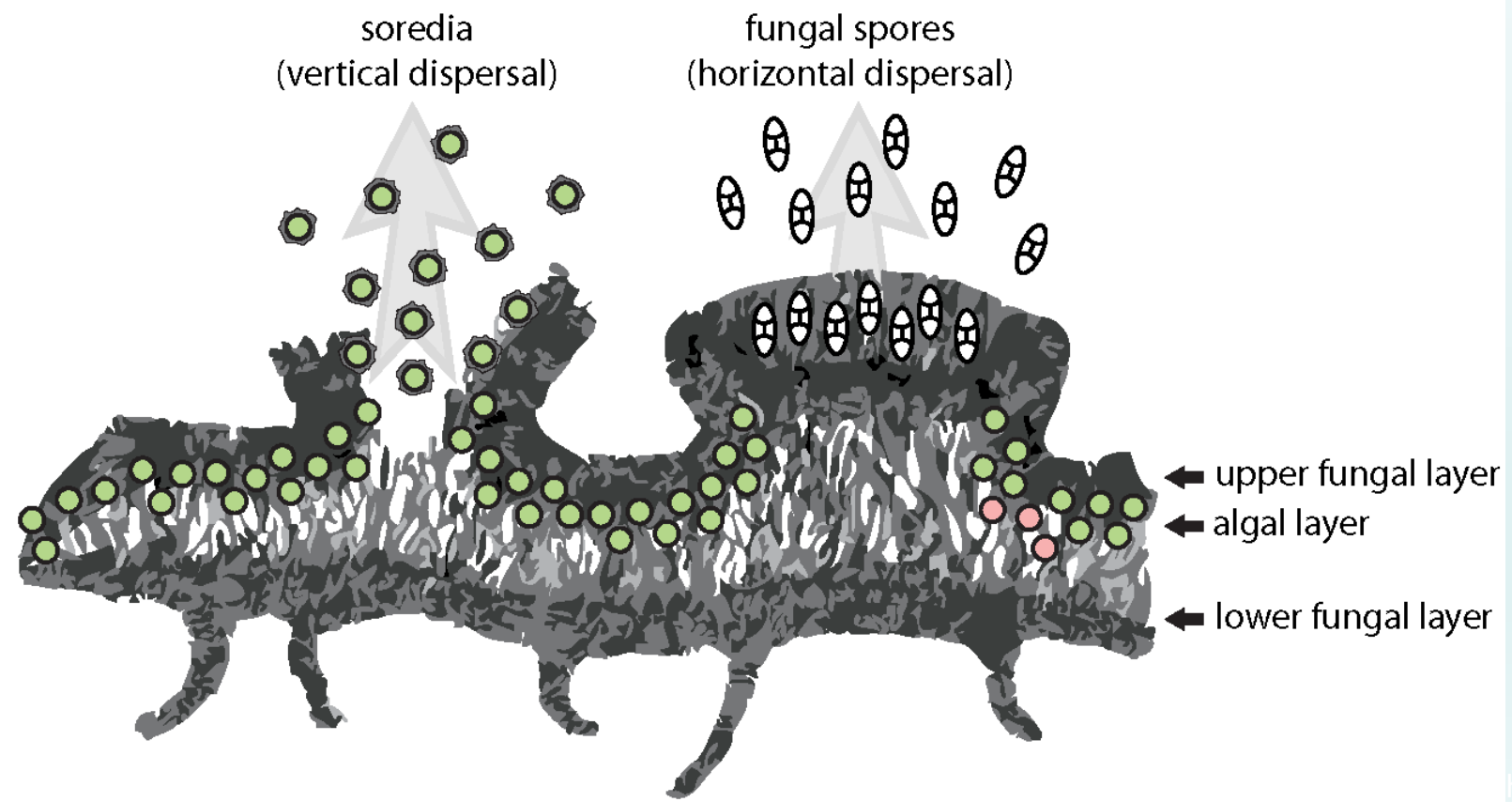
Physconia grisea - vertical dispersal

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.

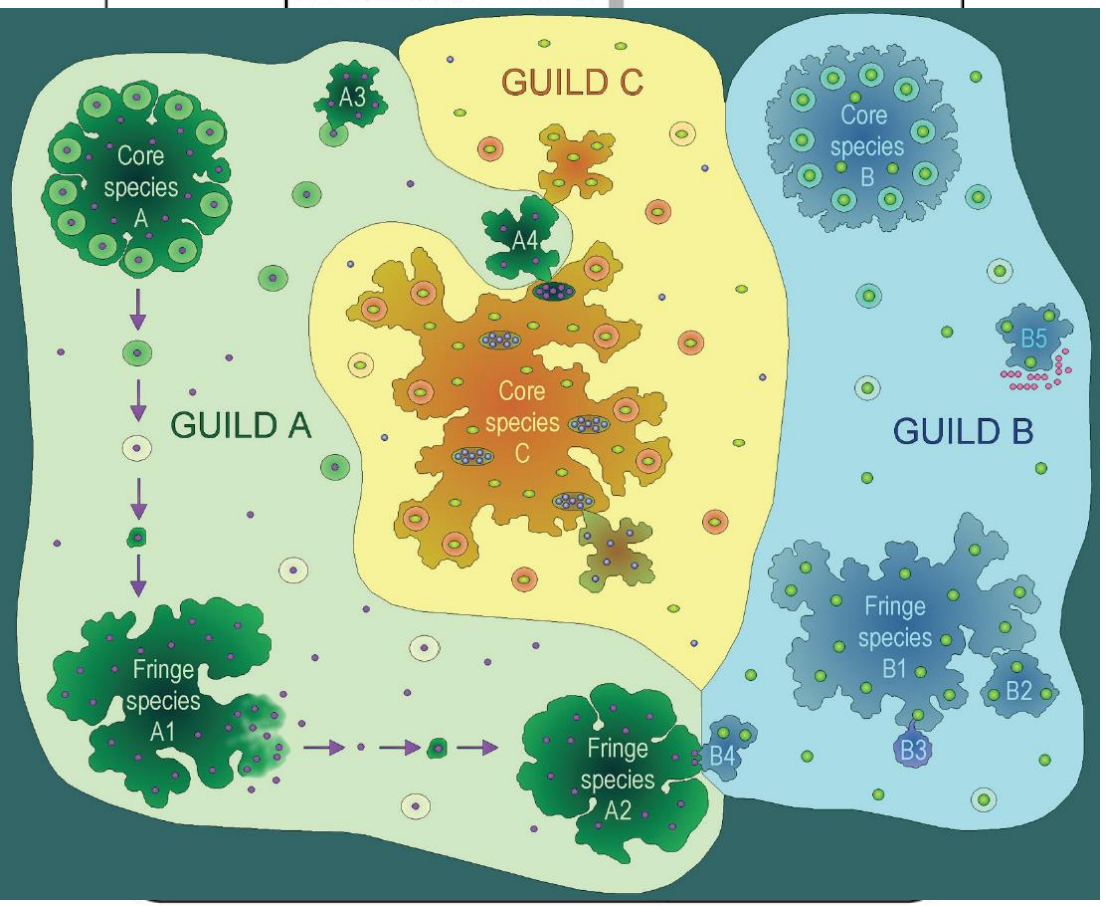
The mode of symbiont dispersal does not affect symbiont diversity

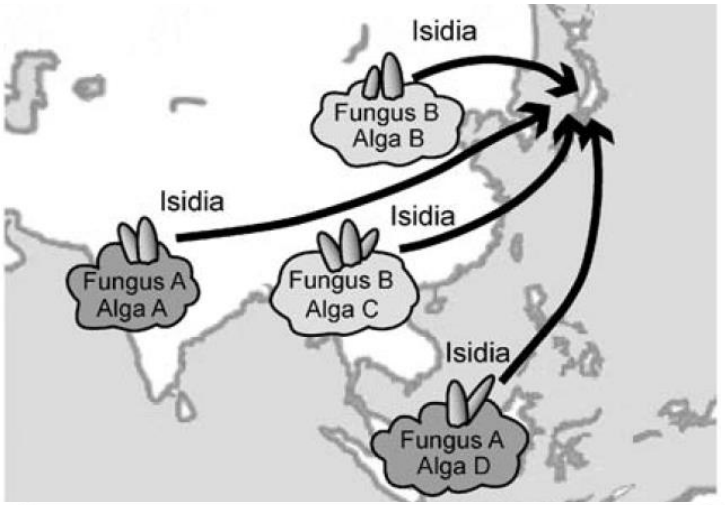
Paradox I.

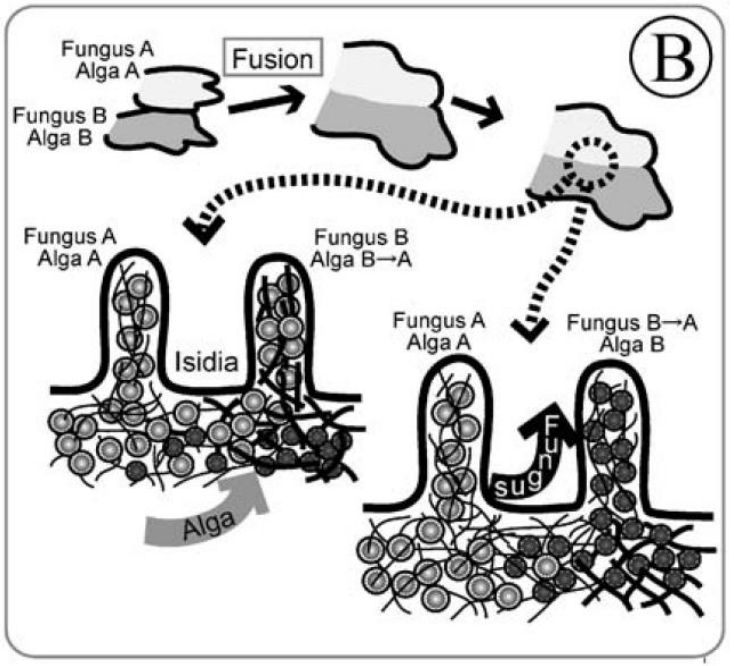
The mode of symbiont dispersal does not affect symbiont diversity

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

*Ohmura 5357C**	**A**	11
*Ohmura 5361A**	**B**	1
Ohmura 5410	**C**	2
*Ohmura 5372**	**D**	3



