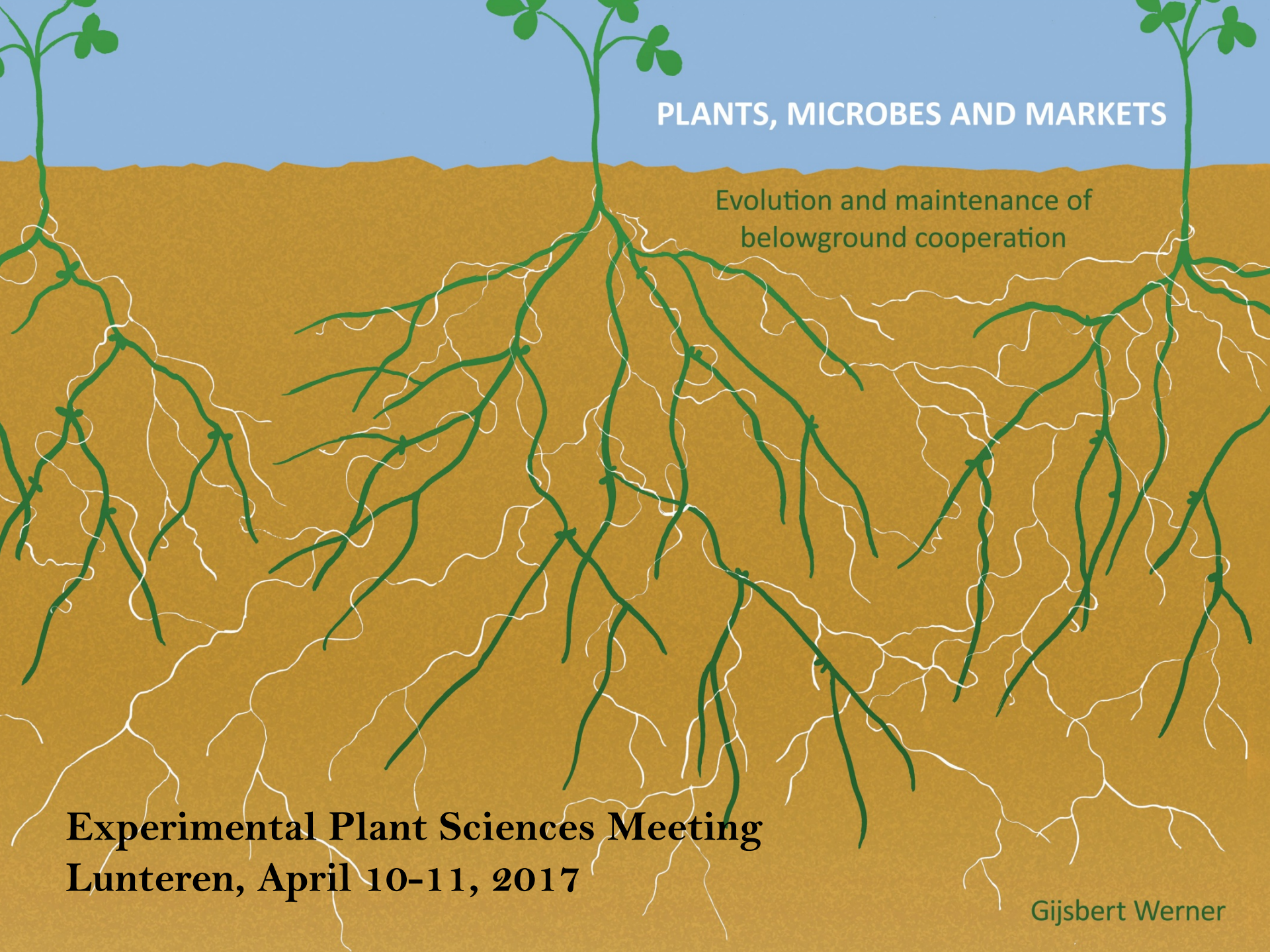


PLANTS, MICROBES AND MARKETS

Evolution and maintenance of belowground cooperation

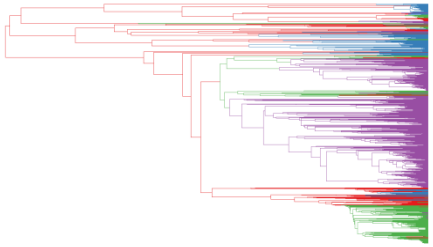
Experimental Plant Sciences Meeting
Lunteren, April 10-11, 2017

Gijsbert Werner

Evolution of Cooperation

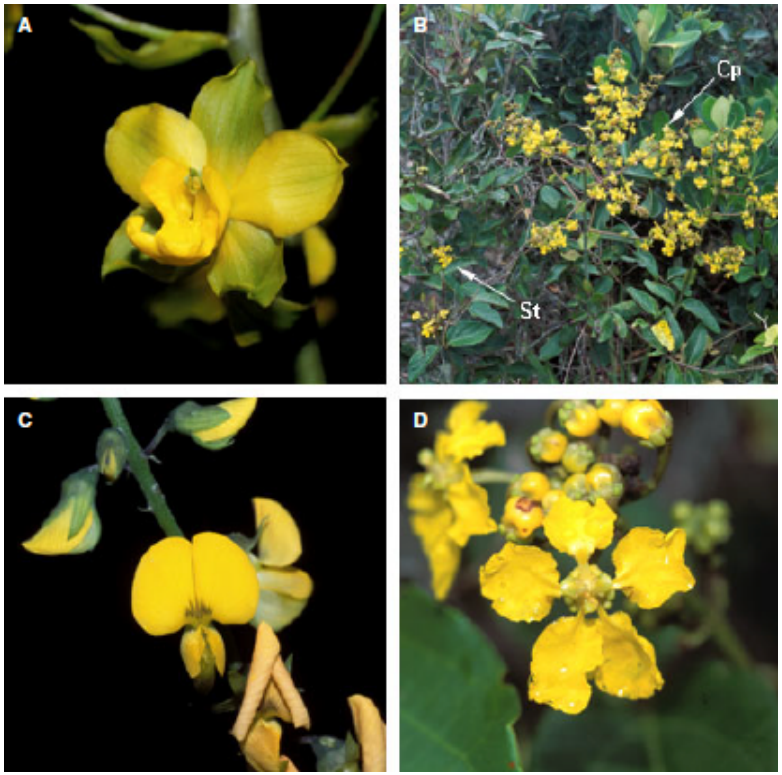
Evolution of Cooperation

$$\left(\frac{\partial^2 \lambda(\alpha_{Res}, \alpha_{Mut})}{\partial \alpha_{Mut}}\bigg|_{\substack{\alpha_{Mut}=\alpha_{Res}{}^* \\ \alpha_{Res}=\alpha_{Res}{}^*}}\right) > 0$$



Plant are the ultimate cooperators..

..but, always risk of cheating and defection



Why conflict? Evolutionary interests not aligned

Pansarin (2008) Reproductive biology of Cyrtopodium polyphyllum (Orchidaceae): a Cyrtopodiinae pollinated by deceit. *Plant Biology*

Plants and soil microbes cooperate belowground

Symbiotic N_2-fixation

Fix atmospheric N_2

Provide N_2 in return for carbon

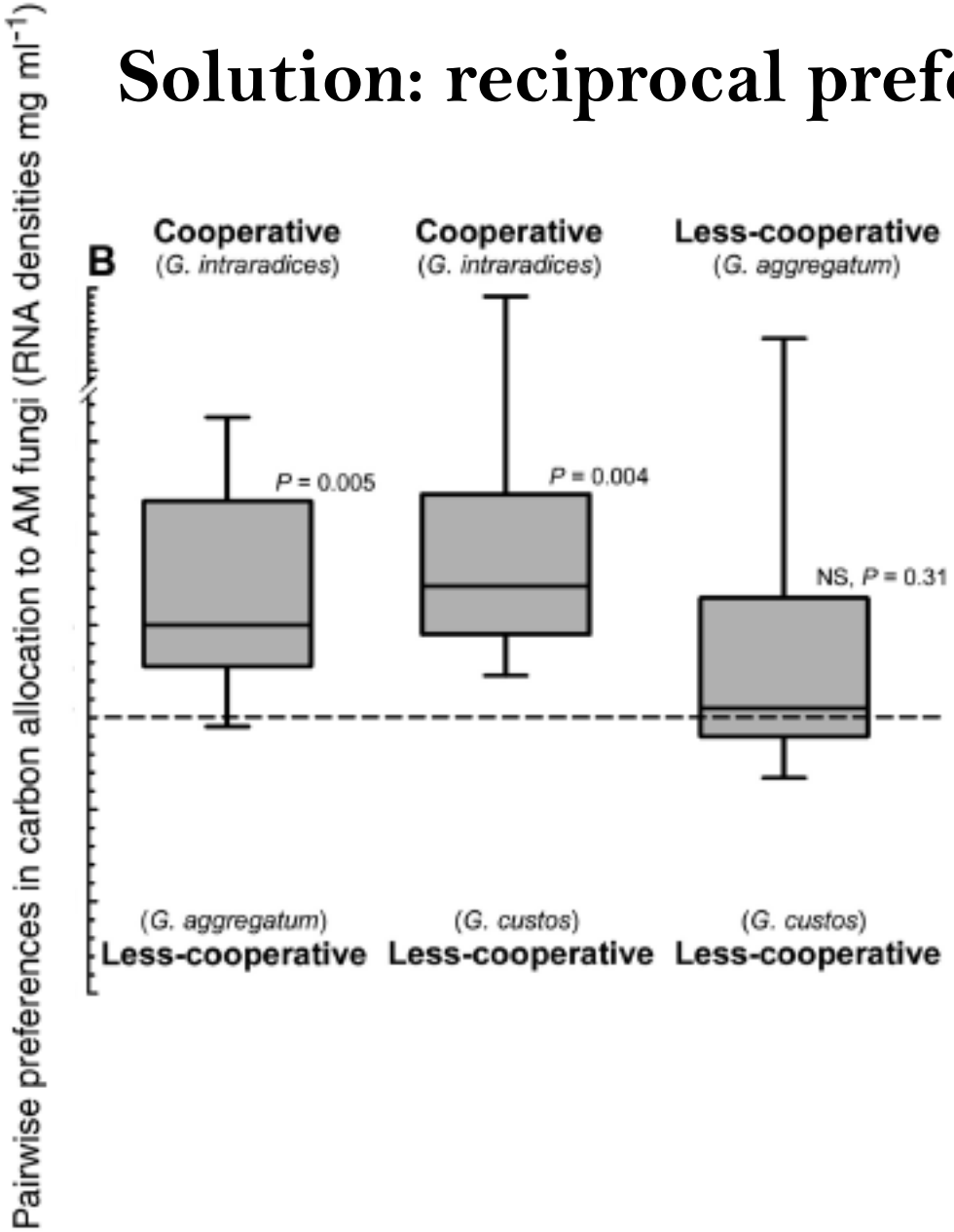
Arbuscular mycorrhizal fungi (AMF)

Scavenge soil for nutrients

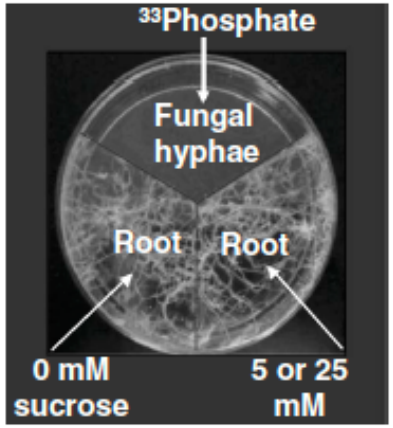
Provide P in exchange for carbon

Why not undermined by lower-quality partners?