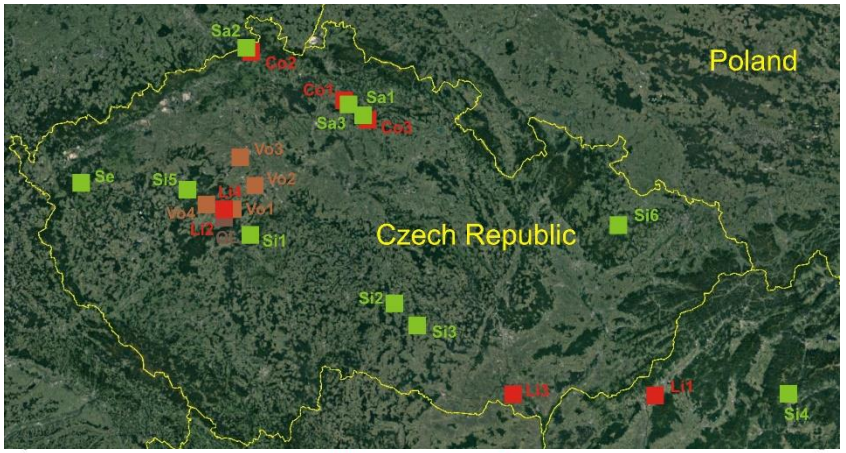


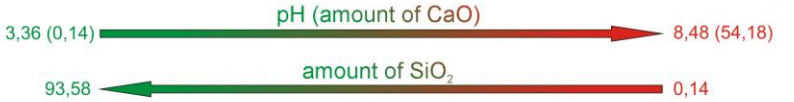


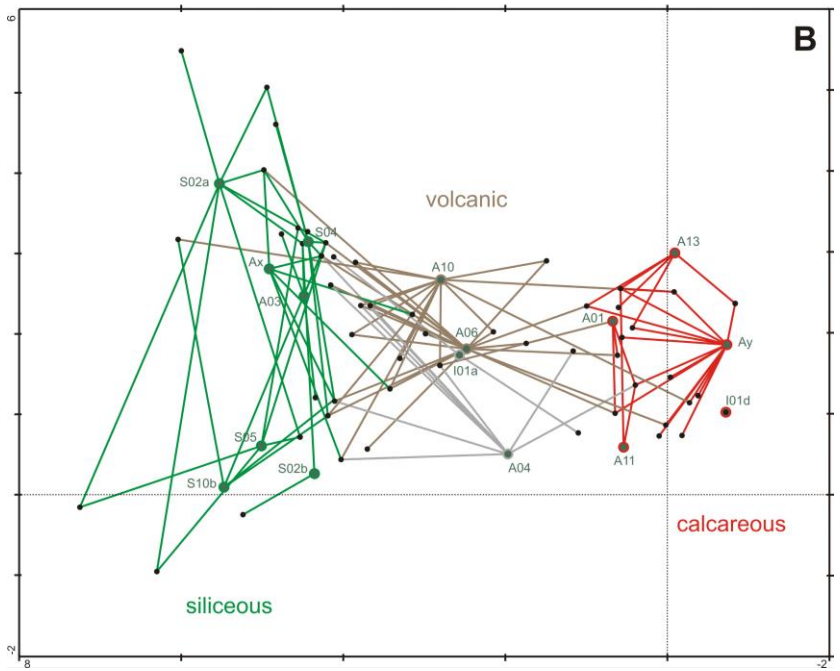
Ohmura et al. (2006): Bryologist

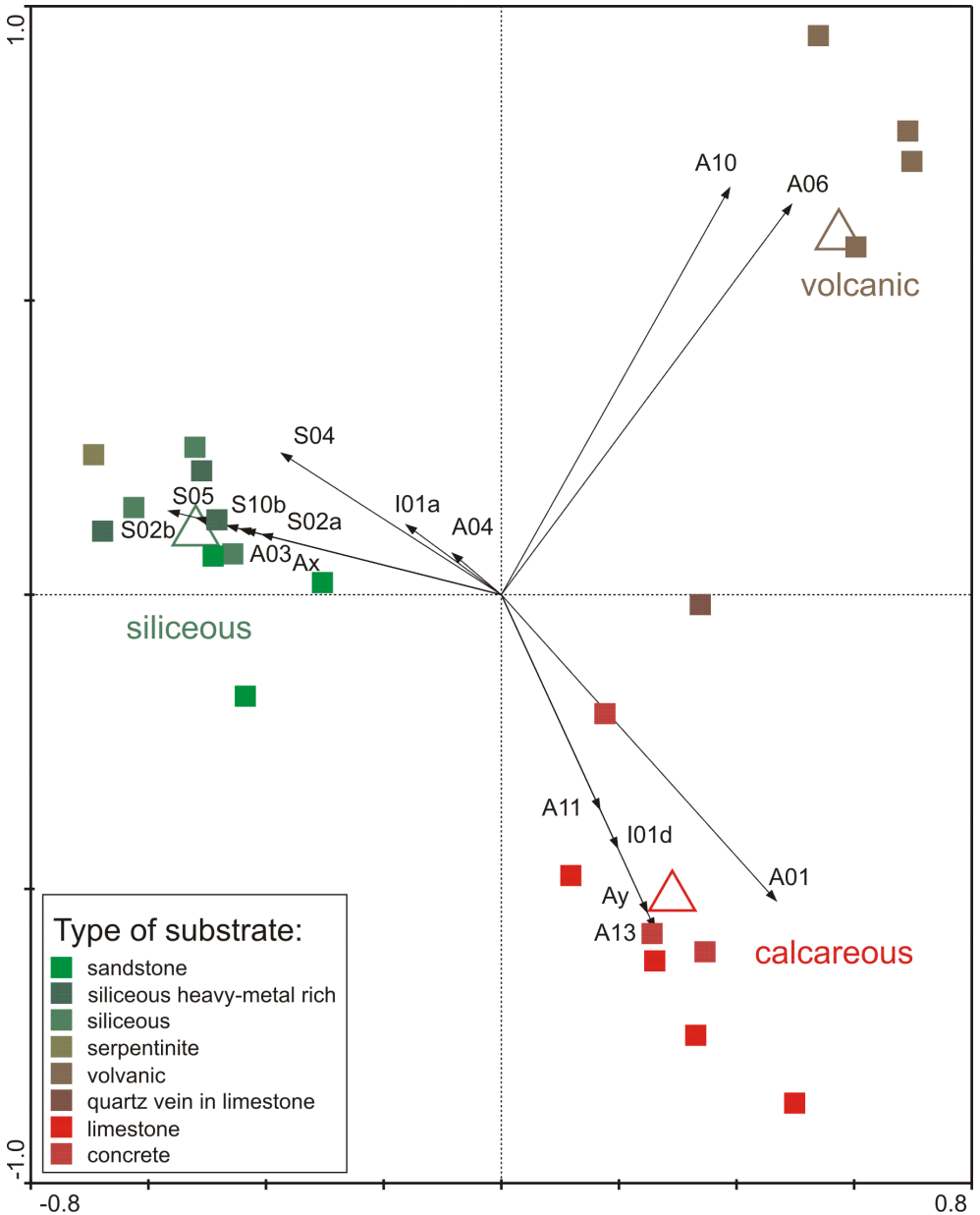
Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity







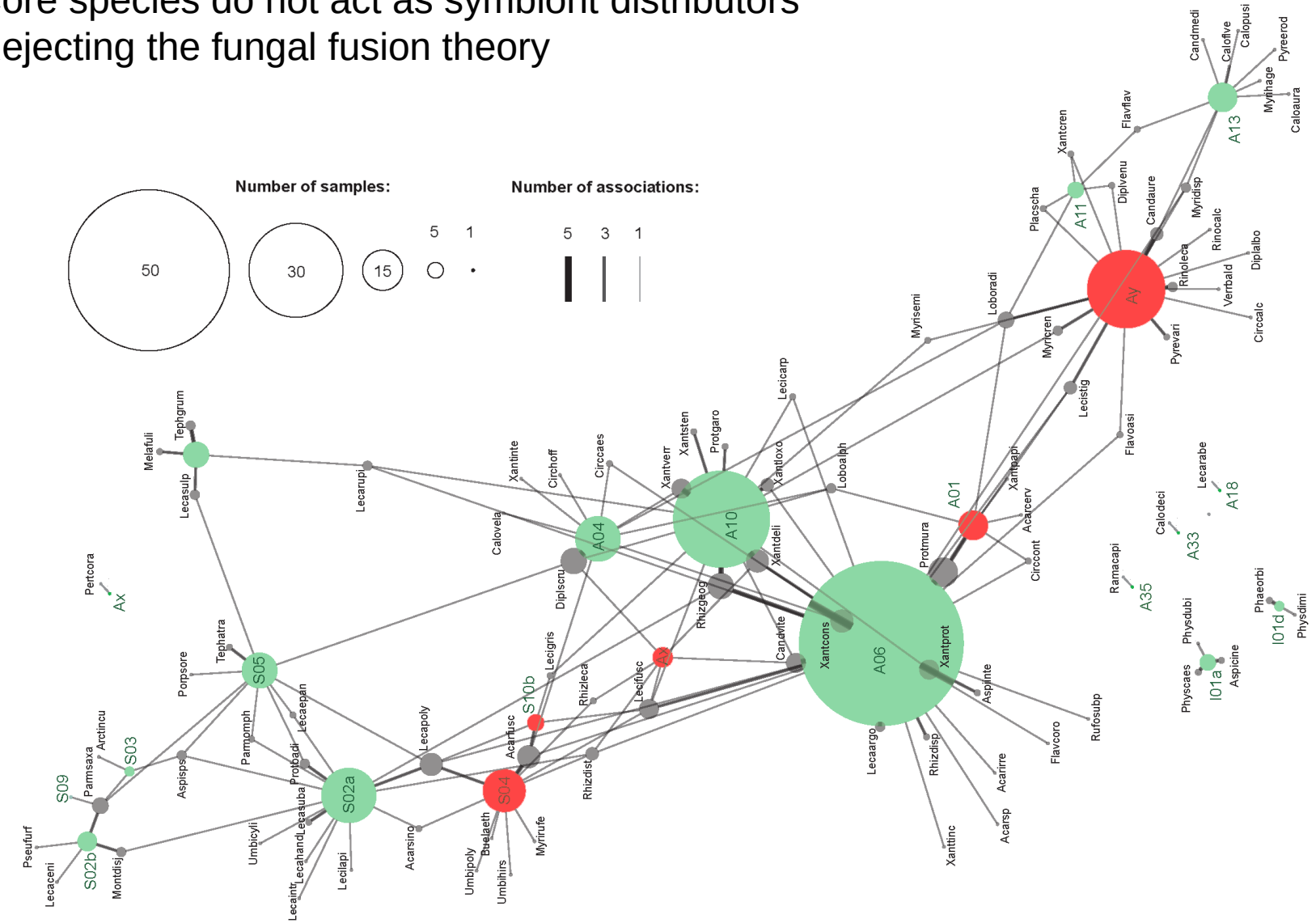


Peksa et al. (submitted)

Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

- A number symbionts were found exclusively in horizontally-dispersed lichens!
- Core species do not act as symbiont distributors
- Rejecting the fungal fusion theory

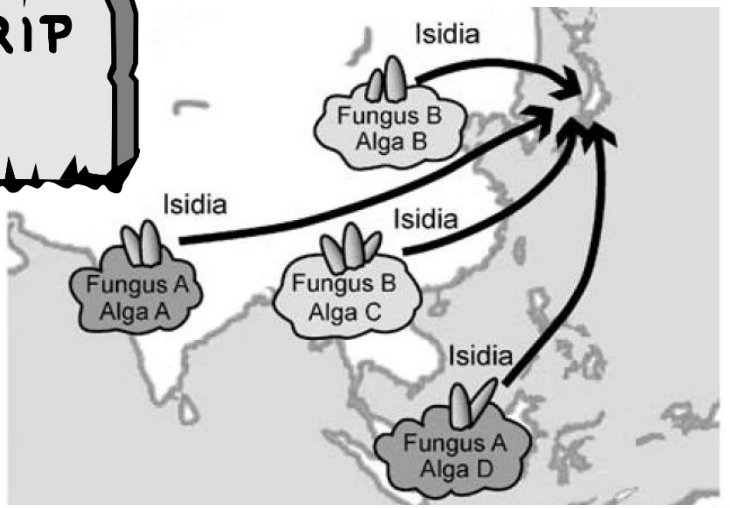


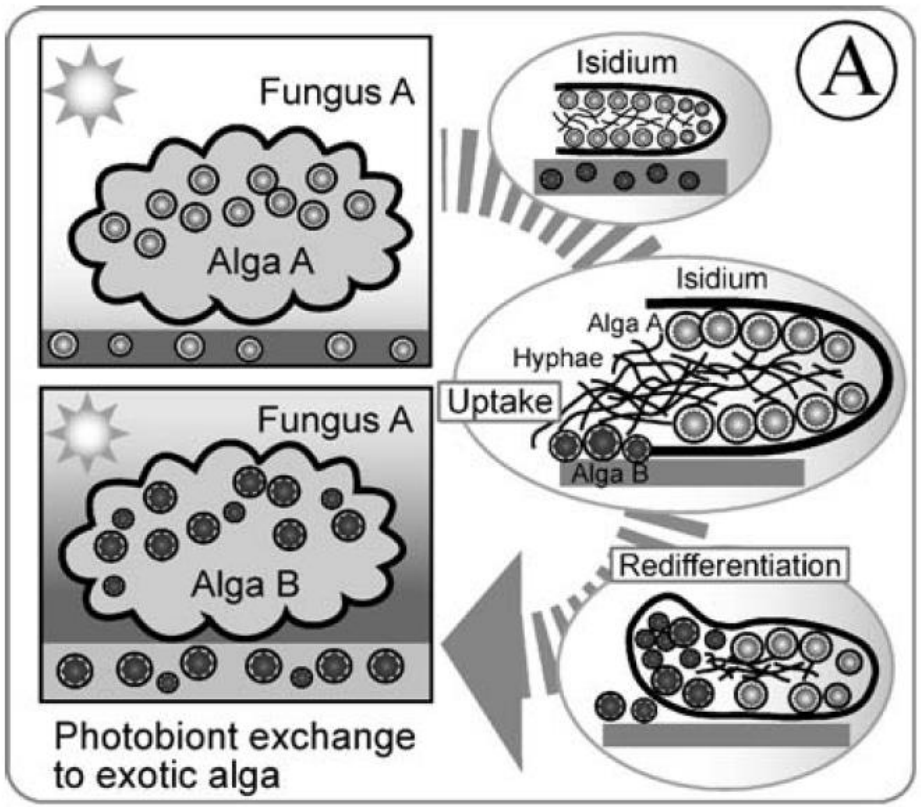
Peksa et al. (submitted)

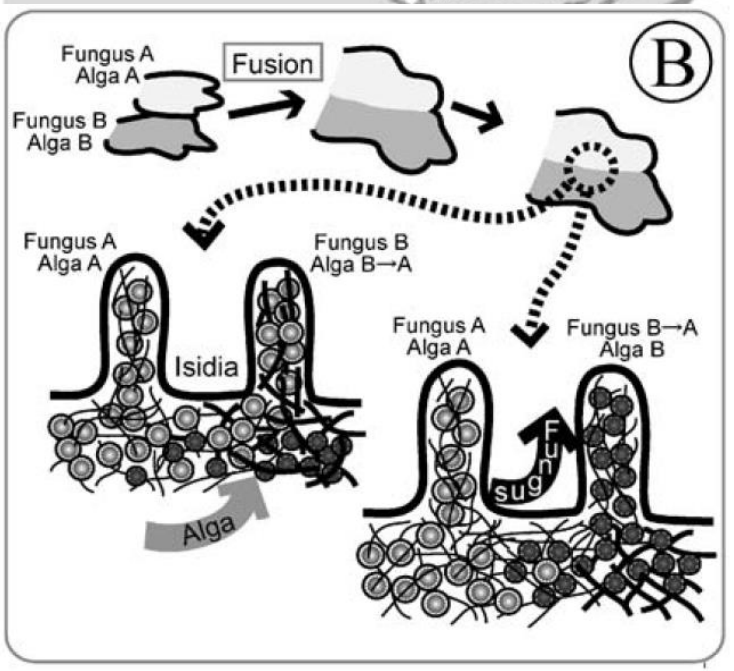
Paradox I.

The mode of symbiont dispersal does not affect symbiont diversity

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





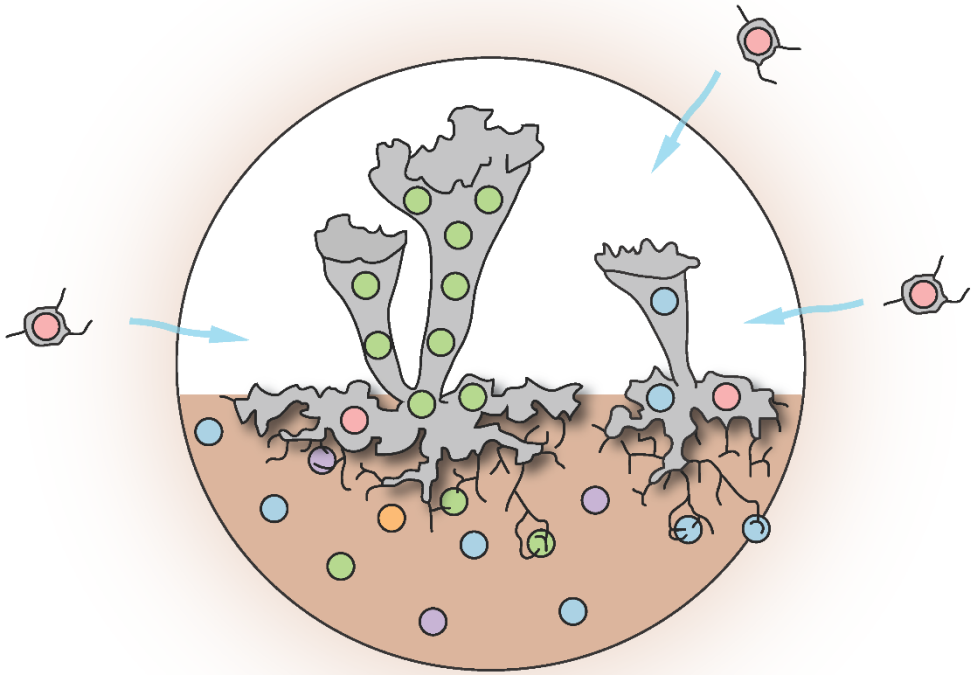


Ohmura et al. (2006): Bryologist

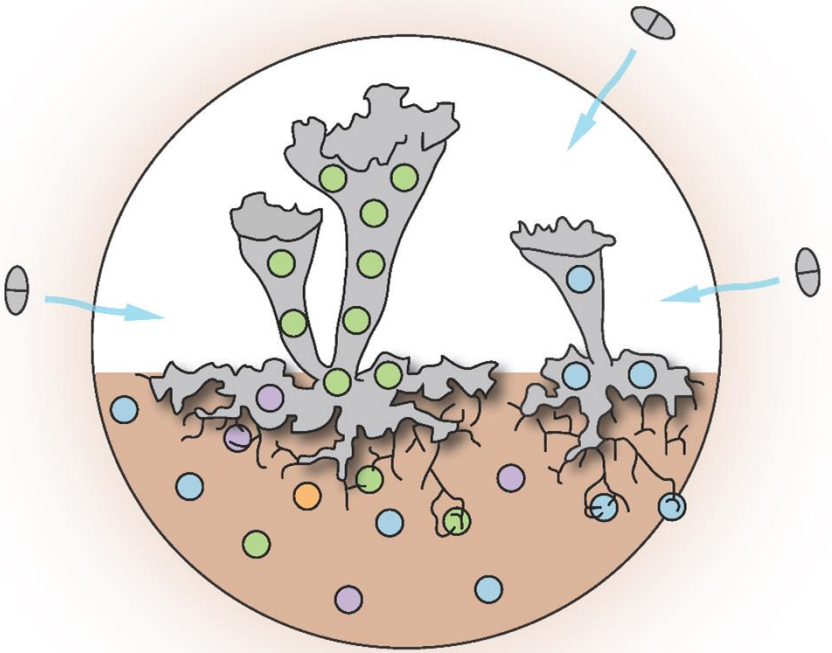
Paradox II.

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



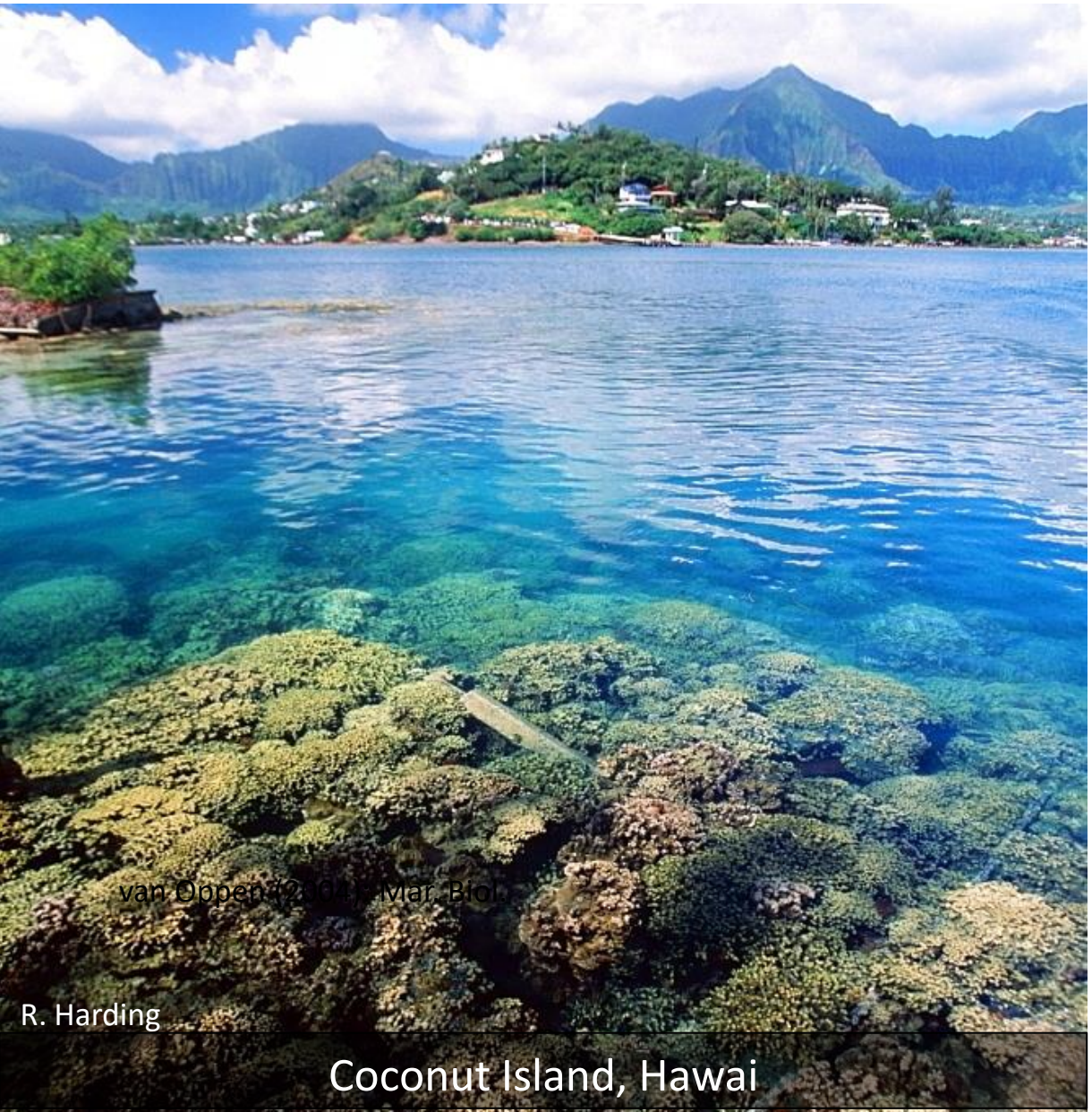
vertical dispersal

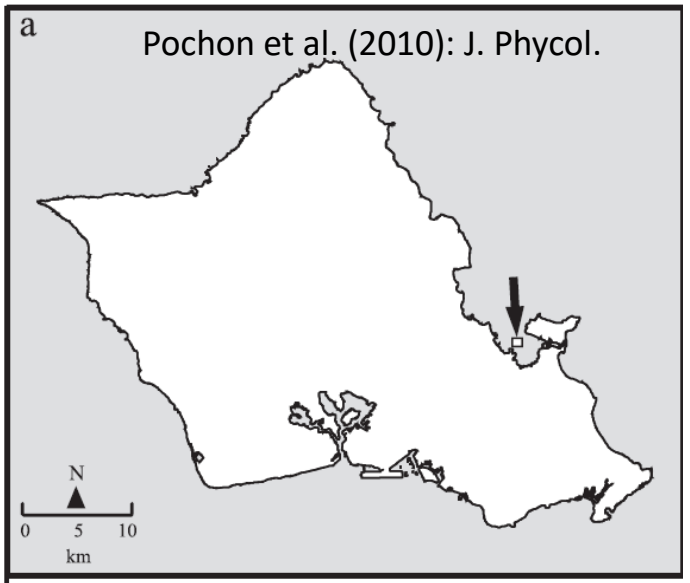


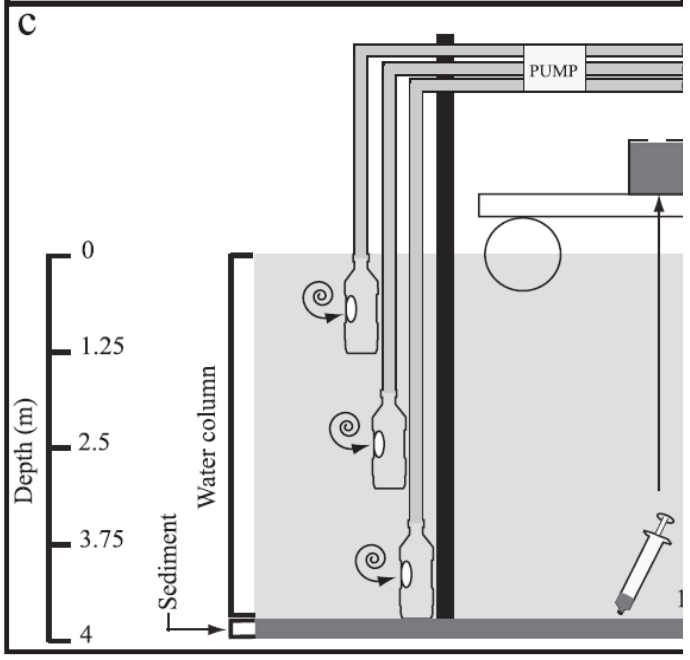
horizontal dispersal

Paradox II.

Host symbionts are physically absent in the environment



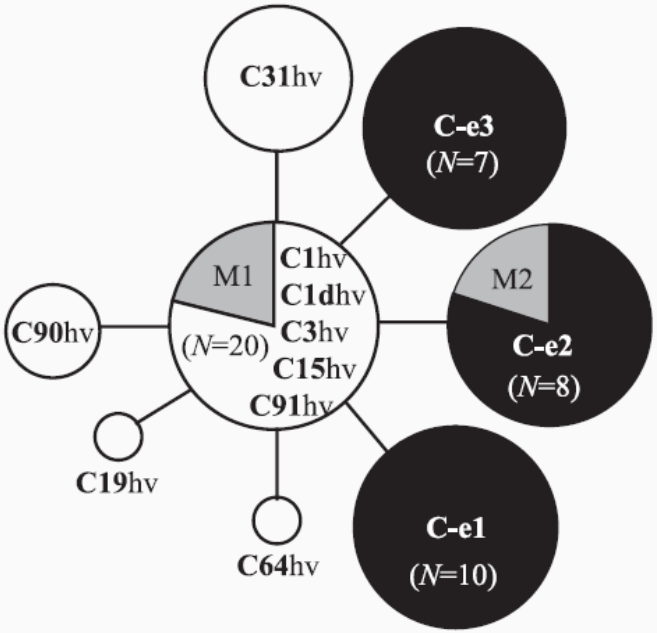


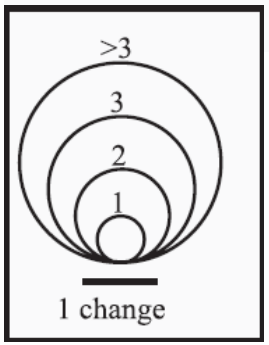


Paradox II.