Solution: reciprocal preferential rewards..

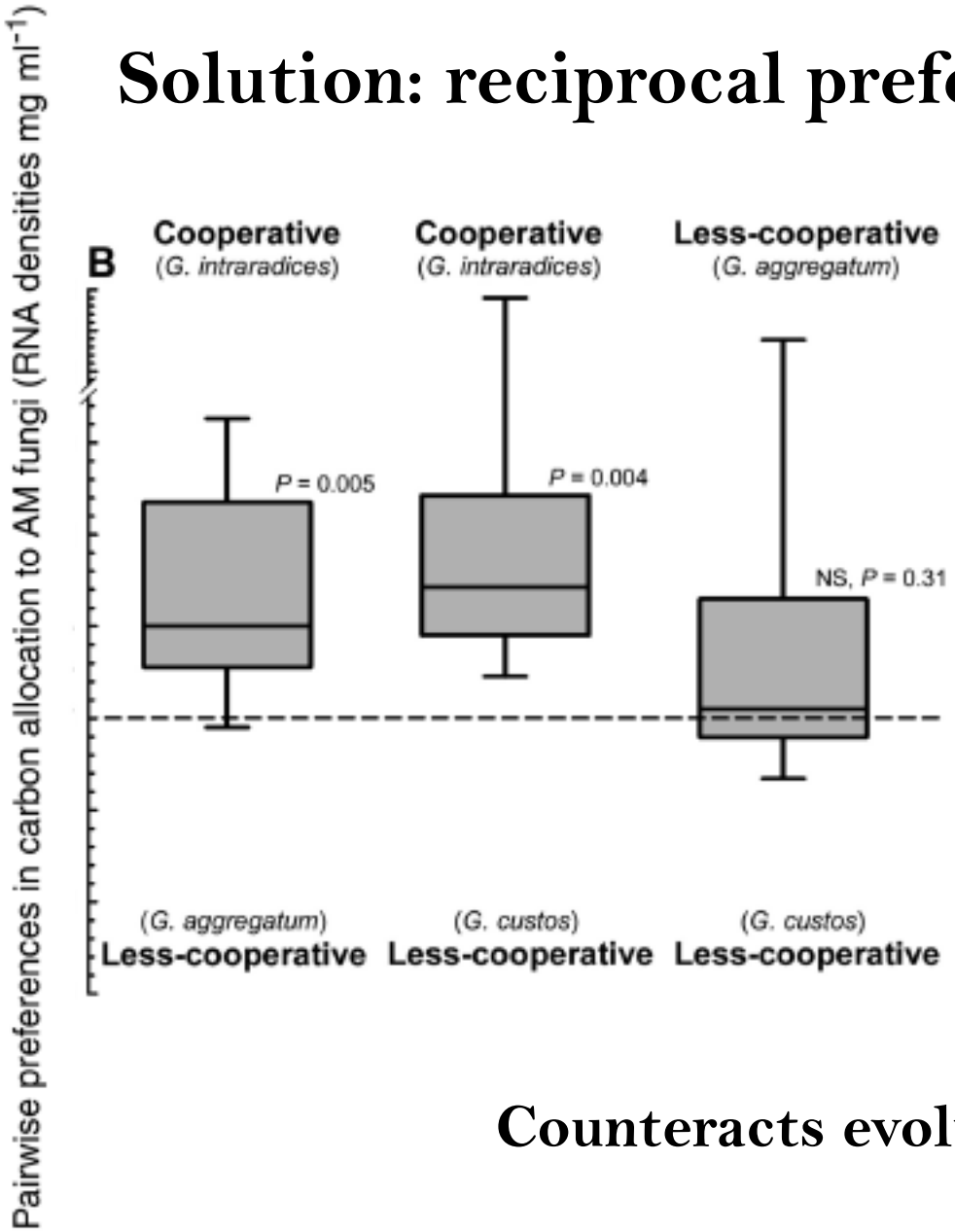


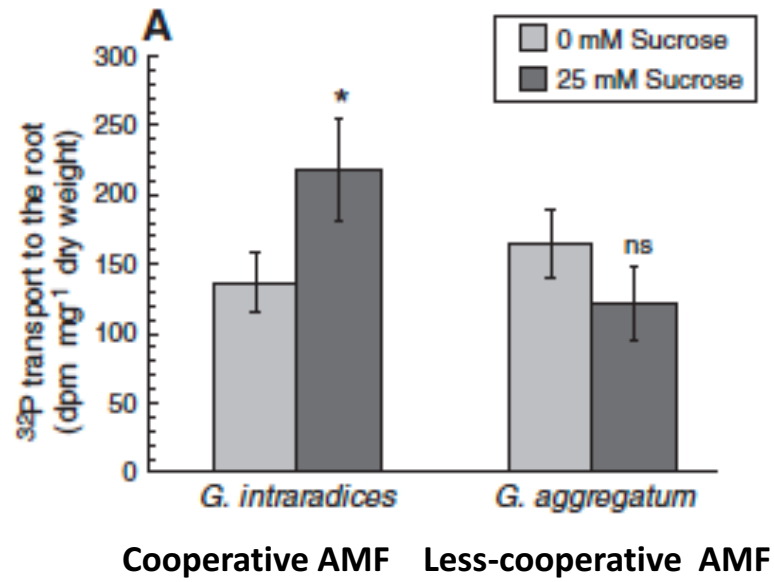
Toby Kiers
VU Amsterdam



Kiers (2011) Reciprocal Rewards Stabilize Cooperation in the Mycorrhizal Symbiosis. *Science*

Solution: reciprocal preferential rewards..





Counteracts evolutionary incentive to 'cheat'

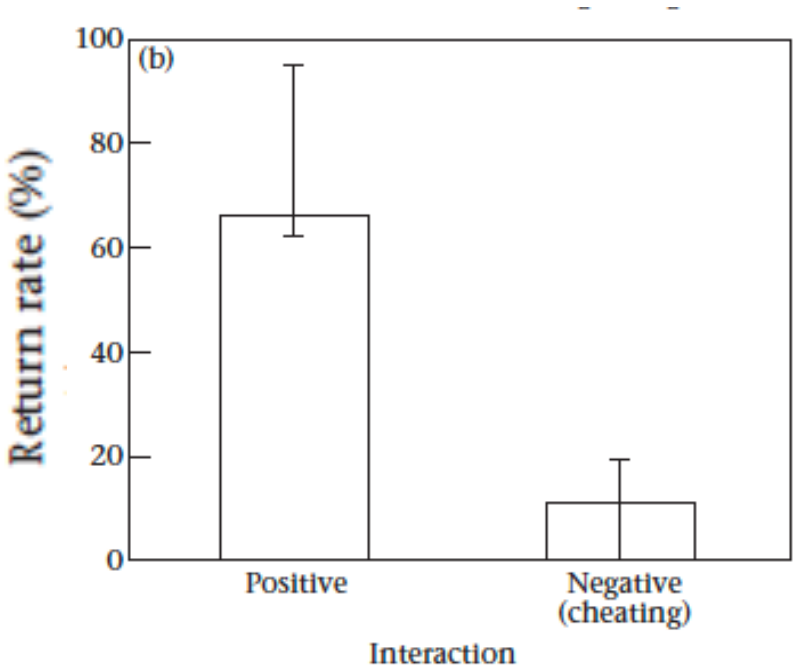
Kiers (2011) Reciprocal Rewards Stabilize Cooperation in the Mycorrhizal Symbiosis. *Science*

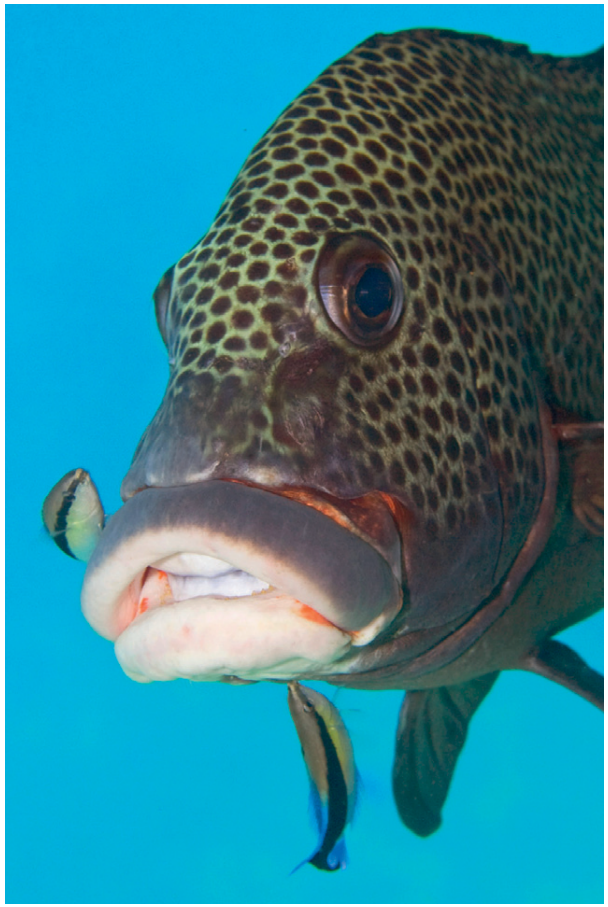
‘Biological markets’ can stabilise cooperation

Preferential rewards

- Based on quality of cooperative service
  - → Incentive to act as better partner
  - → Stabilisation of cooperation

Result: dynamics analogous to markets





Bshary, Schaffer (2002) Choosy reef fish select cleaner fish that provide high-quality service *Animal Behaviour*

Can we apply this framework to microbial interactions?

Four conditions biological markets:

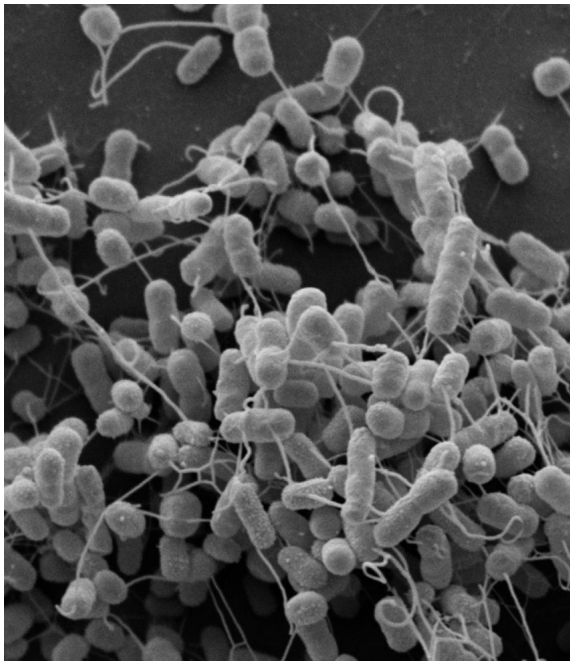
1. Exchange
2. Two distinct classes
3. Variation partner quality
4. Potential partner choice/switch

Chapter 2. Werner *et al.* (2014) Evolution of microbial markets. *PNAS*

Six evolutionary strategies for microbial biological markets…

Six potential microbial 'strategies':

- Avoid bad trading partners
- Build local 'business ties'
- **Diversify or specialise**
- Become indispensable
- Save for a rainy day
- Eliminate the competition