Host symbionts are physically absent in the environment

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





endosymbiotic

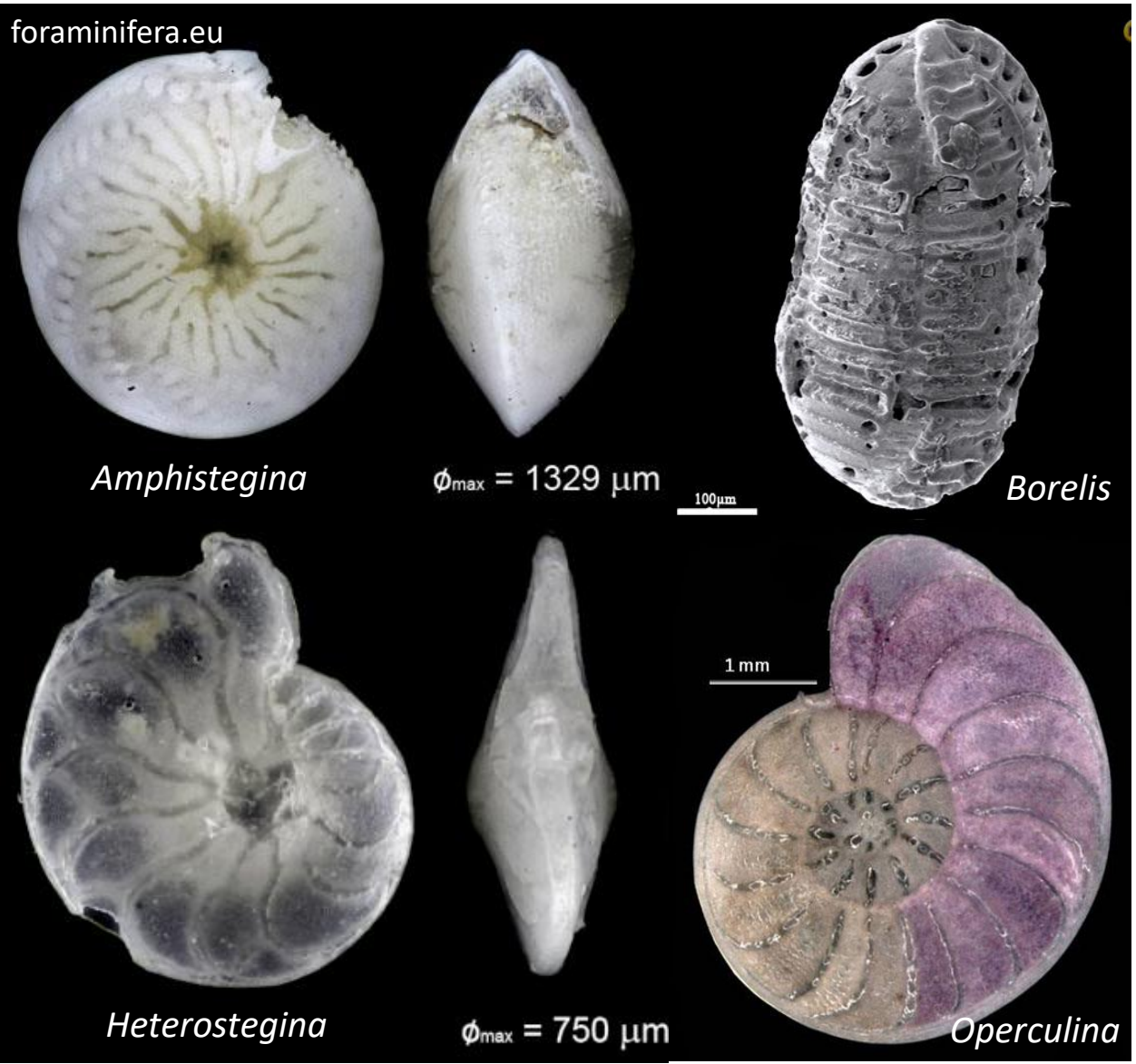
free-living

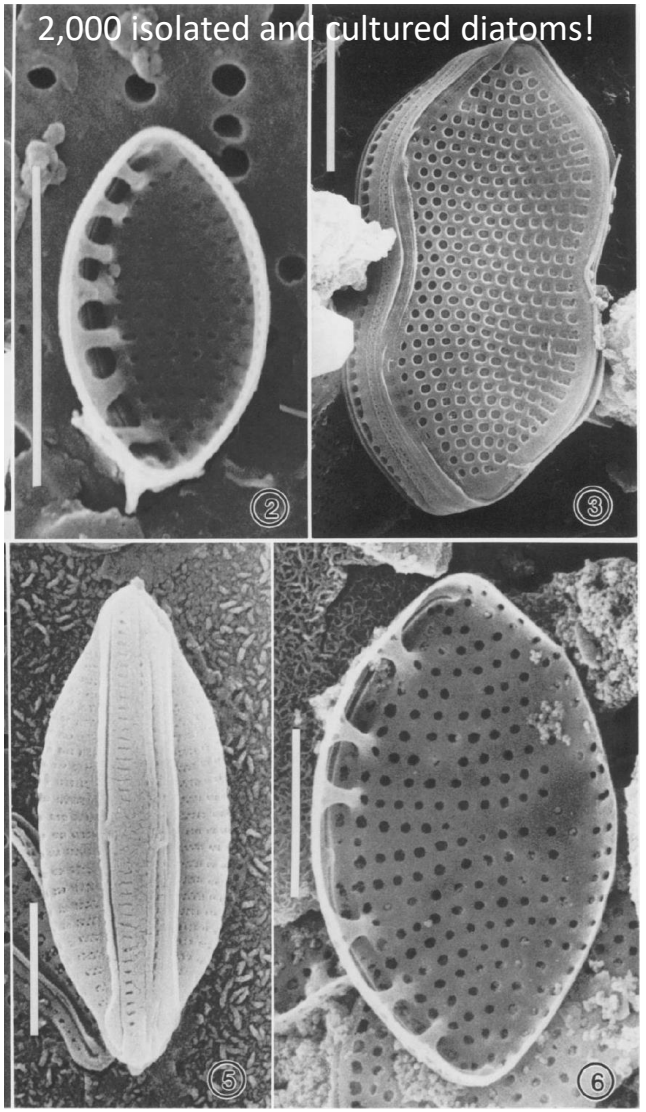
Pochon et al. (2010): J. Phycol.

Paradox II.

Host symbionts are physically absent in the environment

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





Lee et al. (1989): Micropaleontology

Paradox II.

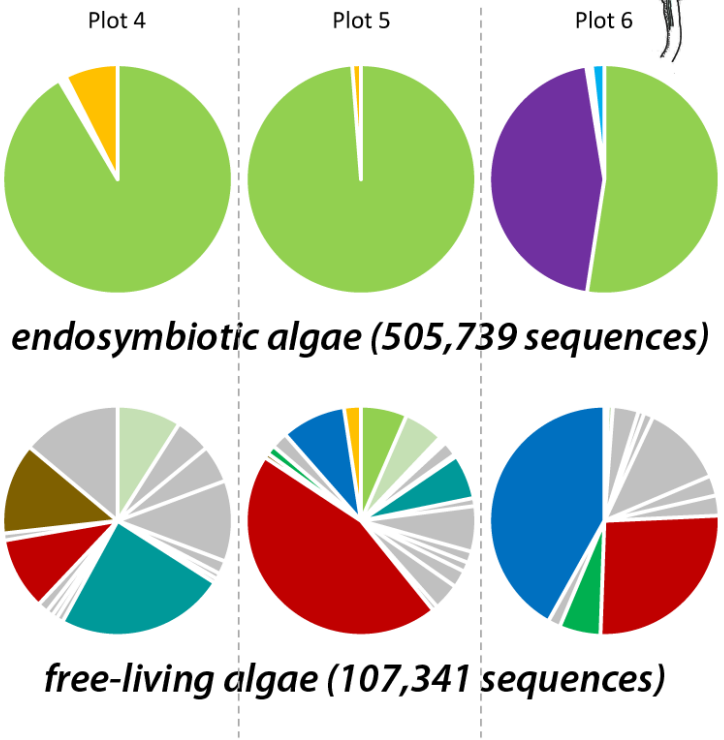
Host symbionts are physically absent in the environment

- 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***

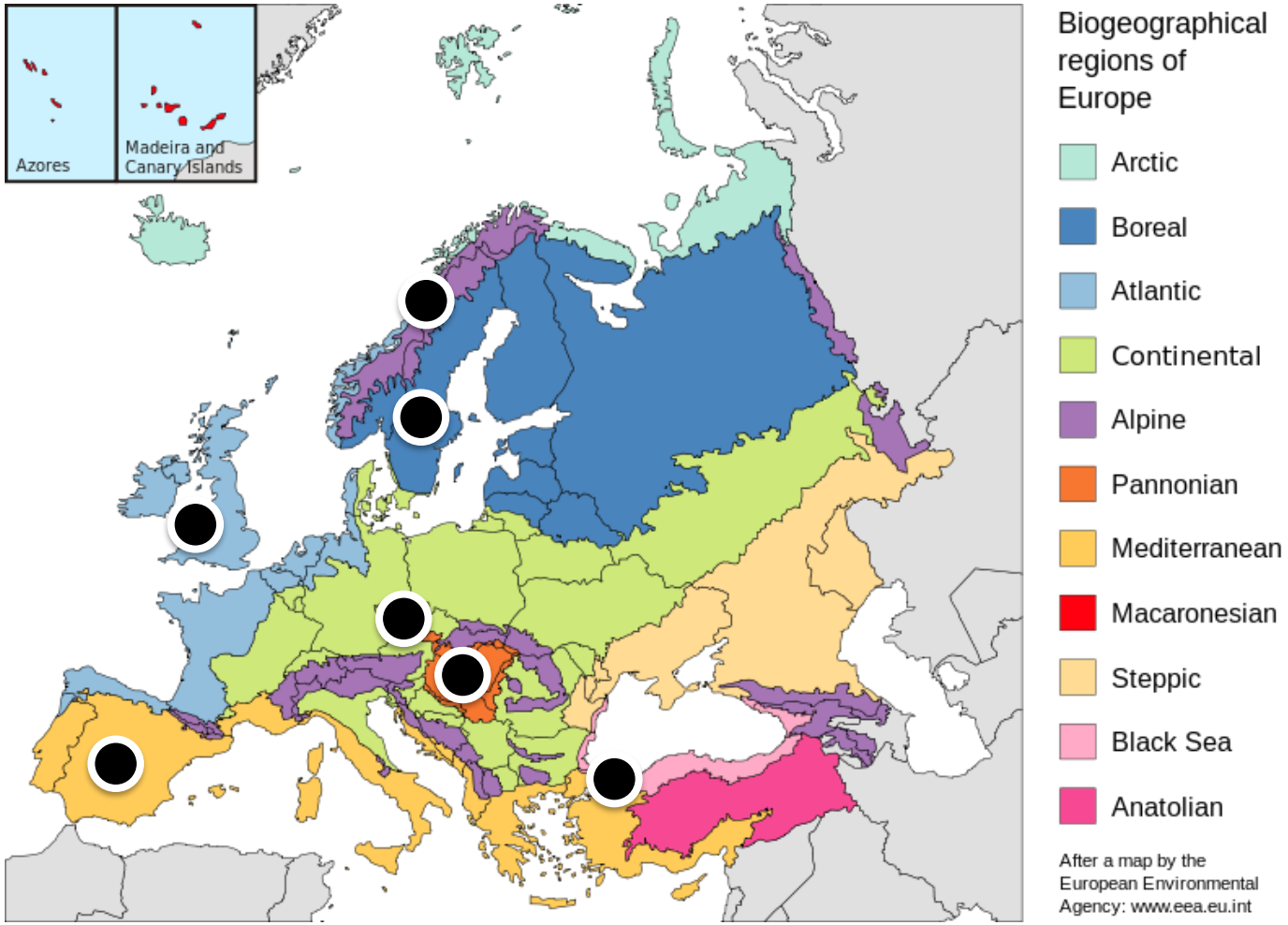
Stereocaulon



Paradox II.

Host symbionts are physically absent in the environment

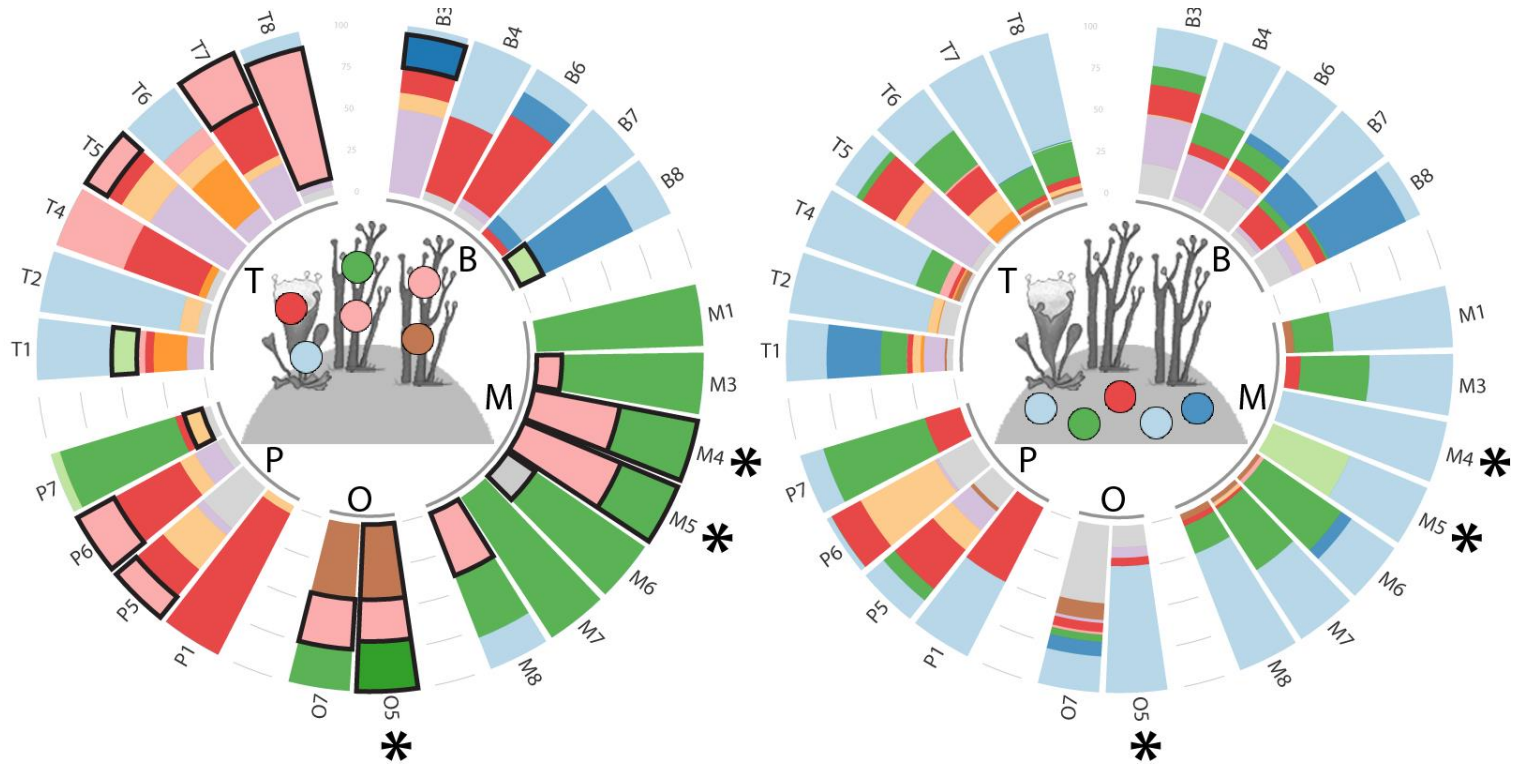
- Sampling *Cladonia* communities in 7 climatically different European regions
  - ➢ 1,120 lichen thalli - Sanger and Illumina sequencing of algal symbionts
  - ➢ 56 composite soil samples - Illumina meta-barcoding of symbionts



Paradox II.

Host symbionts are physically absent in the environment

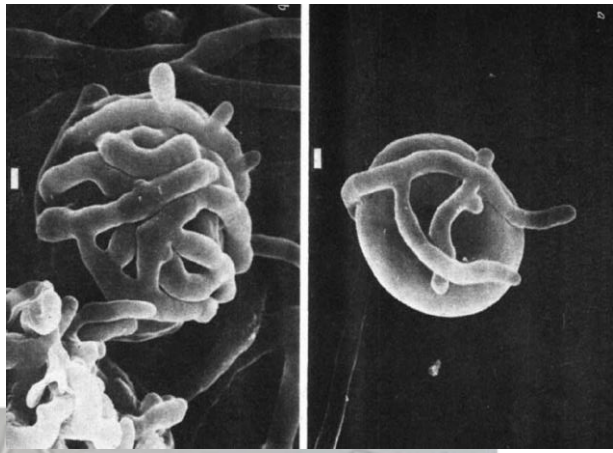
- Limited overlap between endosymbiotic and free-living communities of symbionts
- At three sites, the entire endosymbiotic community was physically absent in the environment



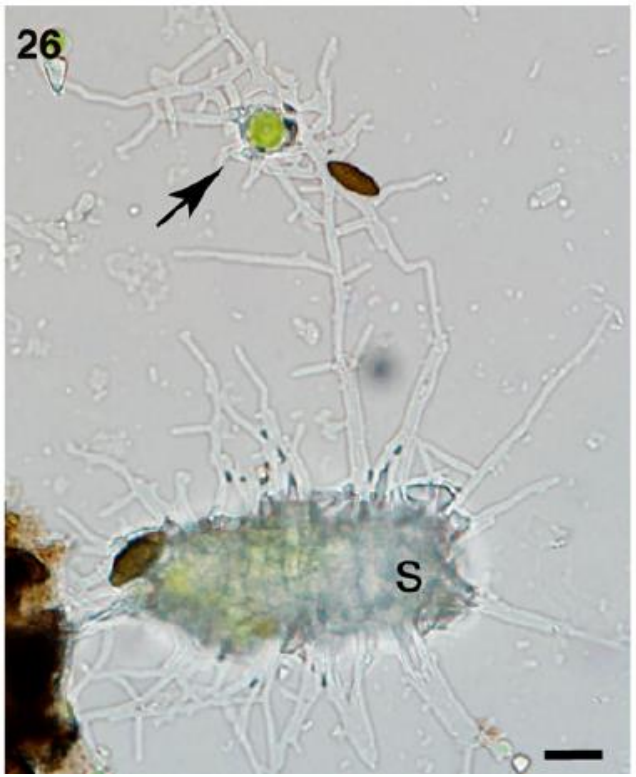
Paradox II.

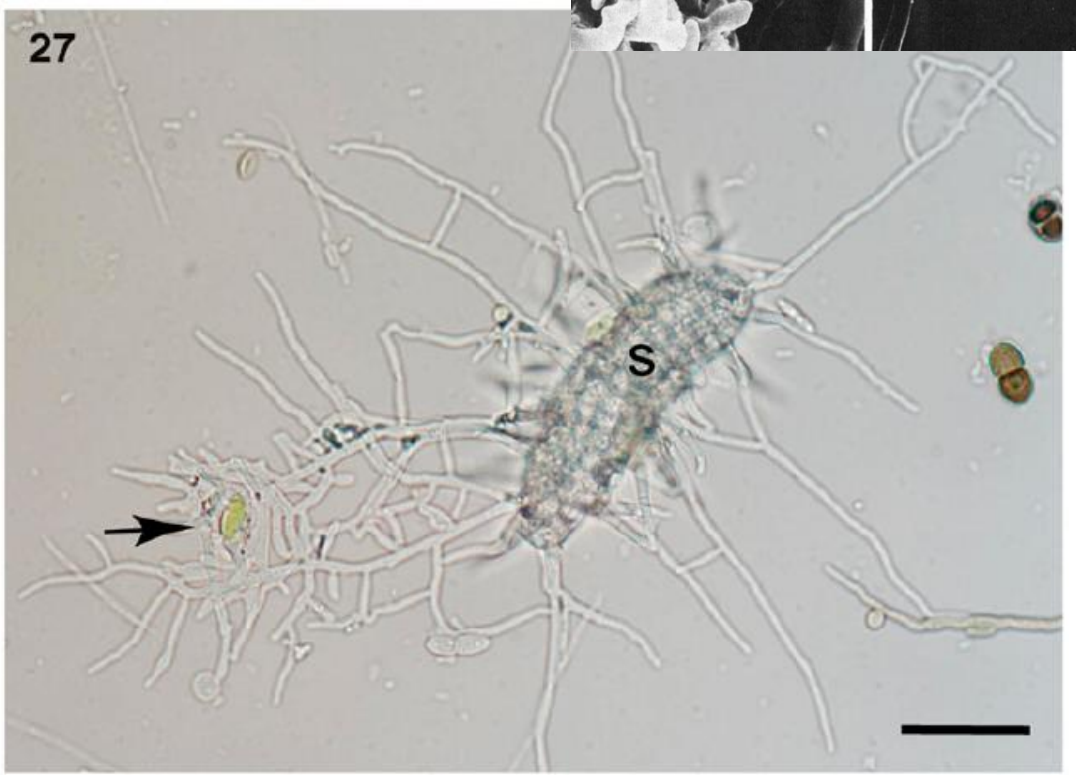
Host symbionts are physically absent in the environment

- 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

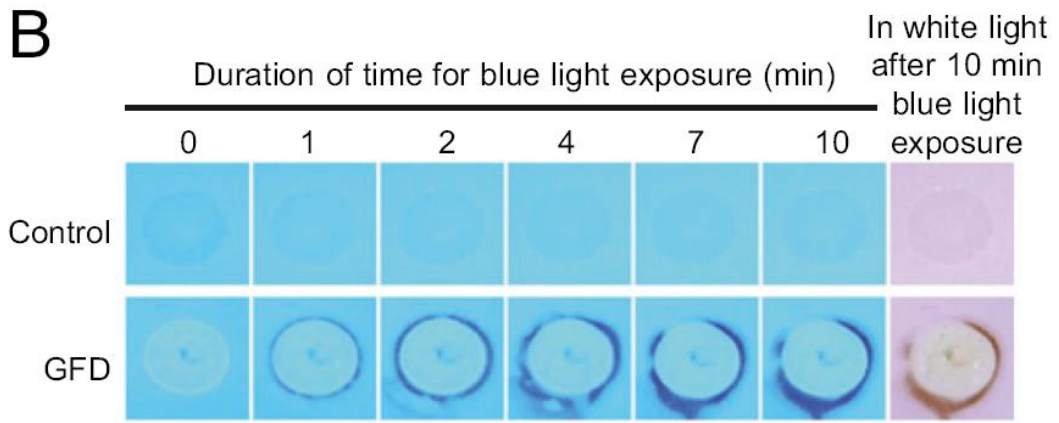


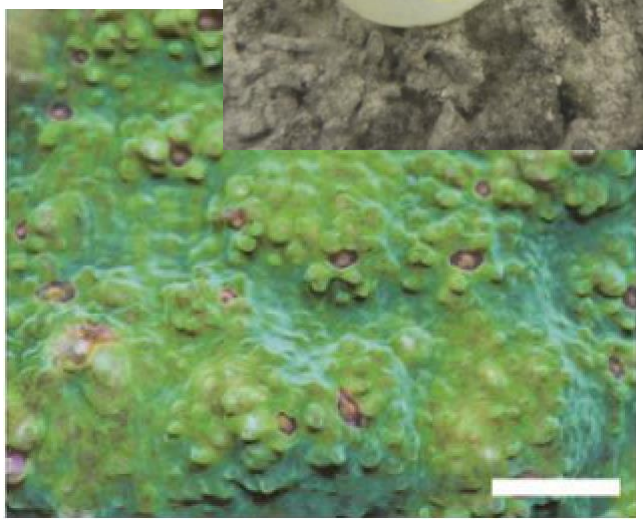


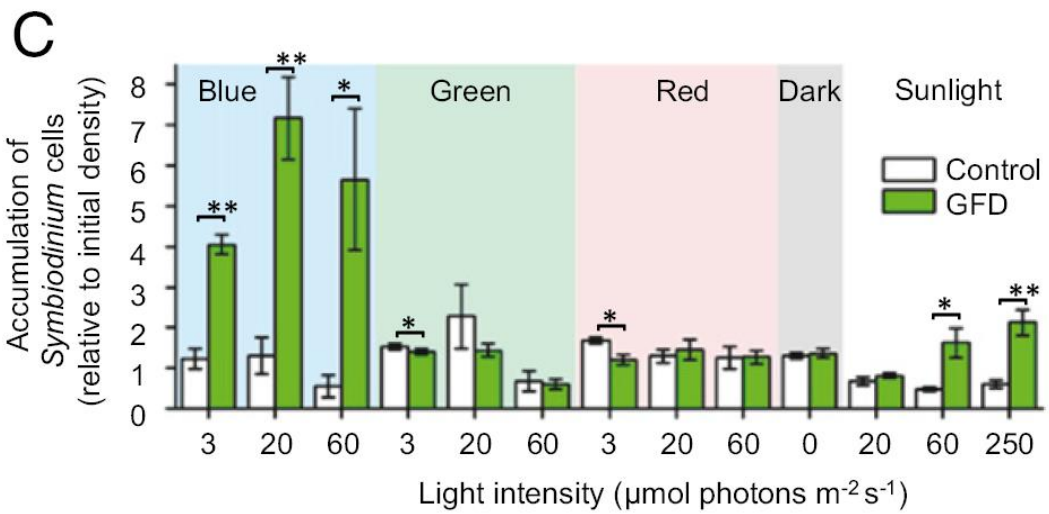
Sanders et al. (2014): Am. J. Bot.

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





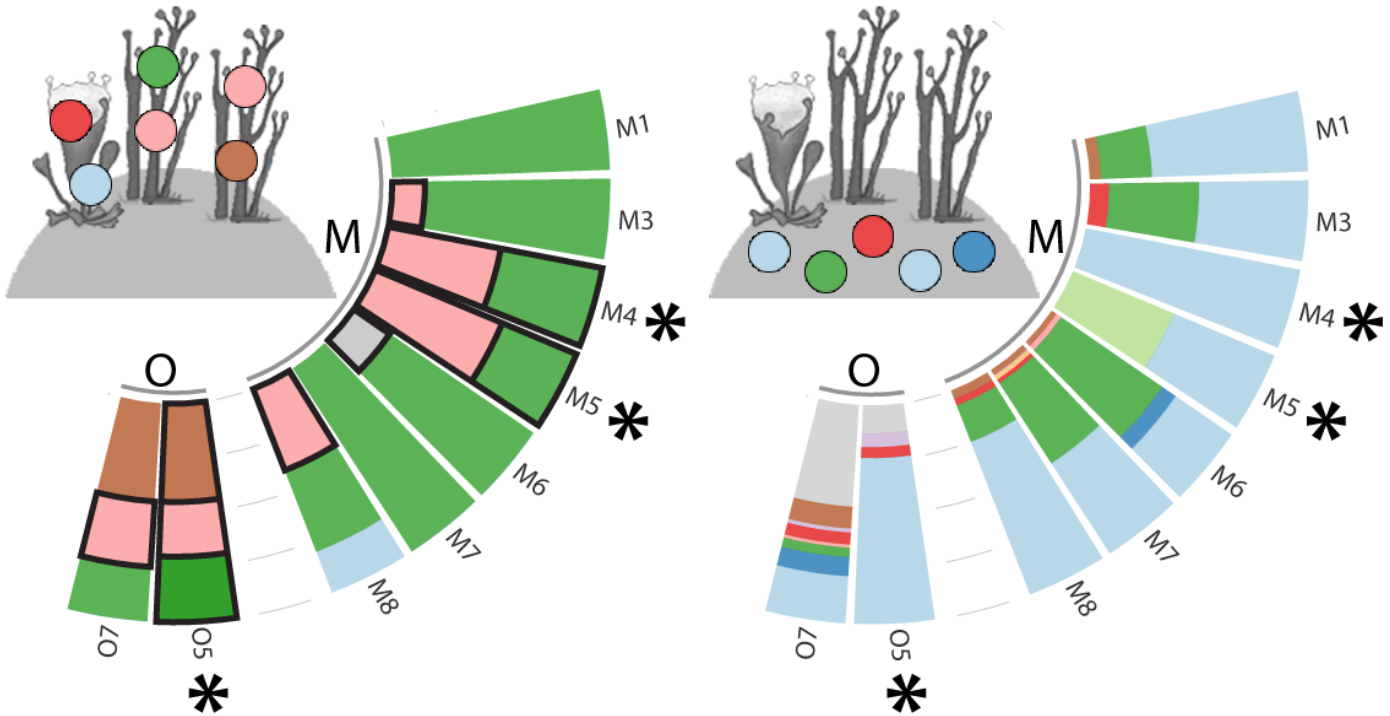


Aihara et al. (2019): PNAS

Paradox II.