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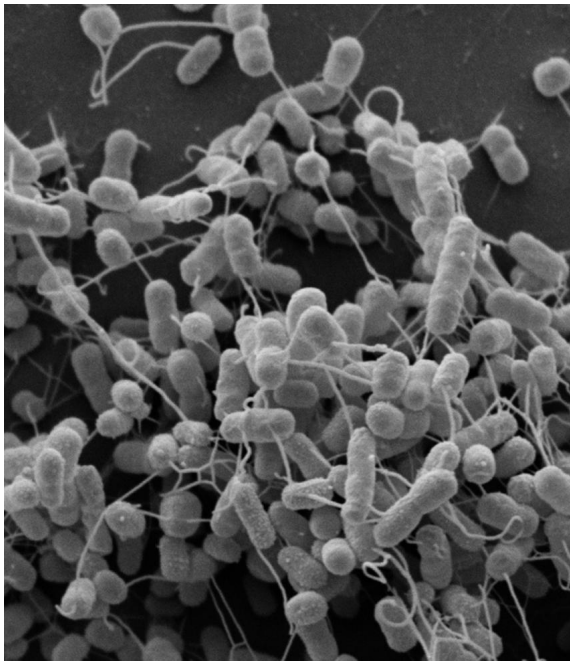
Six evolutionary strategies for microbial biological markets…



Six potential microbial 'strategies':

- Avoid bad trading partners
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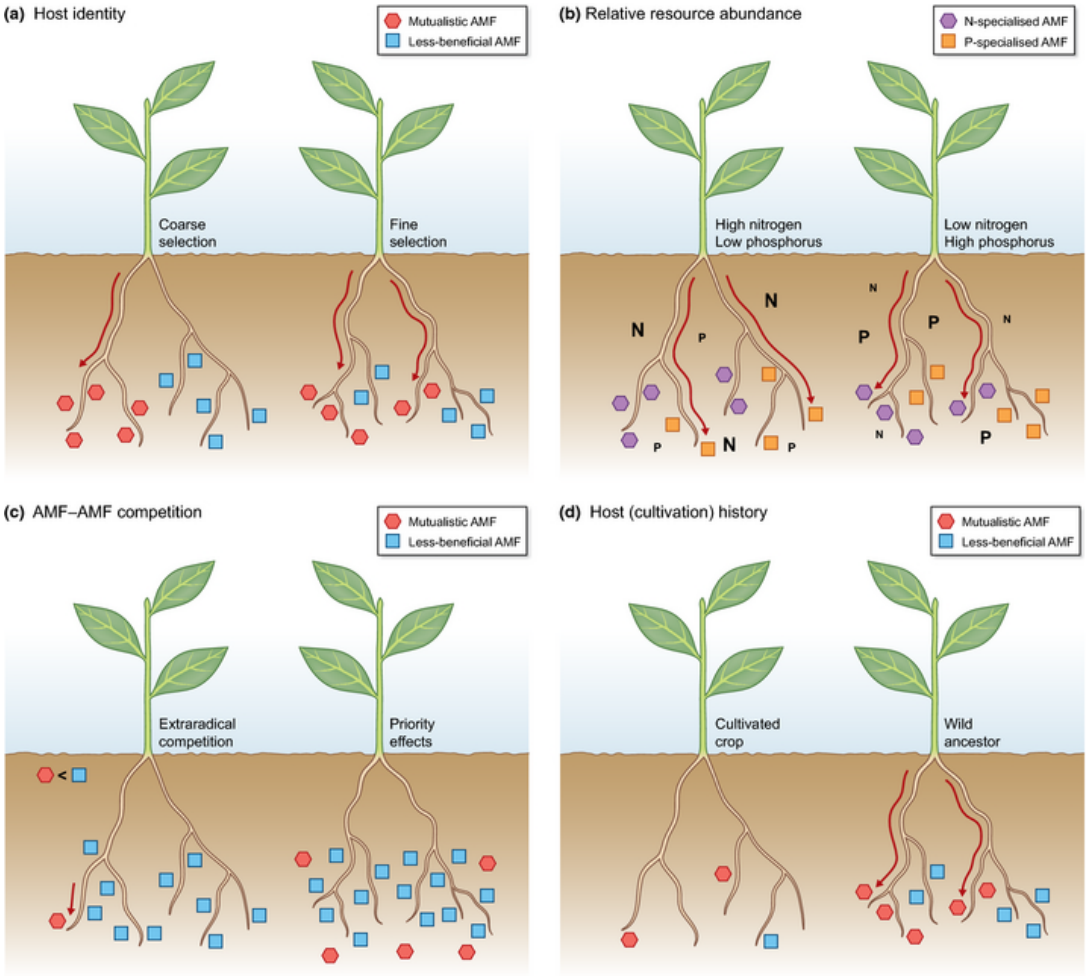
- **Diversify or specialise**
- Become indispensable
- Save for a rainy day
- Eliminate the competition

Key conclusions:

- Biological markets also non-cognitive
- Useful framework (Environmental context).

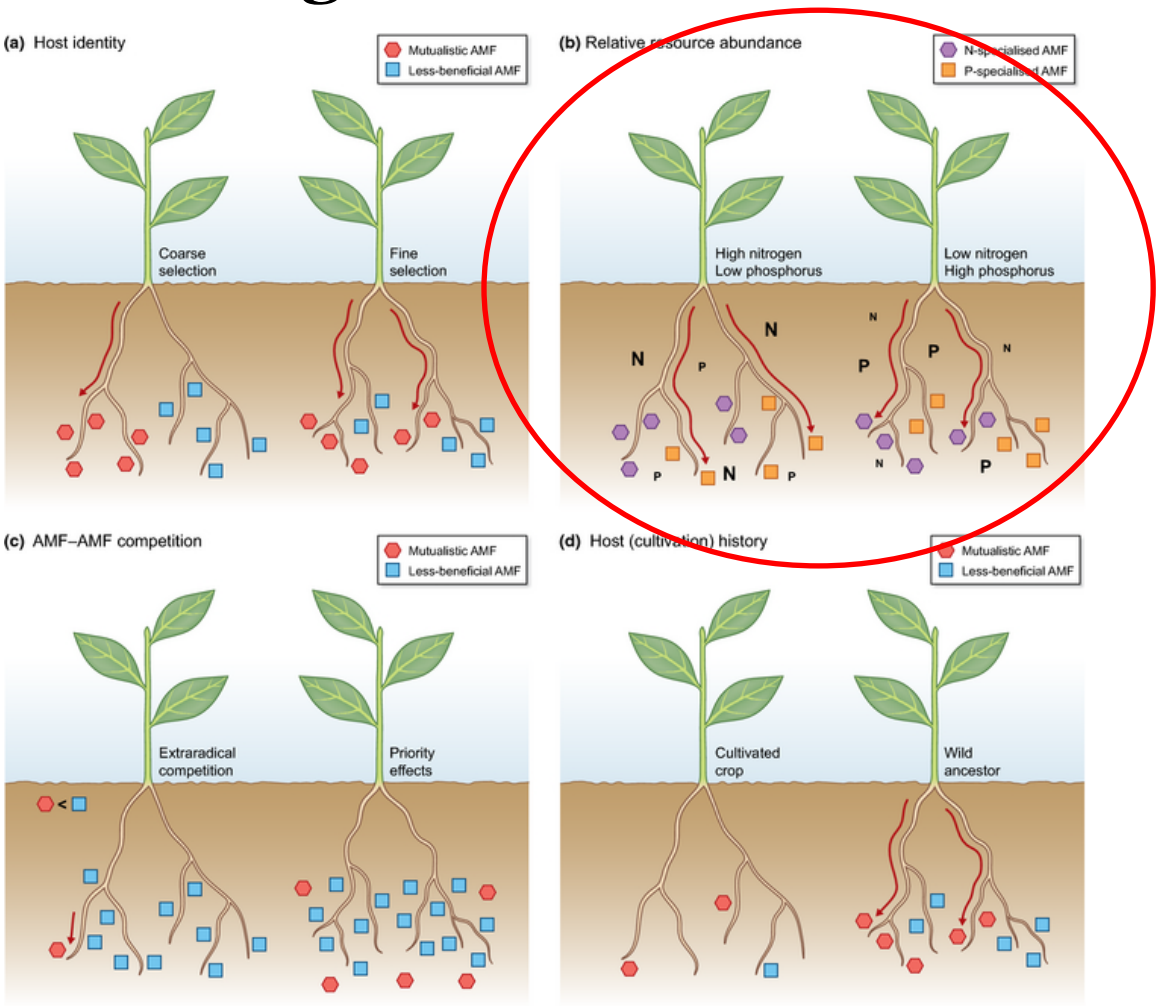
Chapter 2. Werner *et al.* (2014) Evolution of microbial markets. *PNAS*

Rewards vary with environmental and ecological context



Chapter 3. Werner & Kiers (2015) Partner selection in the mycorrhizal mutualism. *New Phytologist*

Rewards vary with environmental and ecological context



Chapter 3. Werner & Kiers (2015) Partner selection in the mycorrhizal mutualism. *New Phytologist*

Does resource abundance affect relative success of high vs. lower-quality AMF?

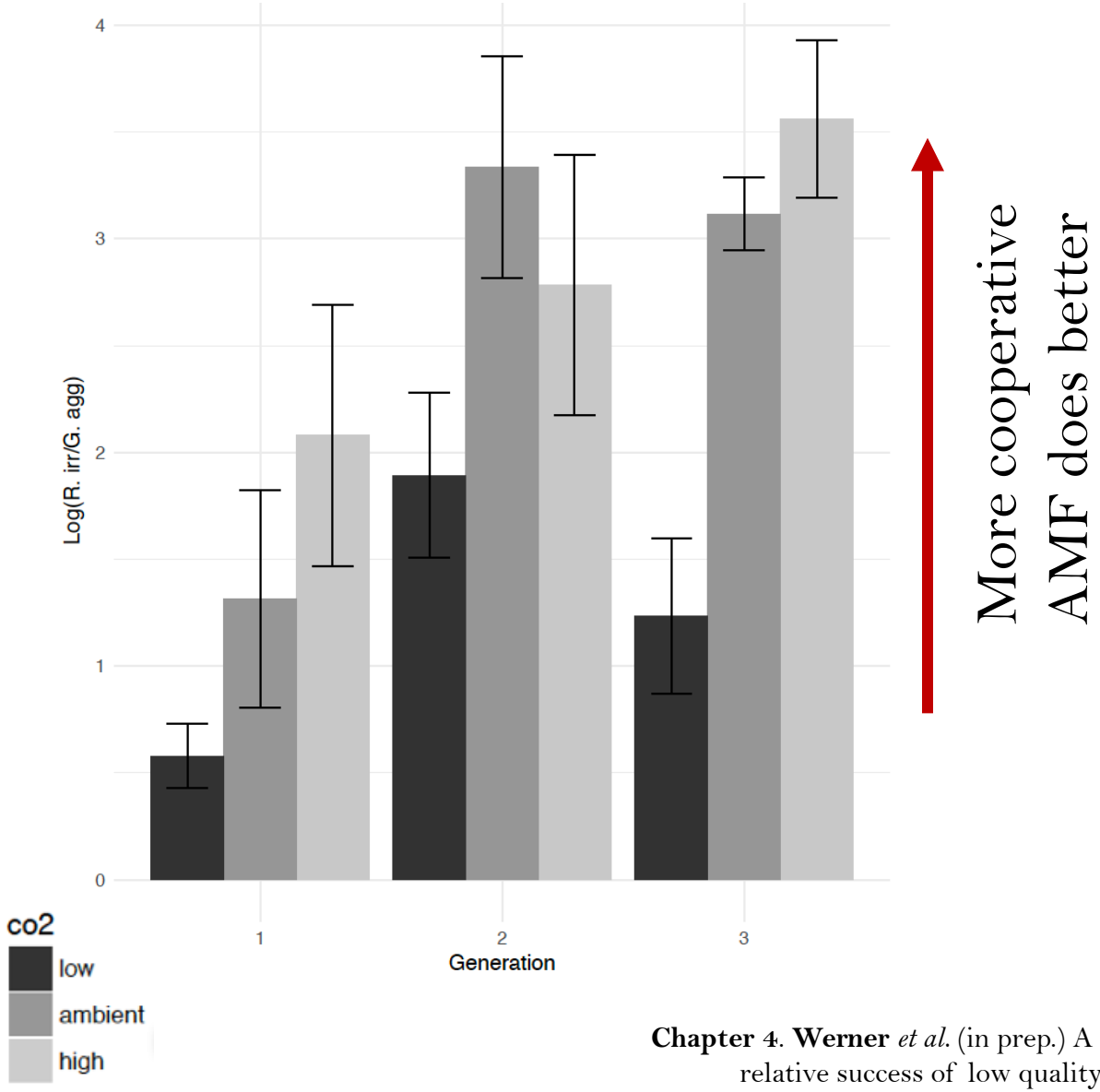
Theoretical prediction:

- More carbon (Light, CO_2), soil nutrients scarcer
  - → more stringent preferential rewards
  - → Higher quality AMF do better

Corné Pieterse
Utrecht University

Bever (2015) Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts. *New Phytologist*. Wyatt et al. (2014) A biological market analysis of the plant-mycorrhizal symbiosis. *Evolution*

Across a CO_2-gradient, increasing carbon favours higher-quality AMF



Chapter 4. Werner *et al.* (in prep.) A gradient of atmospheric CO2-levels influences the relative success of low quality mycorrhizal symbionts over multiple generations.

Across a CO_2-gradient, increasing carbon favours higher-quality AMF

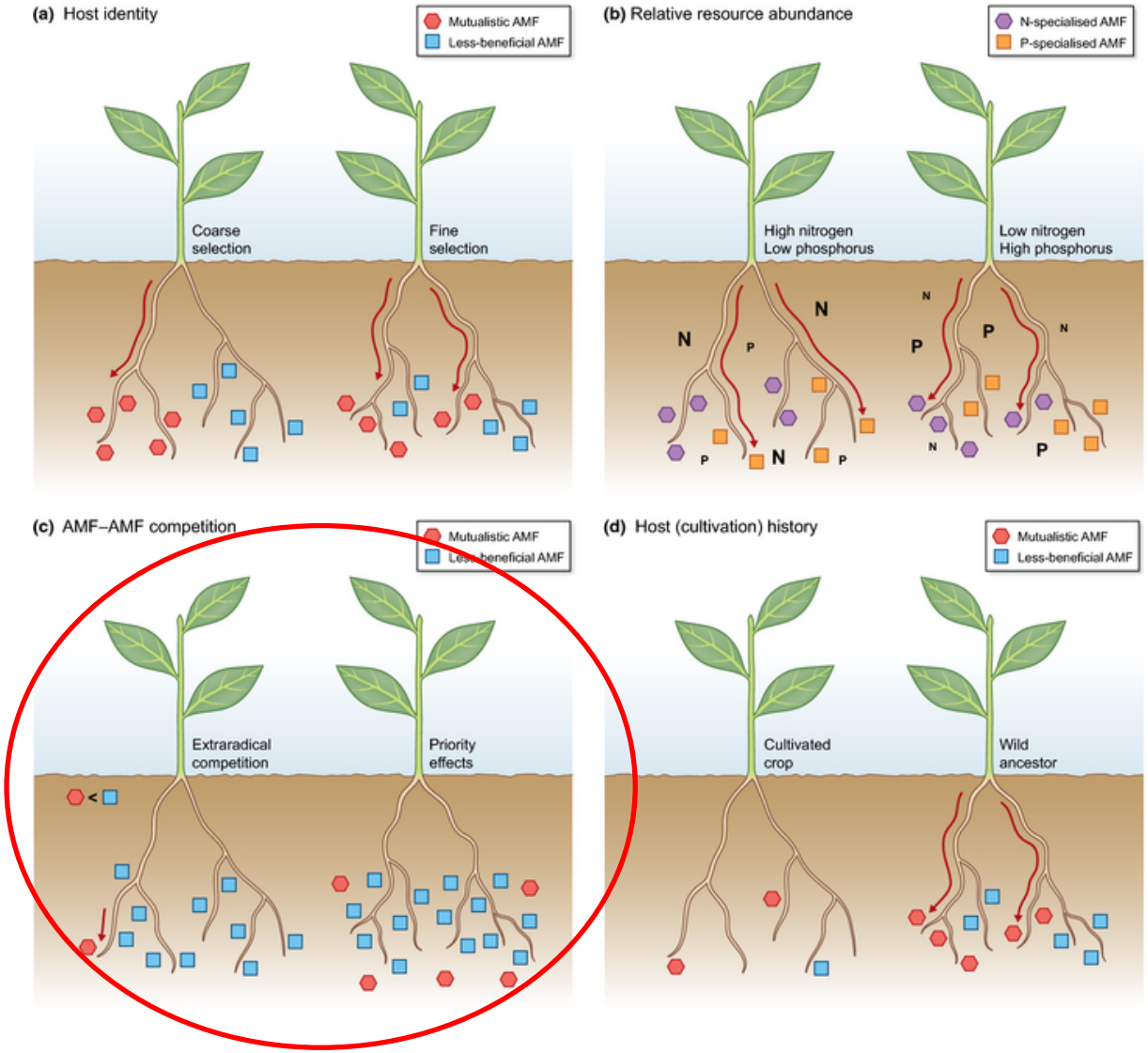
Key conclusions:

- Environmental context affects relative performance AMF
- CO_2 likely affects plant selection higher-quality mutualist
- Potential implication mutualism stability

Open questions:

- Track actual resources
- Range of different quality fungi

An effect of arrival order on partner choice?



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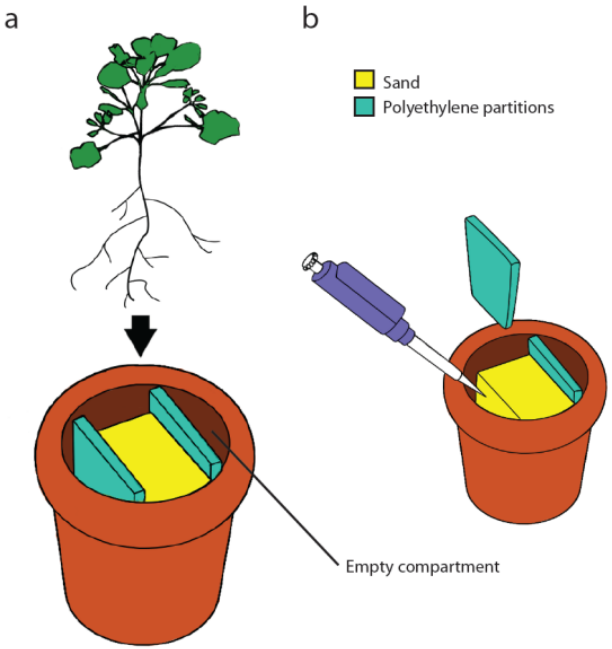
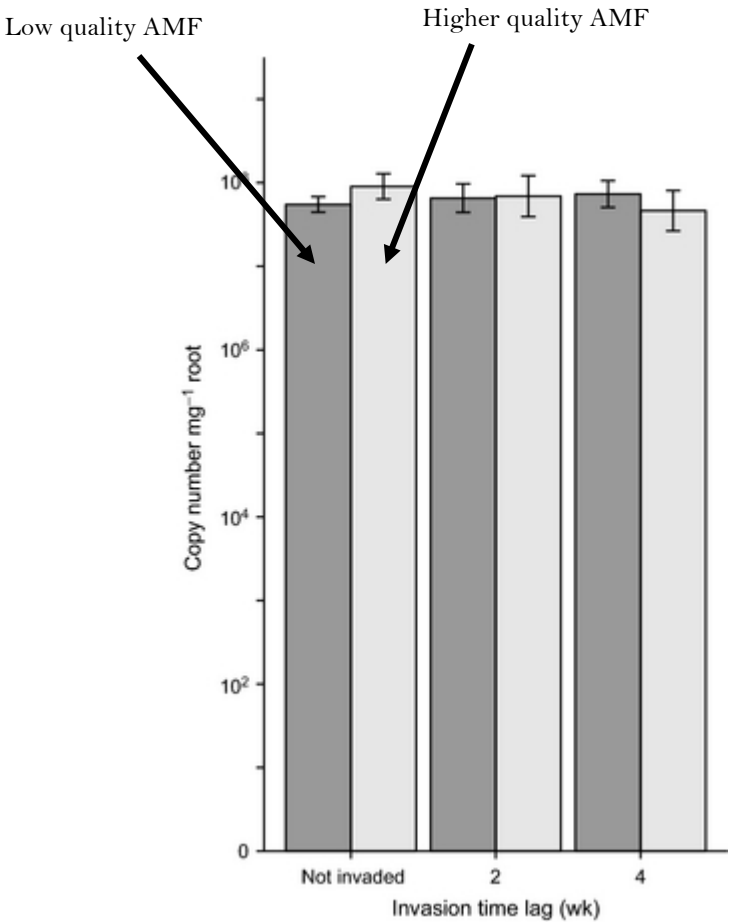
Does arrival order matter?



Chapter 5. Werner & Kiers (2015) Order of Arrival Structures Arbuscular Mycorrhizal Colonisation of Plants. *New Phytologist*

Does arrival order matter?