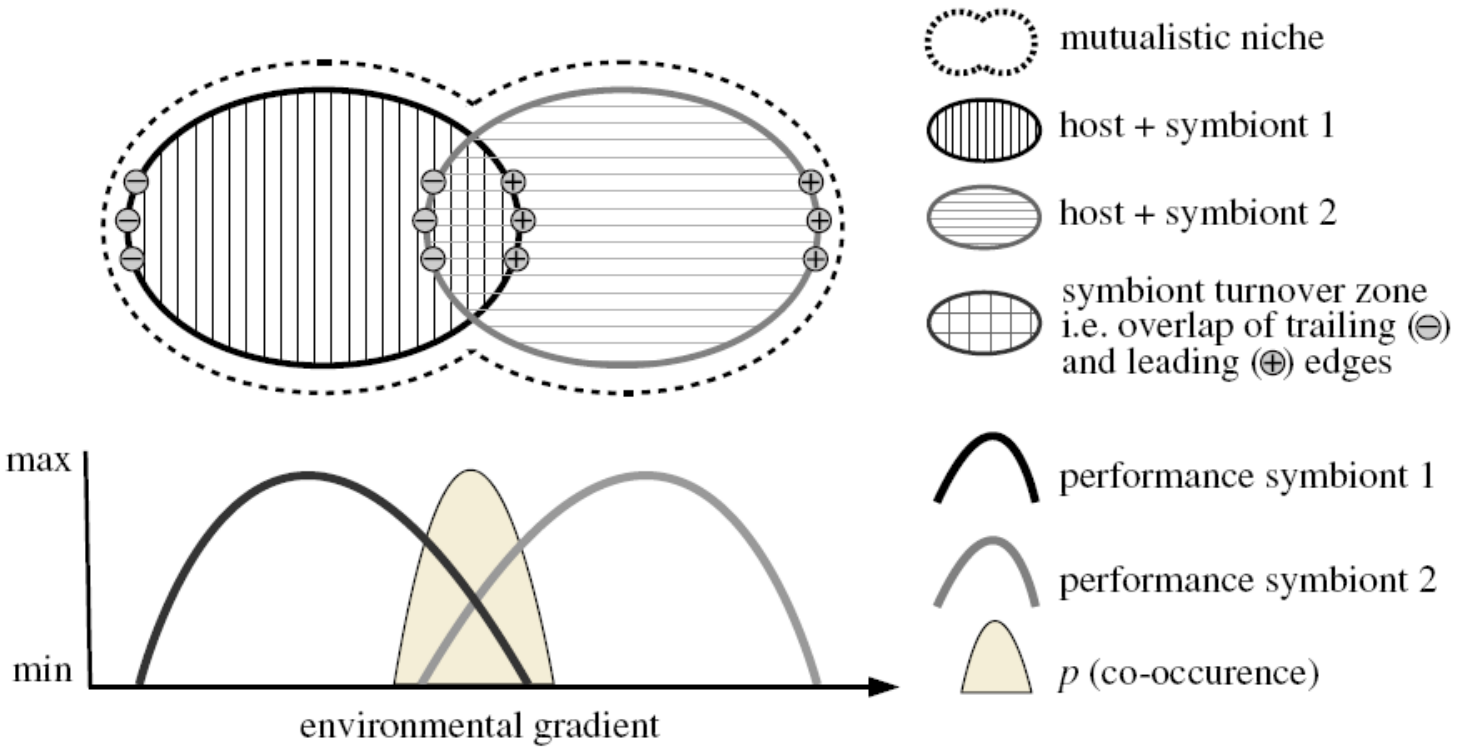
Host symbionts are physically absent in the environment

- Why the common free-living species do not act as endosymbionts at a given site?
  - ➢ The symbionts are ecologically strongly specialized
  - ➢ They are adapted to local environmental conditions
  - ➢ They are indeed able of form symbiotic associations



Paradox II.
Host symbionts are physically absent in the environment

- Why the common free-living species do not act as endosymbionts at a given site?
  - ➢ Symbiotic interactions may significantly shift realized niche of lichen partners, radically influencing the host selectivity during the lichen formation.



Rolshausen et al. (2020): Proc. R. Soc. B

Paradoxes of lichen symbiosis

- Lichens have two types of dispersal propagules, one of them not being used for dispersal
- Lichens are surrounded by a number of locally-adapted, free-living symbionts, which they fully ignore
- 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)
- Though algal symbionts are considered to be ecologically highly specialized and well defined, their real ecological preferences are probably completely different

Ondřej Peksa

Jana Steinová

Lucie Vančurová

Ivana Černajová

Zuzana Škvorová

Tereza Gebouská

Helena Bestová

Thank you for your attention

Patricia Moya

GAČR
GRANTOVÁ AGENTURA ČESKÉ REPUBLIKY

CHARLES UNIVERSITY

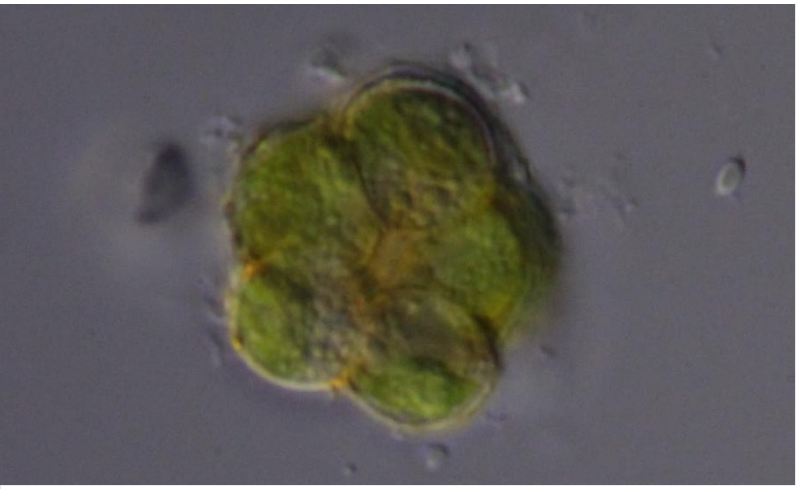
Primus Research Programme

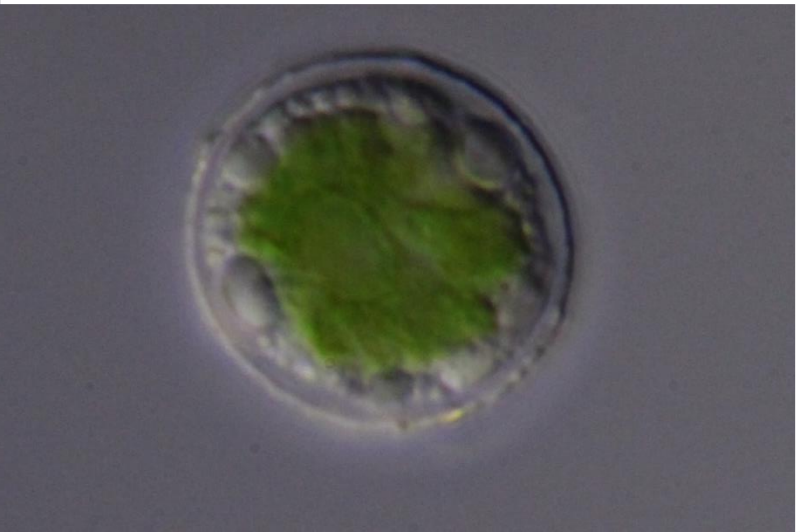
What‘s happening in the soil?

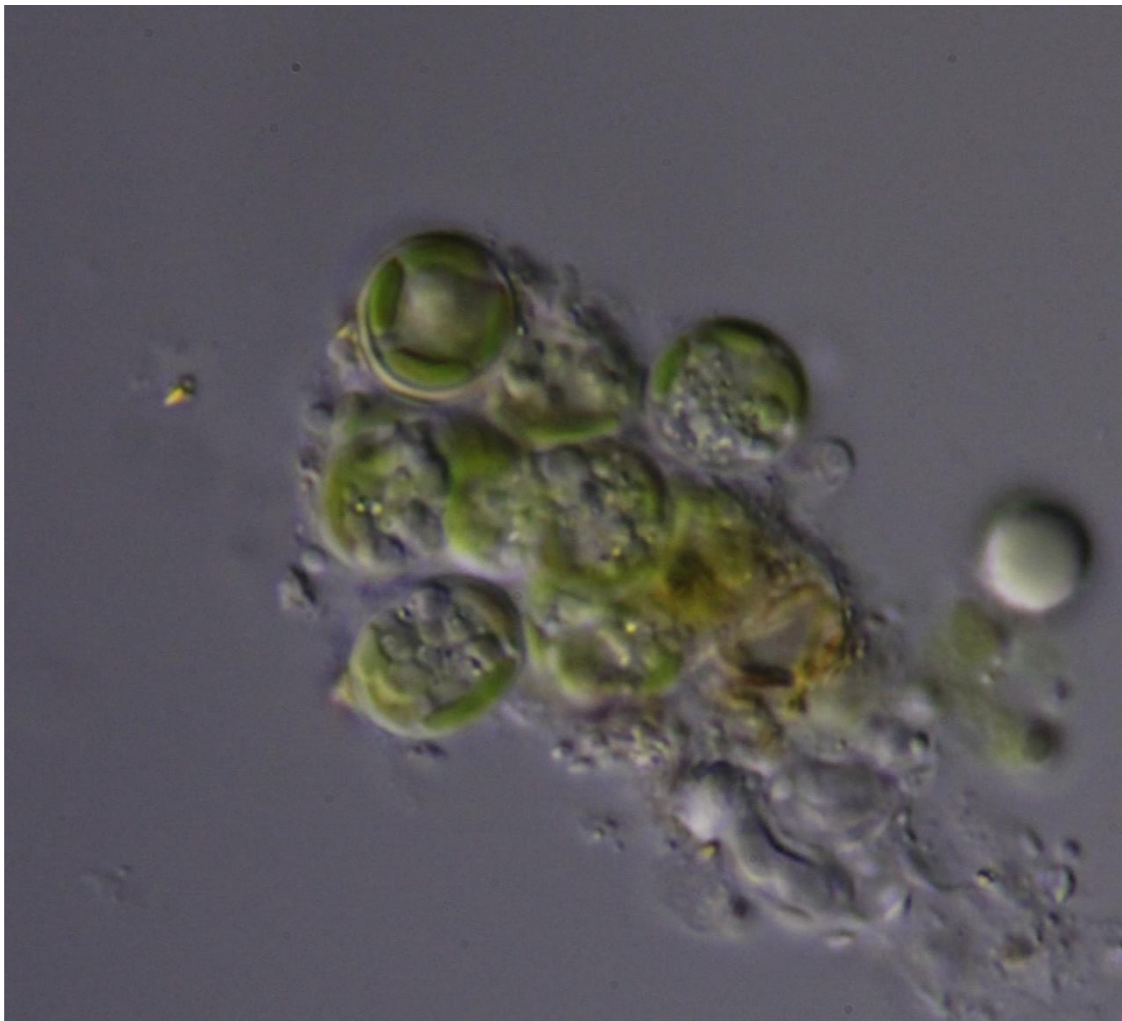
- Complex investigation of free-living symbionts *in situ*
  - A long-term study plot near Vinařice, Central Bohemia

What‘s happening in the soil?

- Complex investigation of free-living symbionts *in situ*
  - Direct observation of living organisms extracted from the soil
  - Algal cultivation
  - Cultivation-free sequencing of isolated algal cells