Resident AMF not affected by second invader…

Chapter 5. Werner & Kiers (2015) Order of Arrival Structures Arbuscular Mycorrhizal Colonisation of Plants. *New Phytologist*

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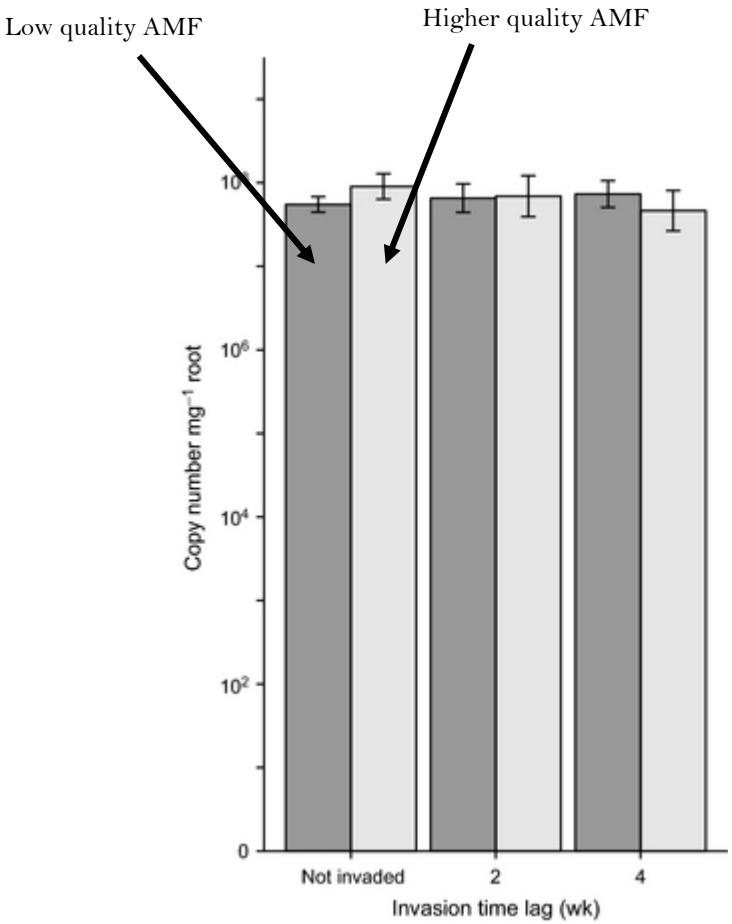

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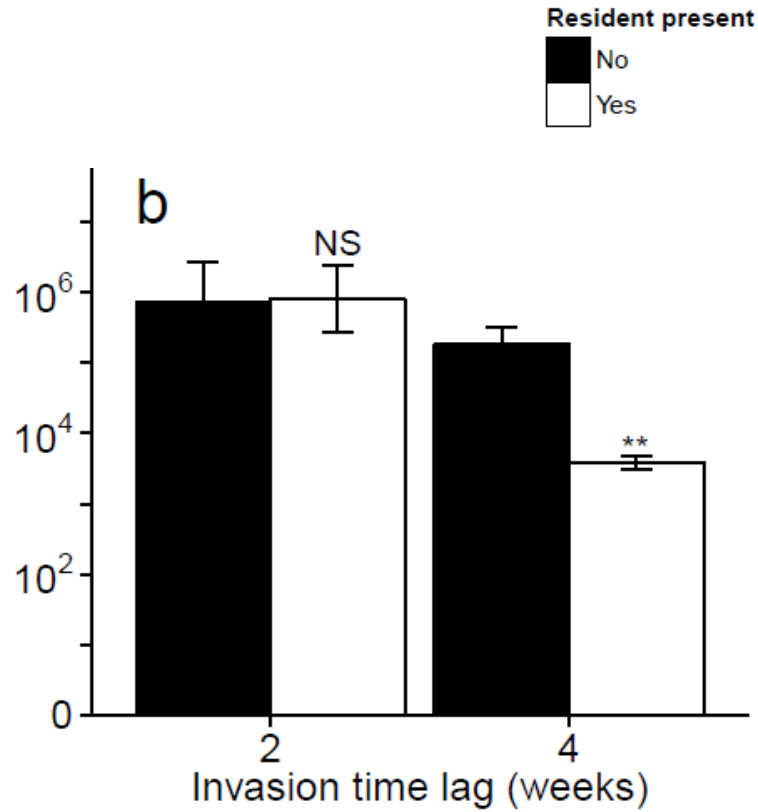


…but, if head start long enough, invader cannot colonise well

Chapter 5. Werner & Kiers (2015) Order of Arrival Structures Arbuscular Mycorrhizal Colonisation of Plants. *New Phytologist*

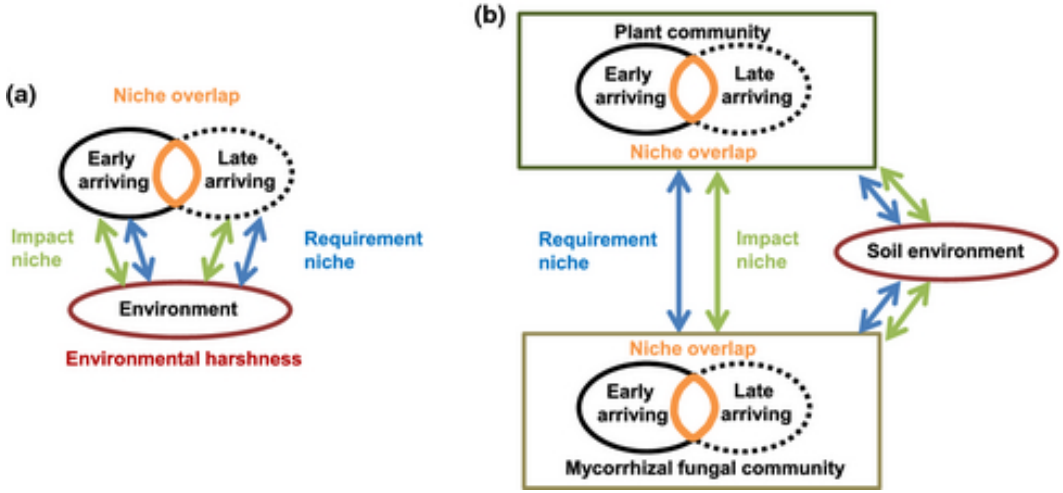
Order of arrival influences AMF colonisation

Key Conclusions:

- Priority effects also belowground
- Could limit effectiveness of reward mechanisms
  - Mutualism / speed trade-offs?

Open Questions:

- Relevant time frame? Fade out?
- Interaction with host plant PE?



Johnson 2015, *New Phytologist*, Commentary

Chapter 5. Werner & Kiers (2015) Order of Arrival Structures Arbuscular Mycorrhizal Colonisation of Plants. *New Phytologist*

When do symbionts specialise or diversify?

Specialist – one service (N_2)

Generalist – Phosphorus, Nitrogen, H_2O, Pathogen Protection

Fitness of strategy depends on other 'player' → Evolutionary game theory

What is the Evolutionary Stable Strategy (ESS)?

$$\left(\frac{\partial^2 \lambda(\alpha_{Res}, \alpha_{Mut})}{\partial \alpha_{Mut}} \bigg|_{\substack{\alpha_{Mut}=\alpha_{Res}^* \\ \alpha_{Res}=\alpha_{Res}^*}} \right) > 0$$

When do symbionts specialise or diversify?

Specialist – one service (N_2)

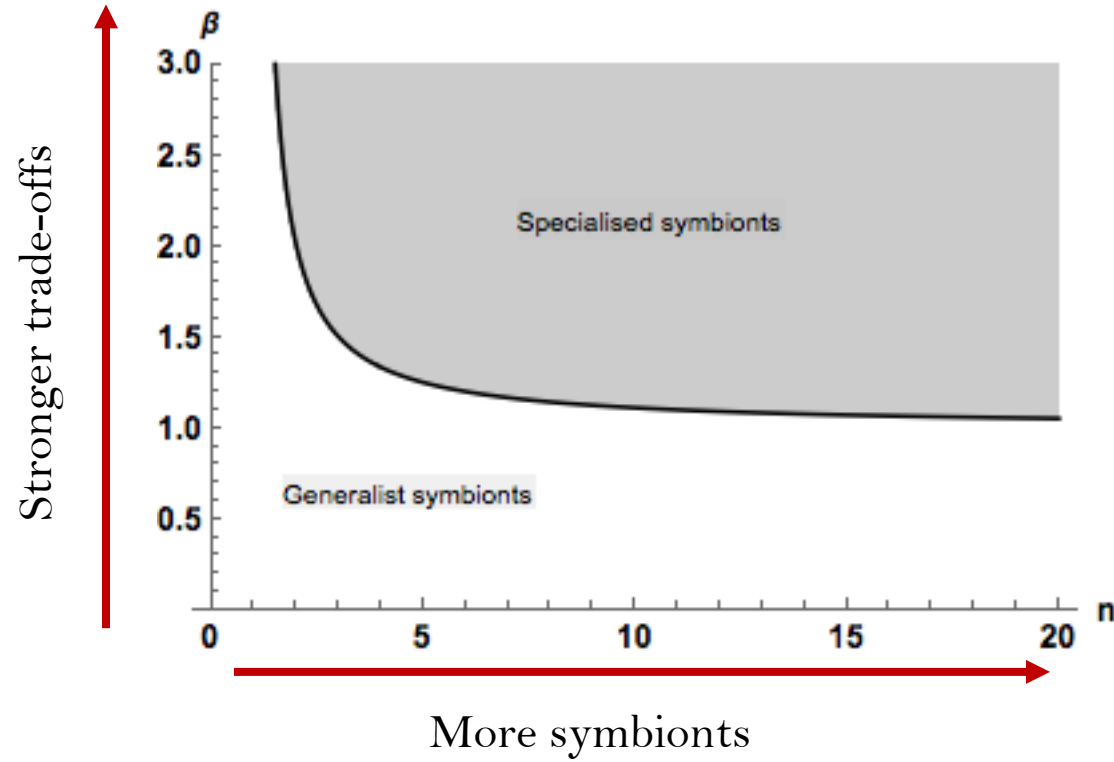
Generalist – Phosphorus, Nitrogen, H_2O, Pathogen Protection

Prof. Stuart West,
University of Oxford

Gregory Wyatt,
University of Oxford

Specialist – one service

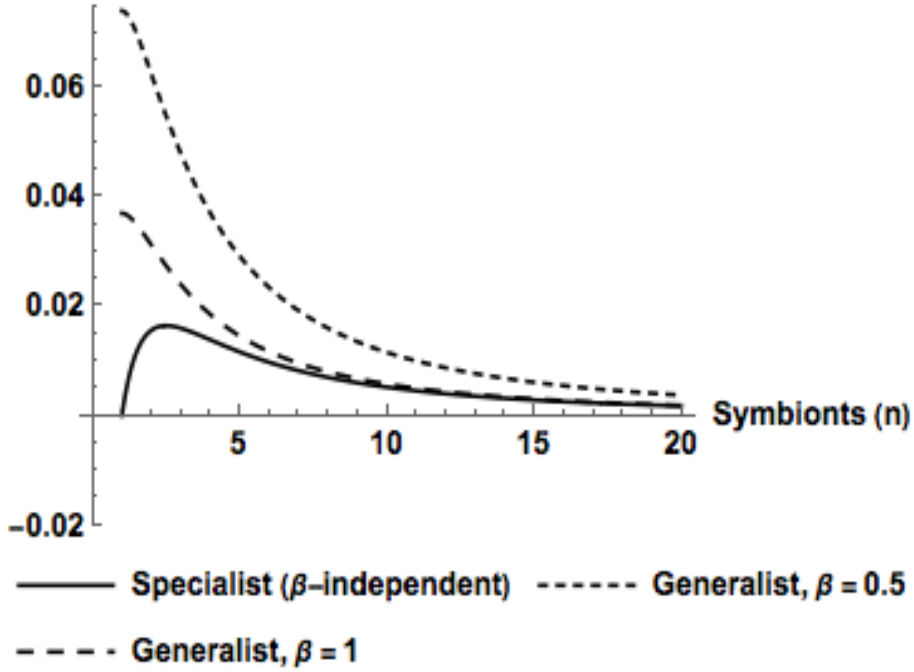
$$\beta > 1 + \frac{1}{n}$$



Specialization on single benefit, if:

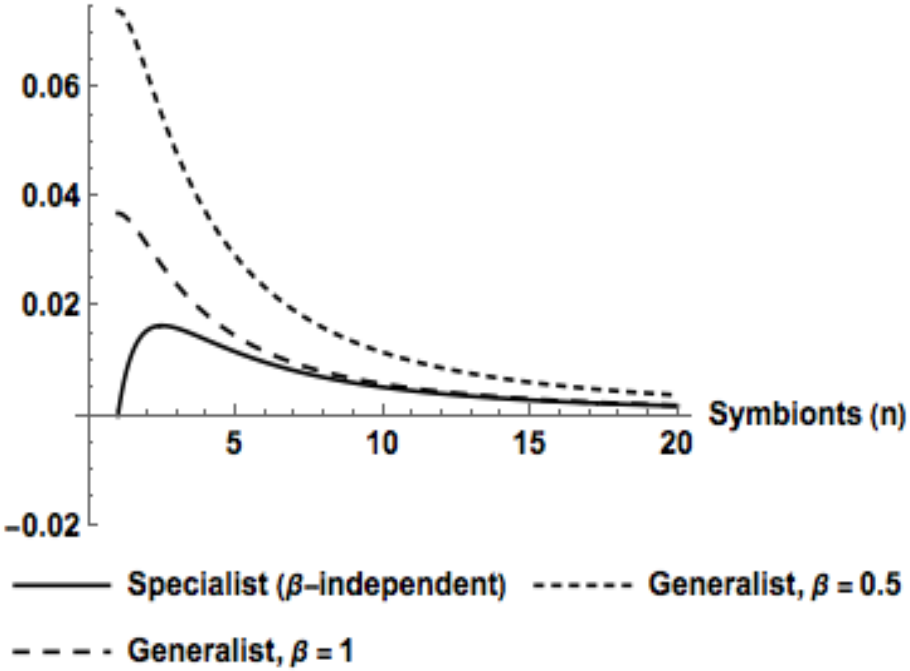
- Strong trade-offs
- Many symbionts per host

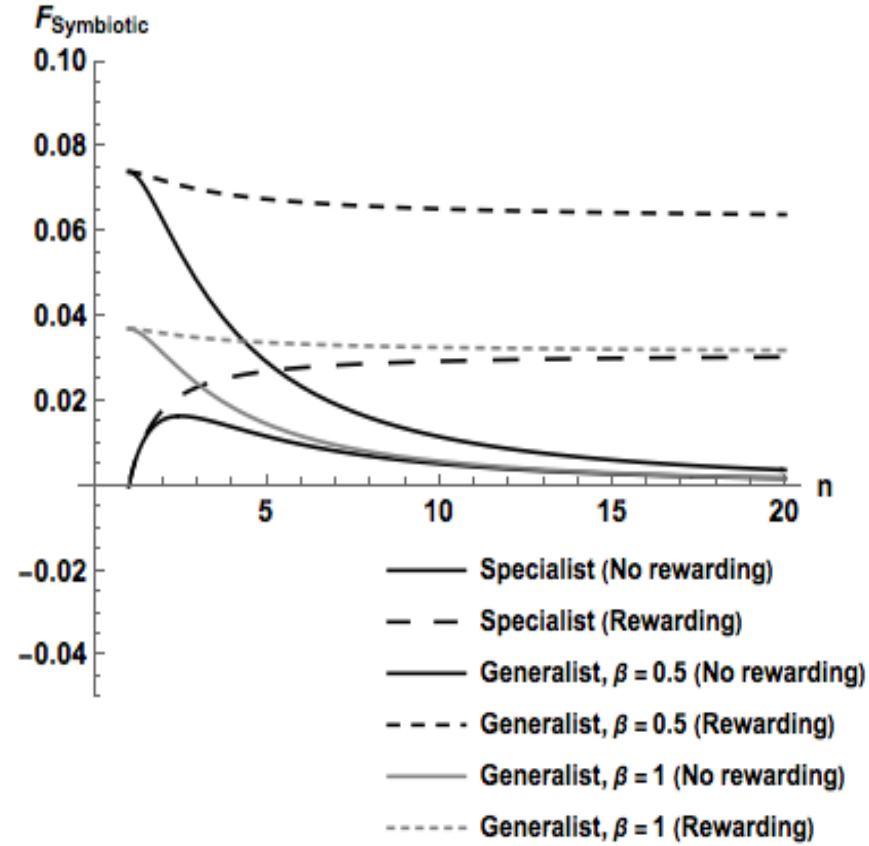
Chapter 6. Werner *et al.* (in sub) Should symbionts provide multiple benefits or specialise on a single mutualistic service?



More symbionts

But this also undermines cooperation & drives cheating…





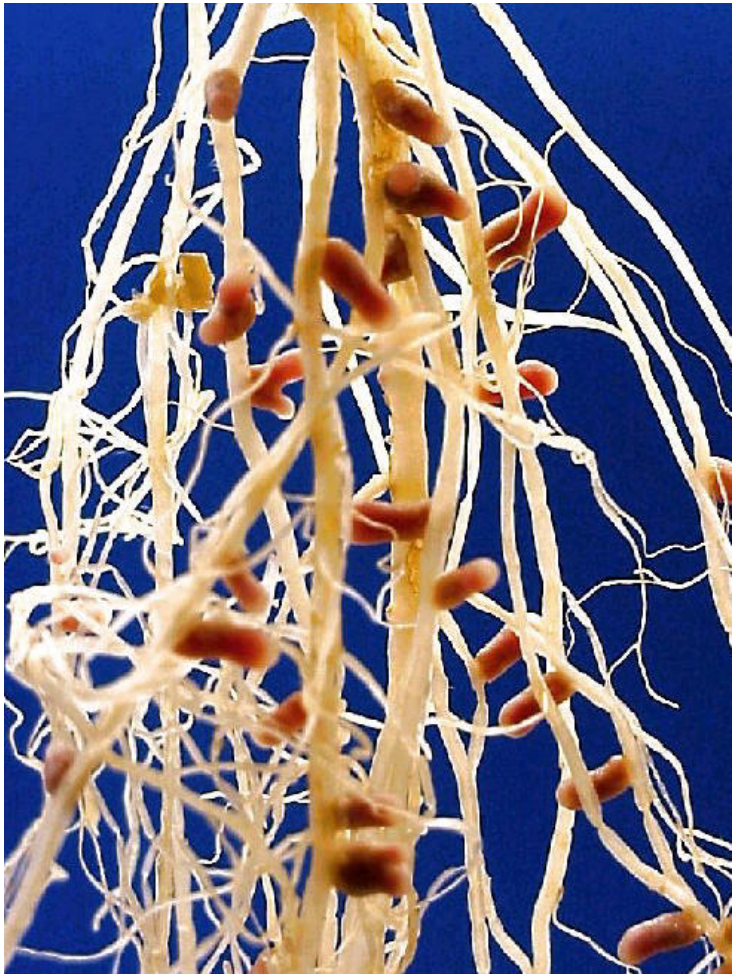
But this also undermines cooperation & drives cheating…

…rewards for cooperative partners can stabilise (specialised) symbioses

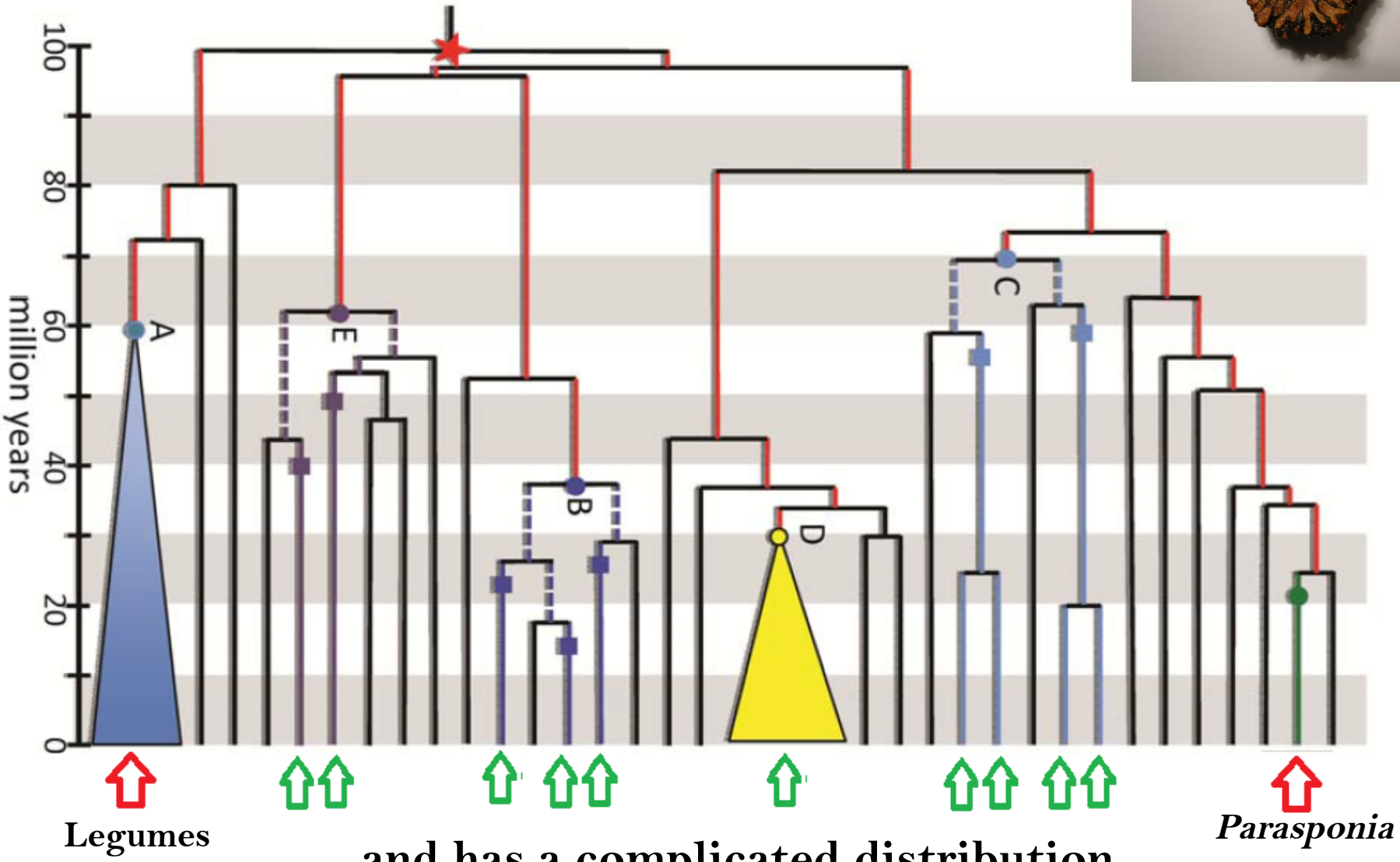
Key conclusions:

- Trade-offs & symbiont n key for specialisation vs generalism
- Rewards can shape both *level* & *type* of mutualistic cooperation

Ancient evolutionary history symbiotic N_2-fixation

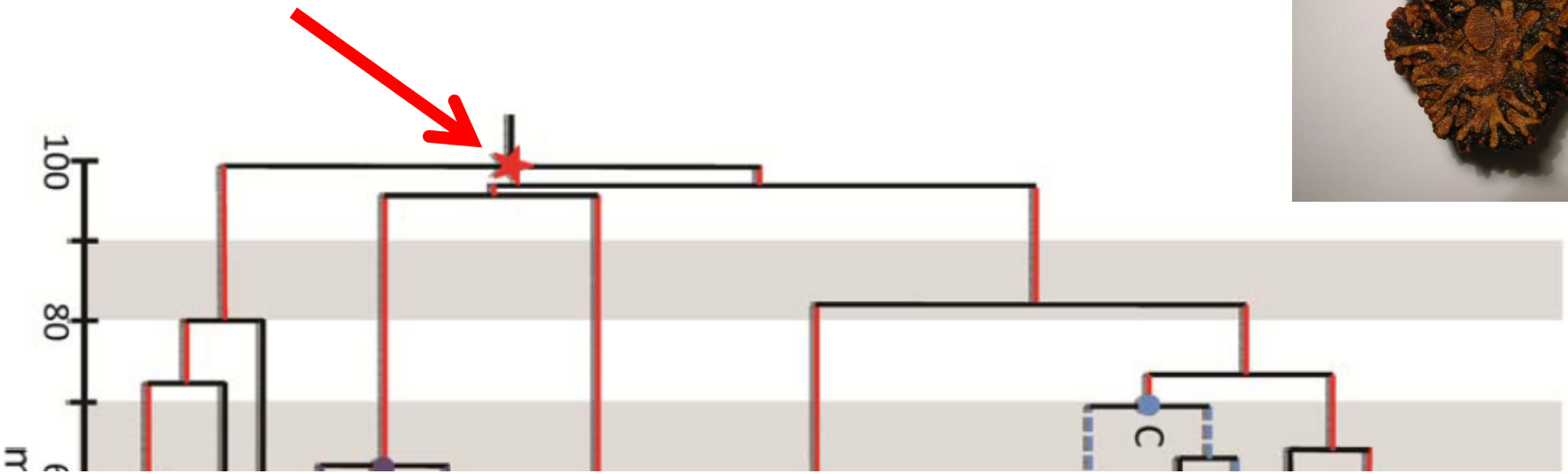


Symbiotic N_2-fixation in angiosperms is rare...

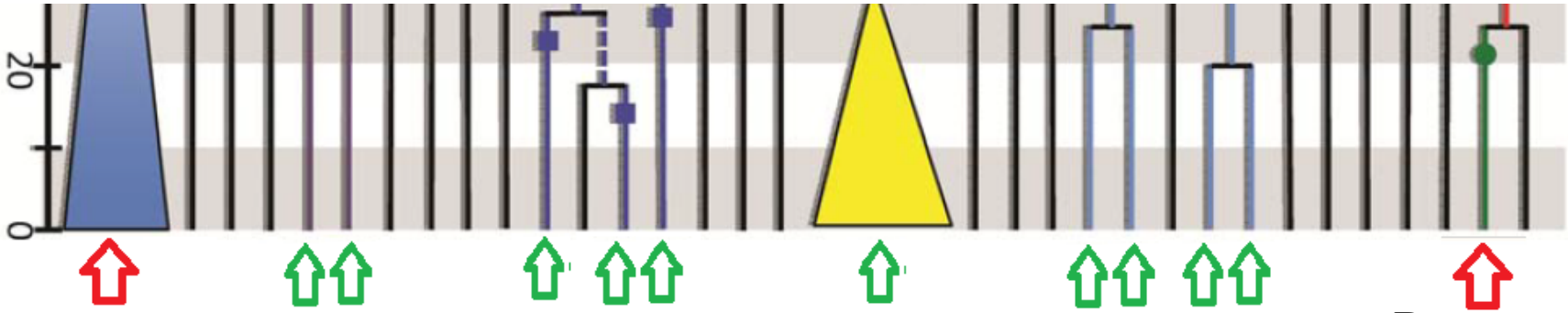


…and has a complicated distribution

Adapted from: Doyle 2011 MPMI



From verbal accounts to quantitative reconstruction



Legumes

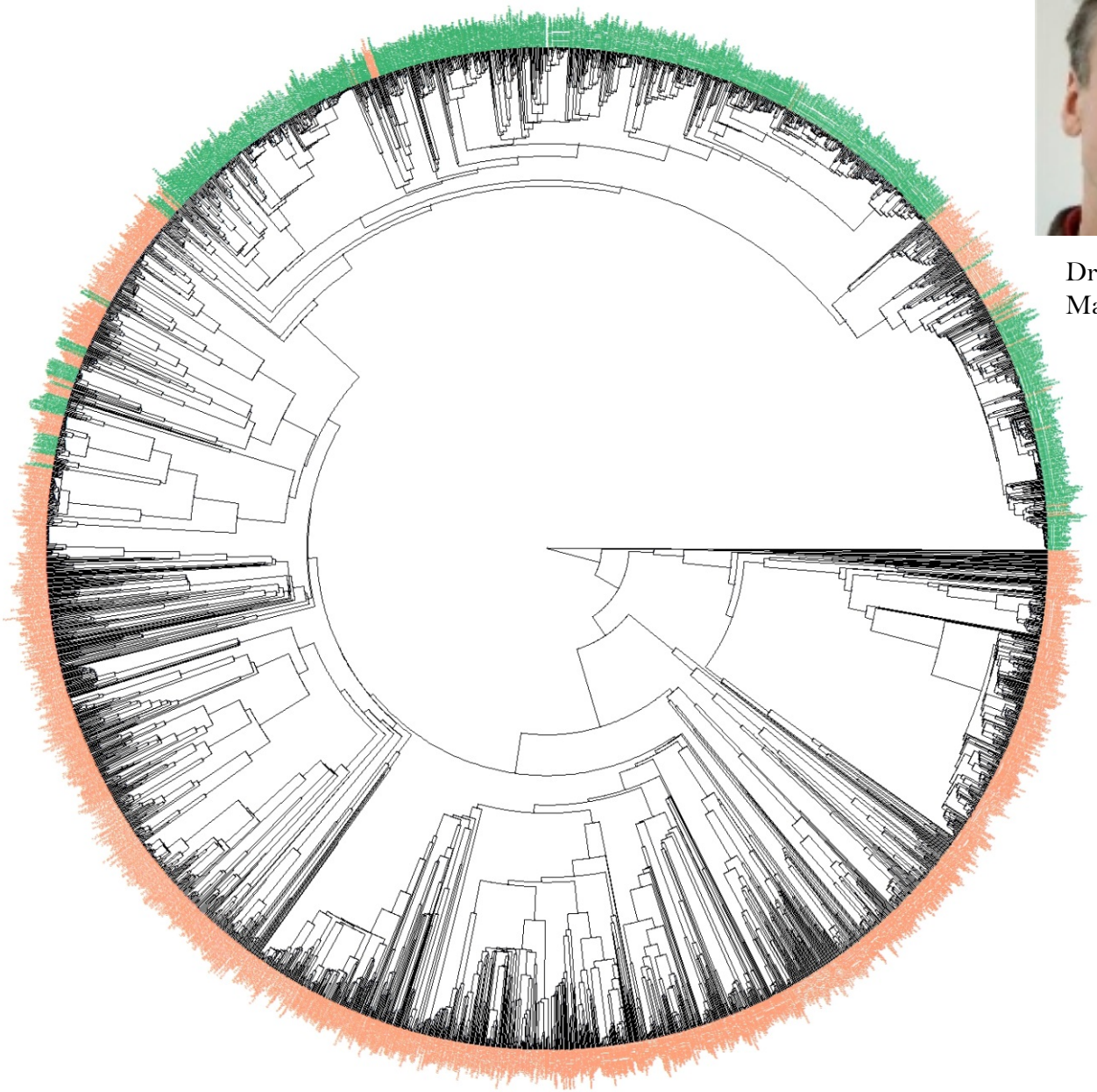
Parasponia

…and has a complicated distribution

Adapted from: Doyle 2011 MMI

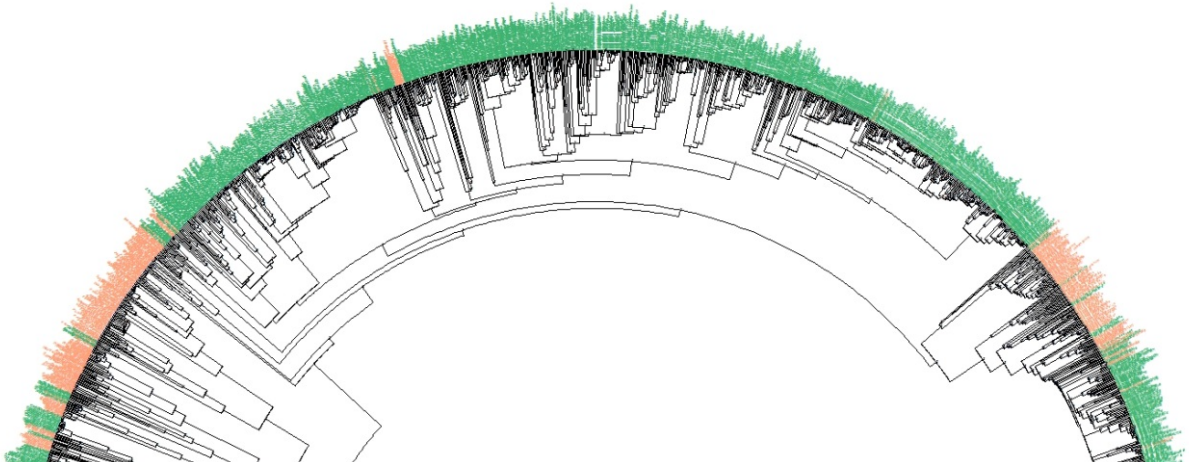
Dr. William Cornwell,
UNSW Australia

Dr. Jens Kattge
Max Planck, Jena



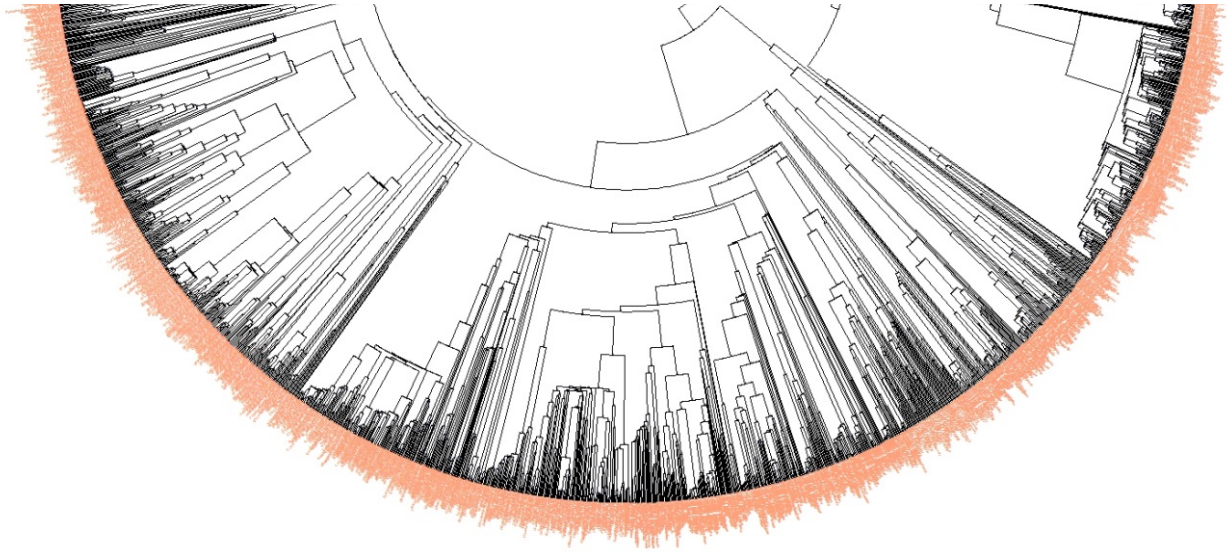
Prof. Janet Sprent
University of Dundee

Chapter 7. Werner *et al.* (2014) A single evolutionary innovation drives the deep evolution of symbiotic N2-fixation in angiosperms. *Nature Communications*



Single Speed Model: Very bad fit (AIC-weight <0.01%)

Best: Model with 2 speeds of evolution (AIC-weight 55%)