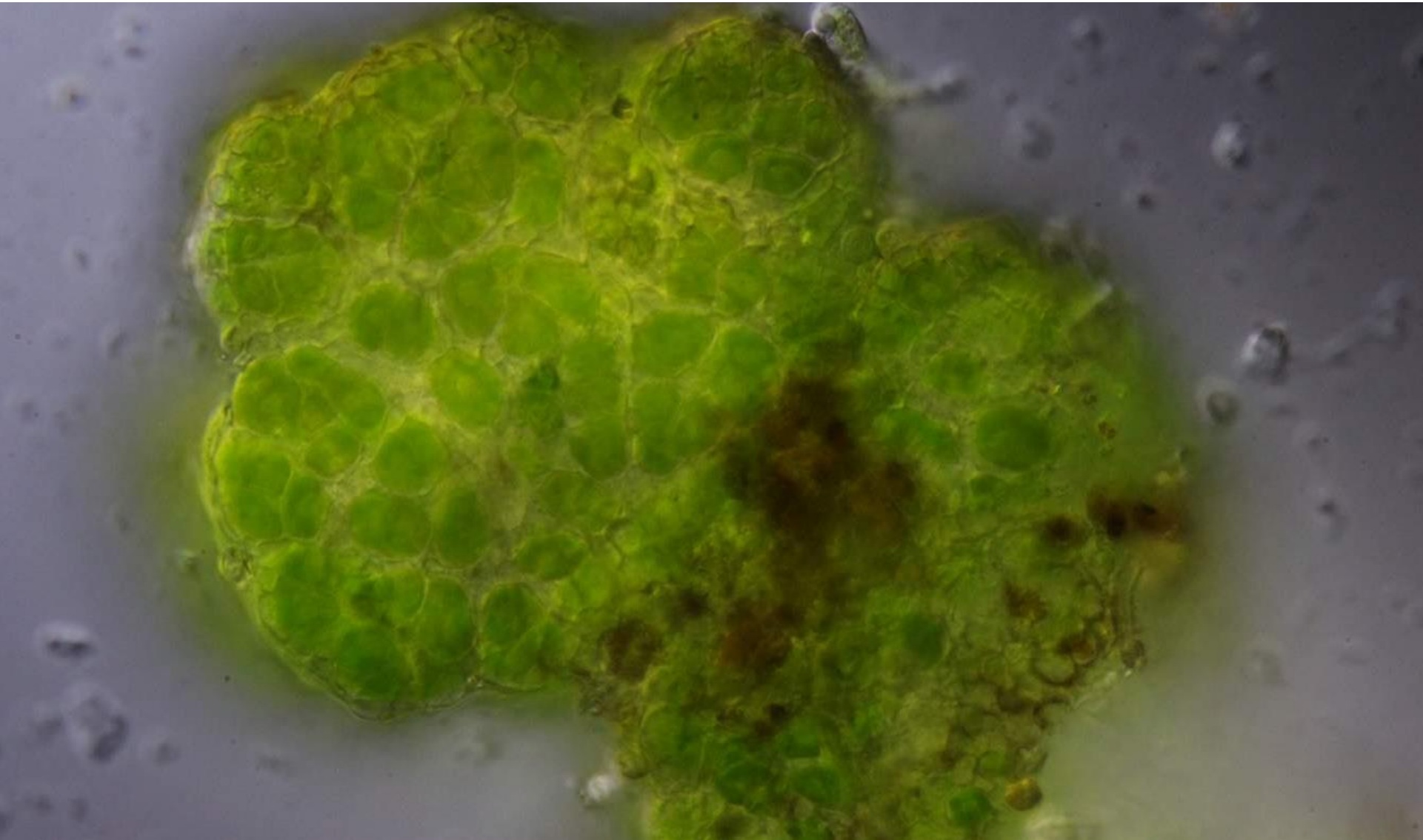






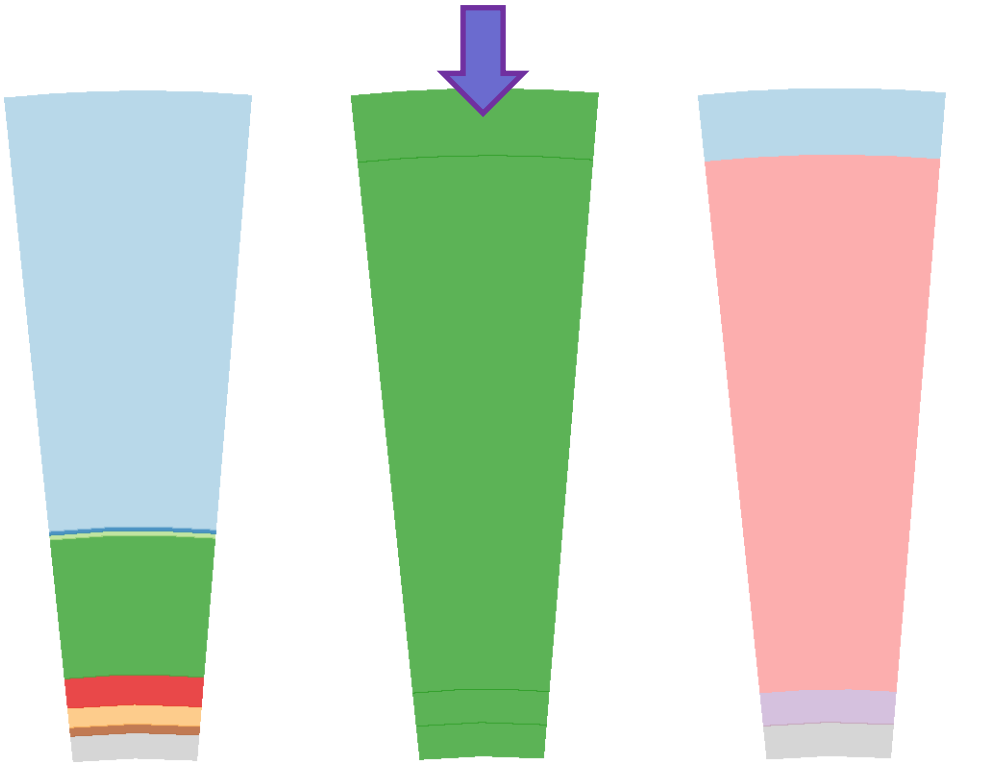
What‘s happening in the soil?

- Complex investigation of free-living symbionts *in situ*
  - ➢ Detection of microscopic, juvenile lichens



What‘s happening in the soil?

- Complex investigation of free-living symbionts *in situ*
  - ➢ Detection of juvenile lichen symbioses?



free-living algae

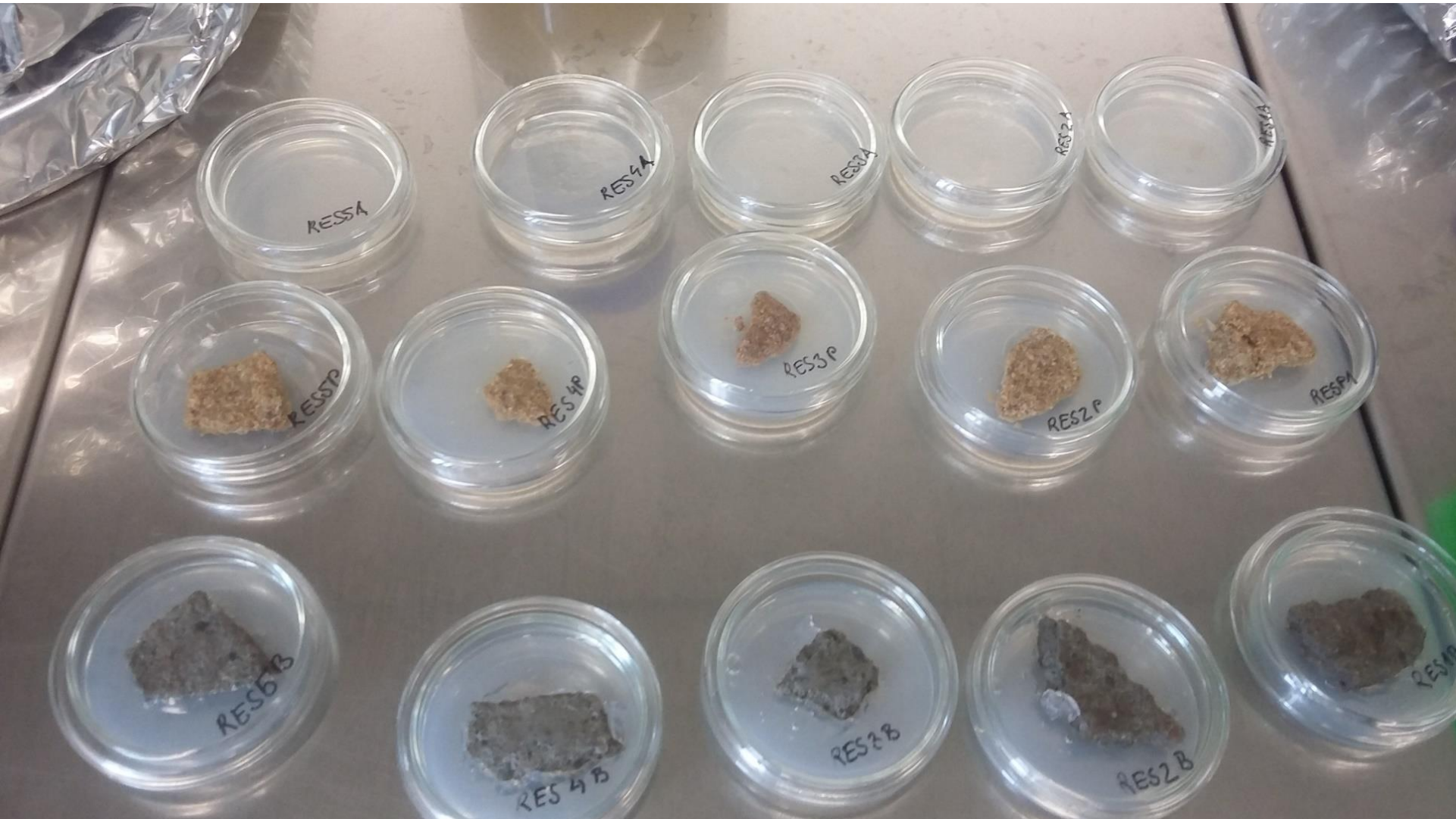
algae in juvenile lichens

endosymbiotic algae

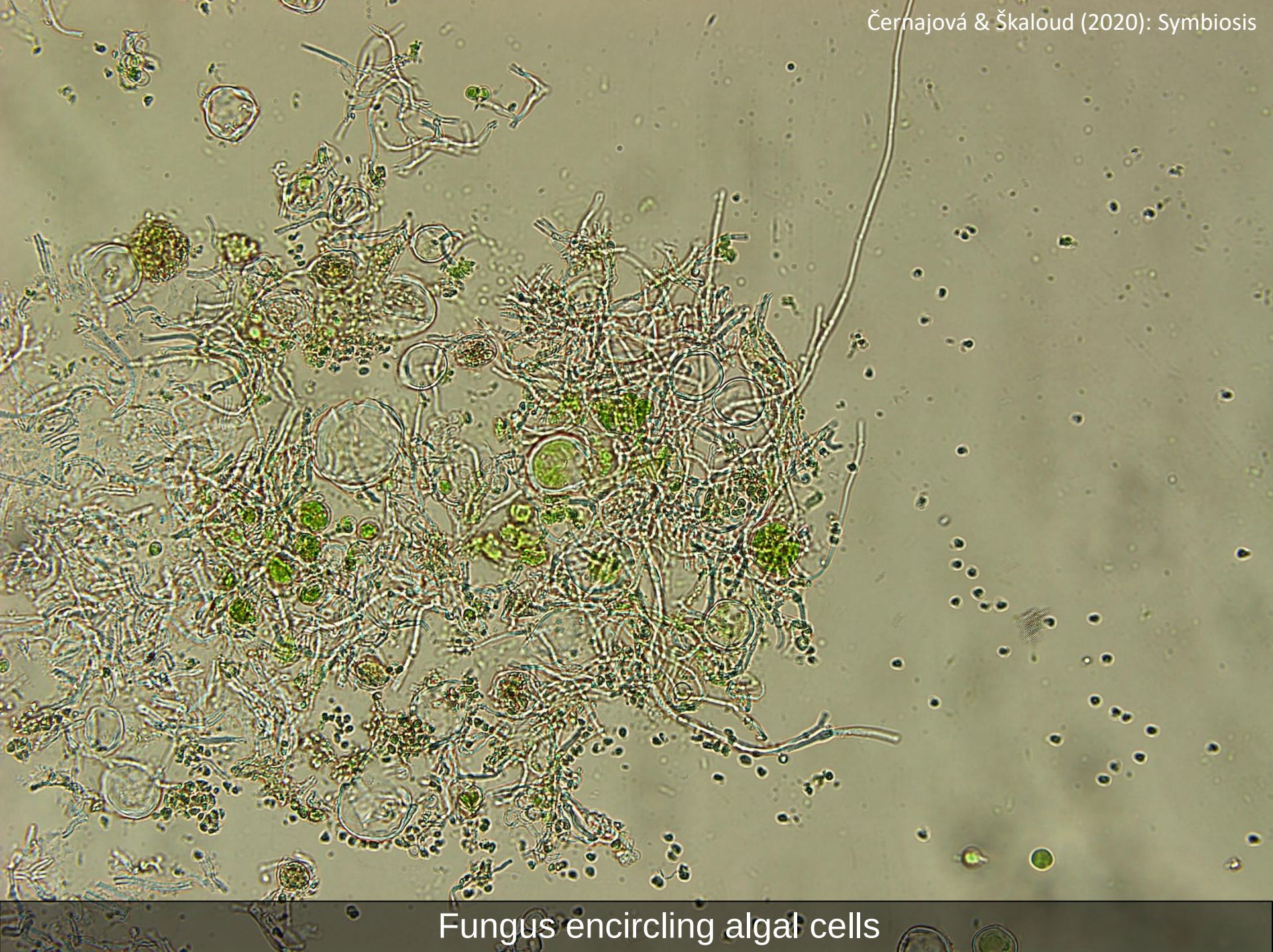
A. glomerata
A. irregularis
A. aff. *irregularis*
A. mediterranea
A. woessiae
clade 8
A. lobophora
A. italiana
clade 12
clade WKQ1A
others

Let‘s build a lichen!

- Artificial lichen synthesis using pure fungal and algal cultures



Fungal and algal pure cultures



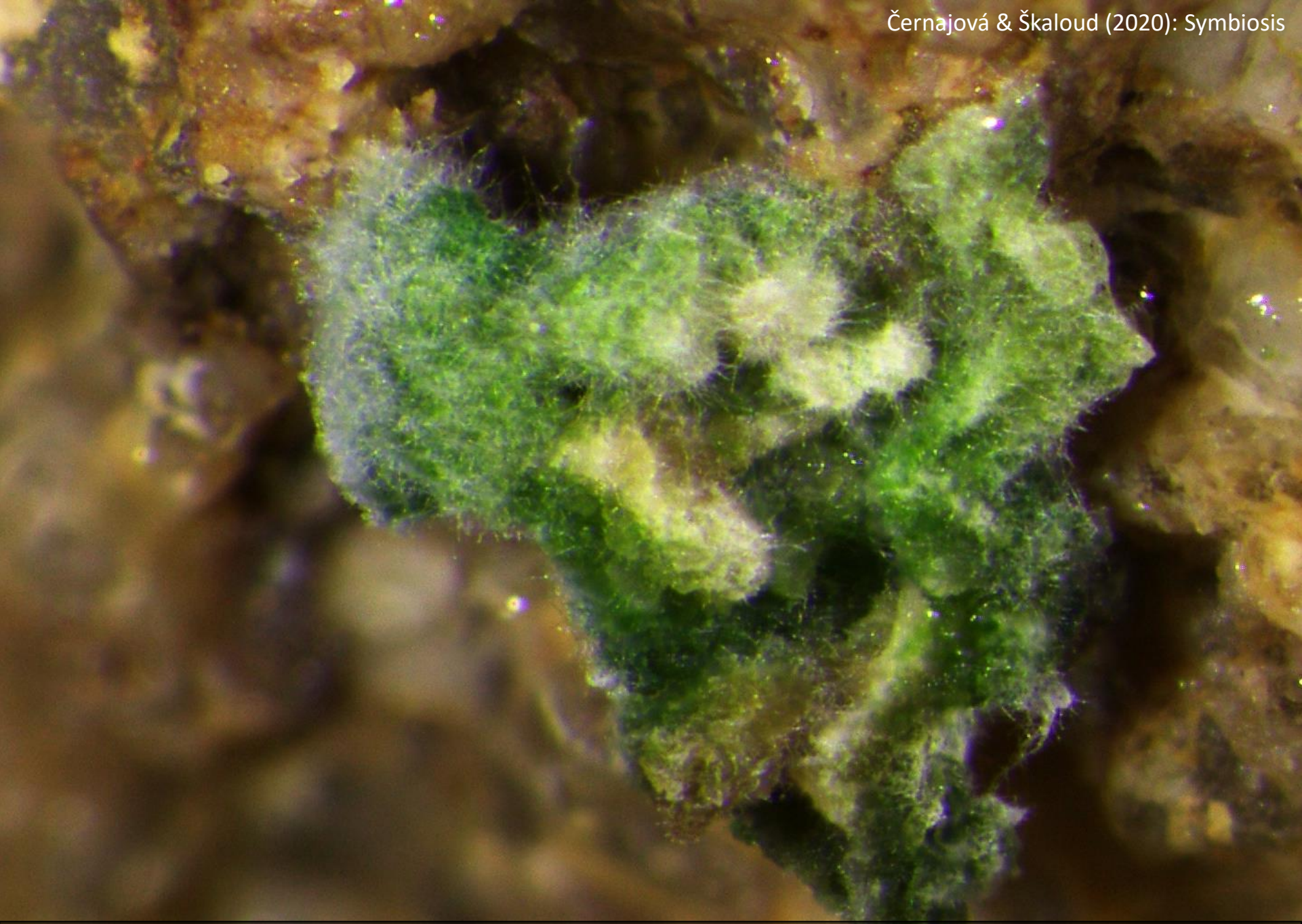
Fungus encircling algal cells

Černajová & Škaloud (2020): Symbiosis

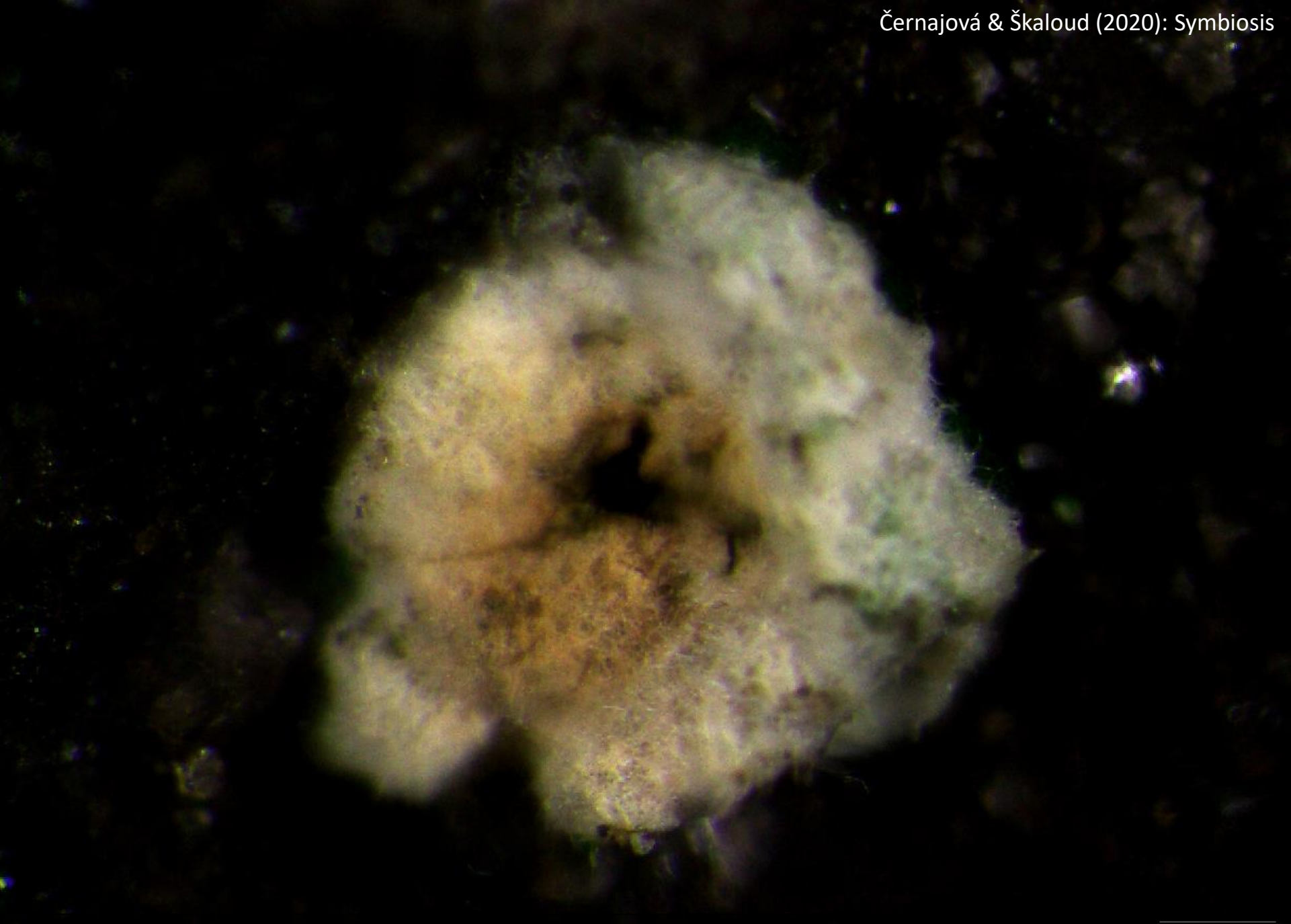
A mass of predominantly algal cells with a few interwoven fungal hyphae

Fungus starts to take over

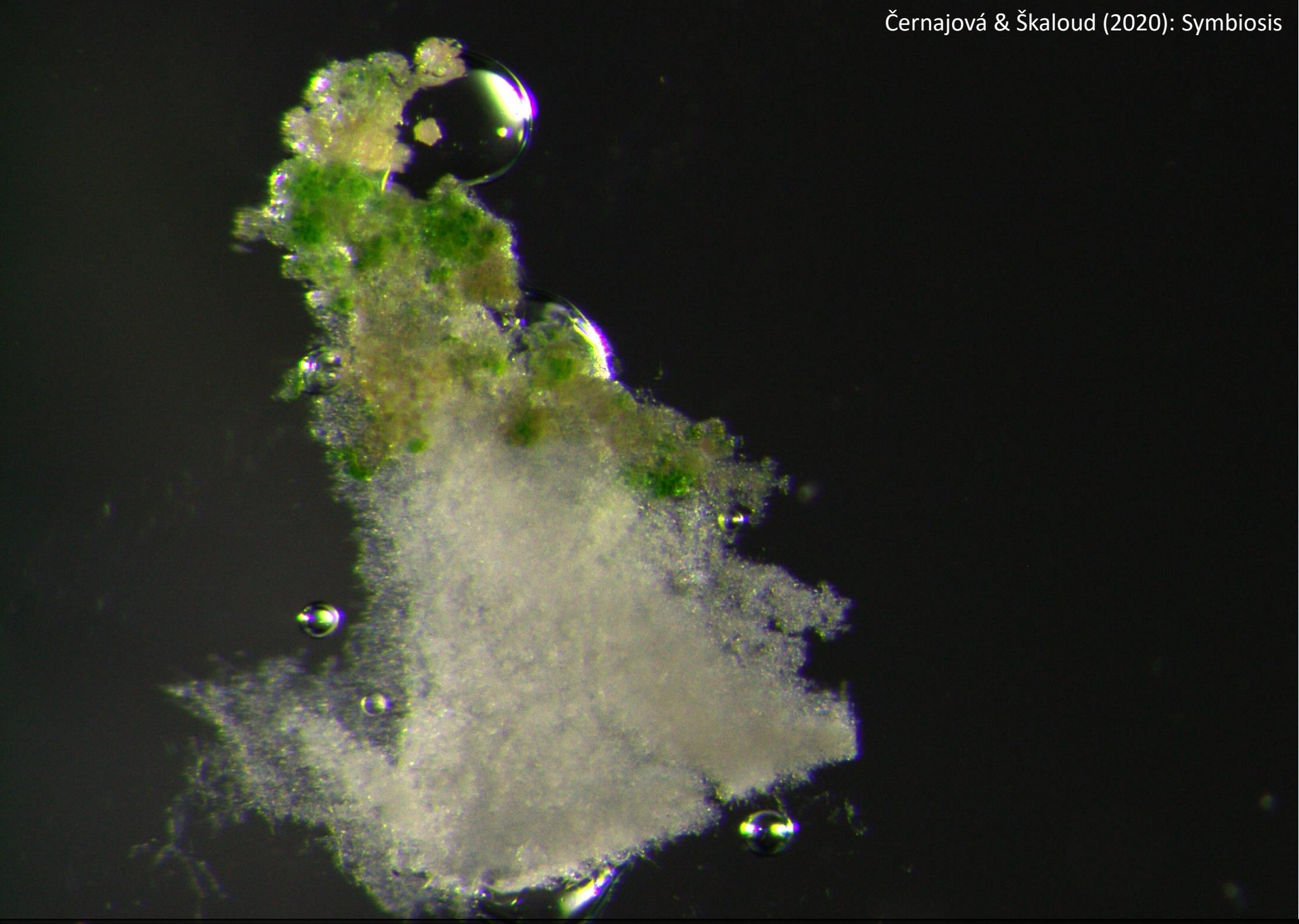
Fungus forms a superficial layer enclosing the algae inside



Transfer on the soil, development of rhizine-like structures



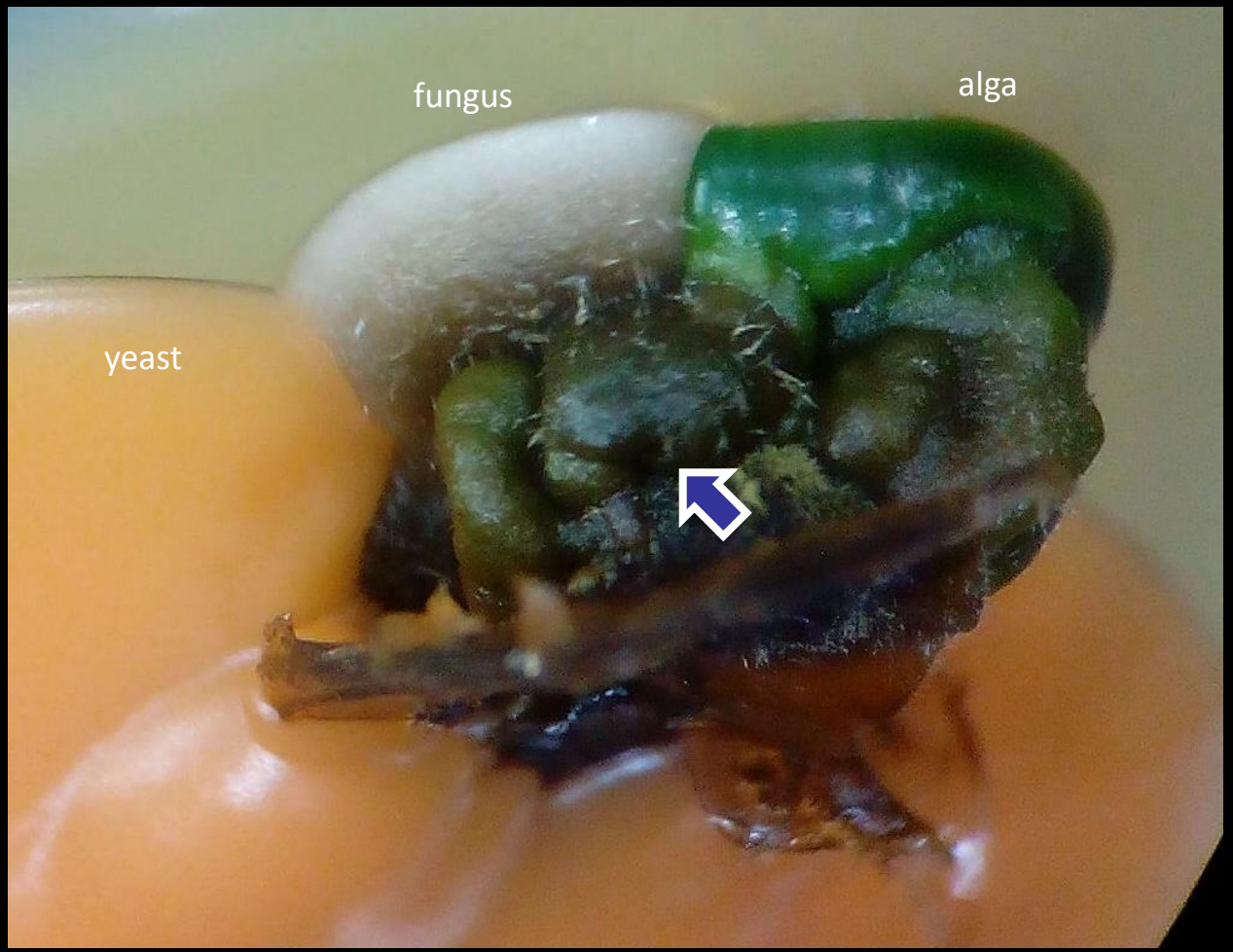
A young lichen – fungus completely enclosed the algae



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

Let‘s build a lichen!

- The yeast profits on the symbiosis, but probably does not involve the thallus formation



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Thank you for your attention

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