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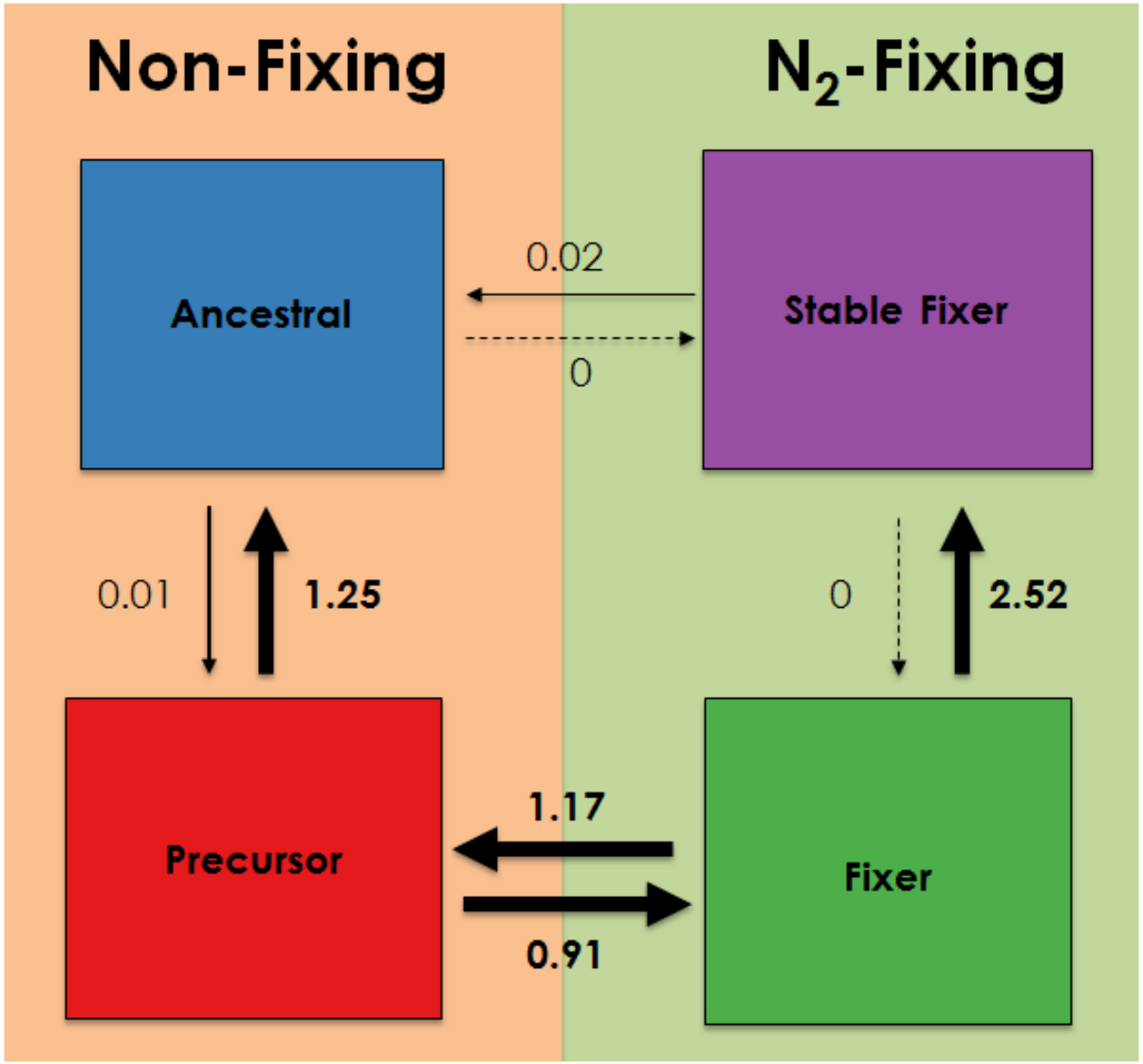

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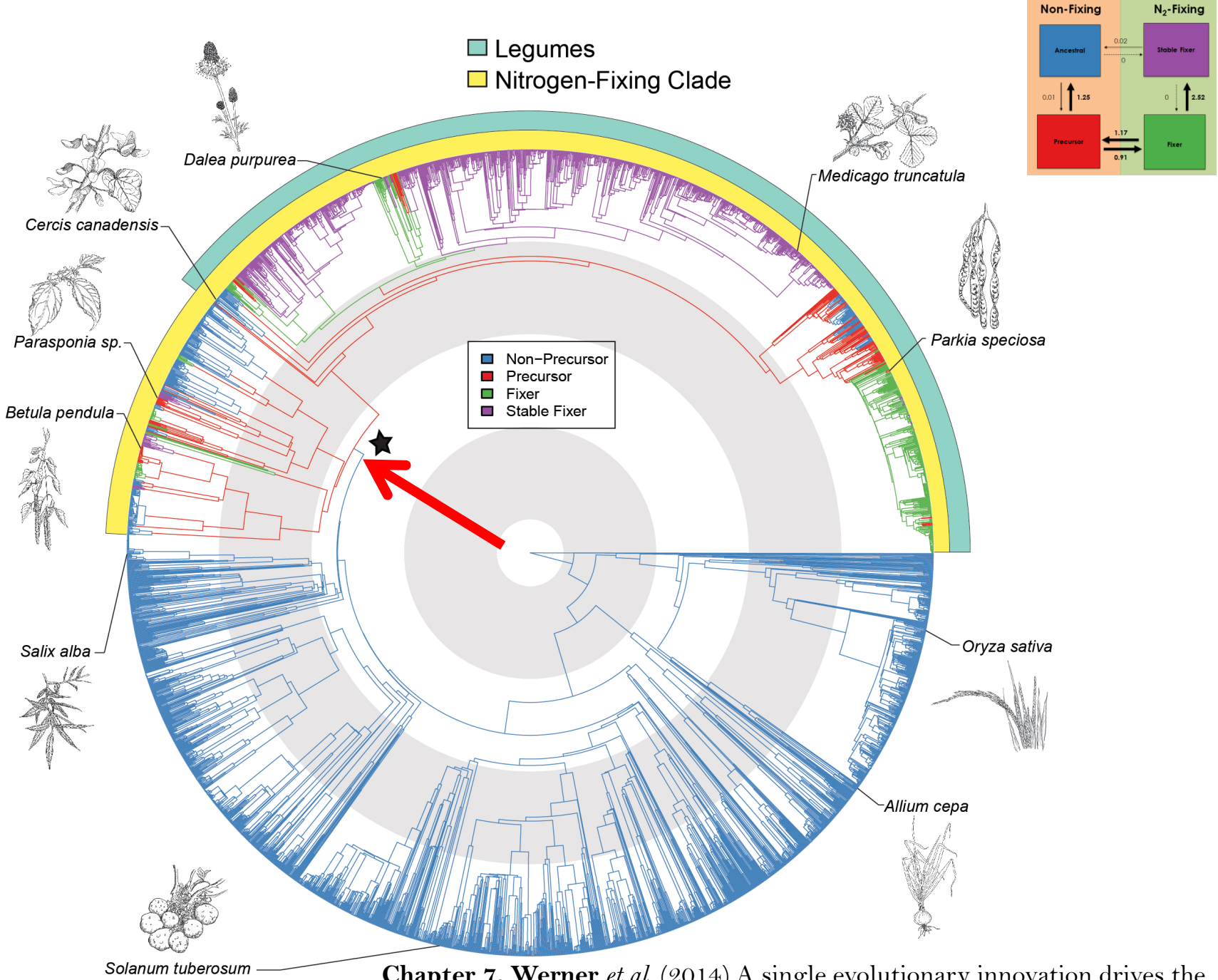

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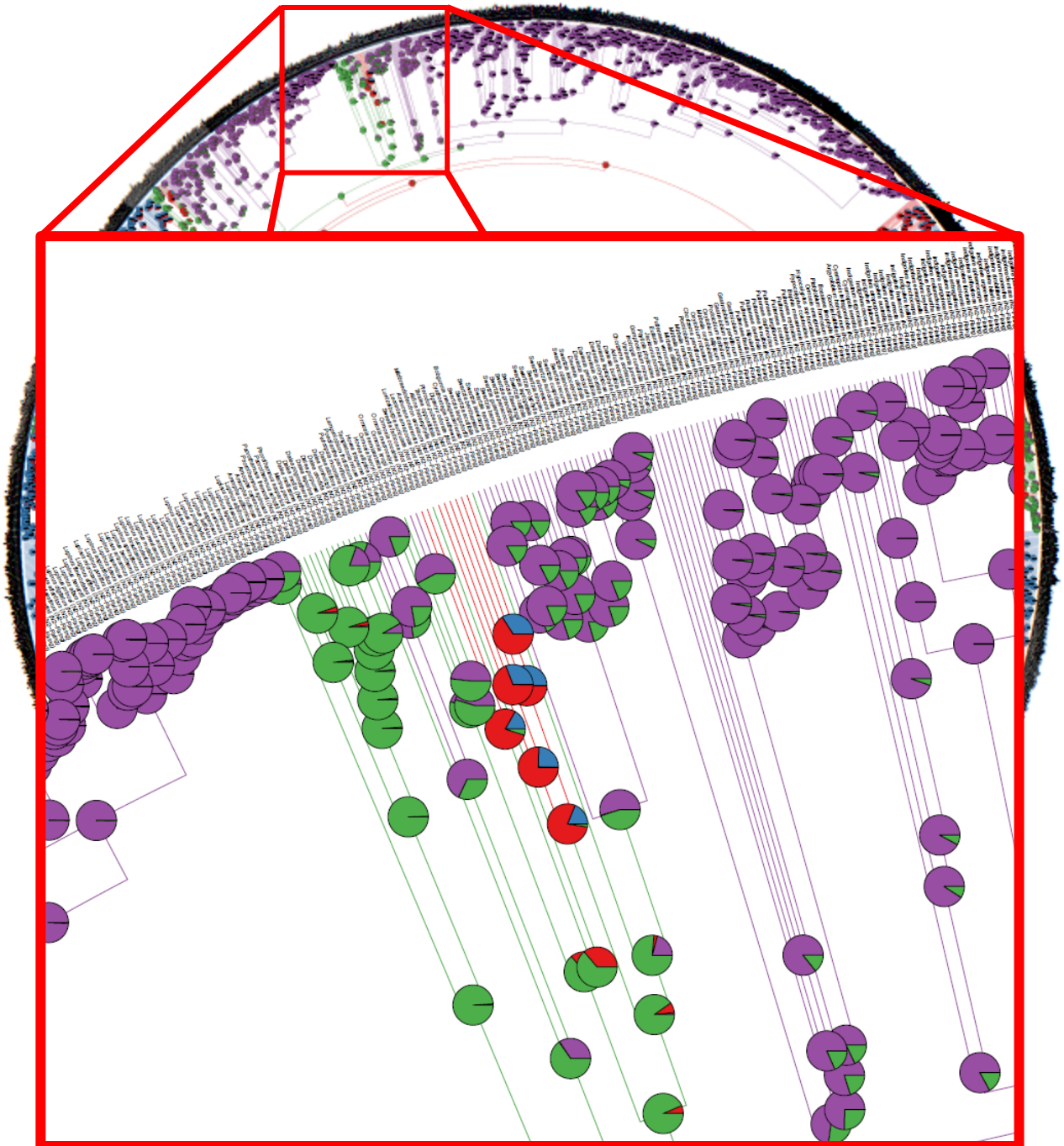
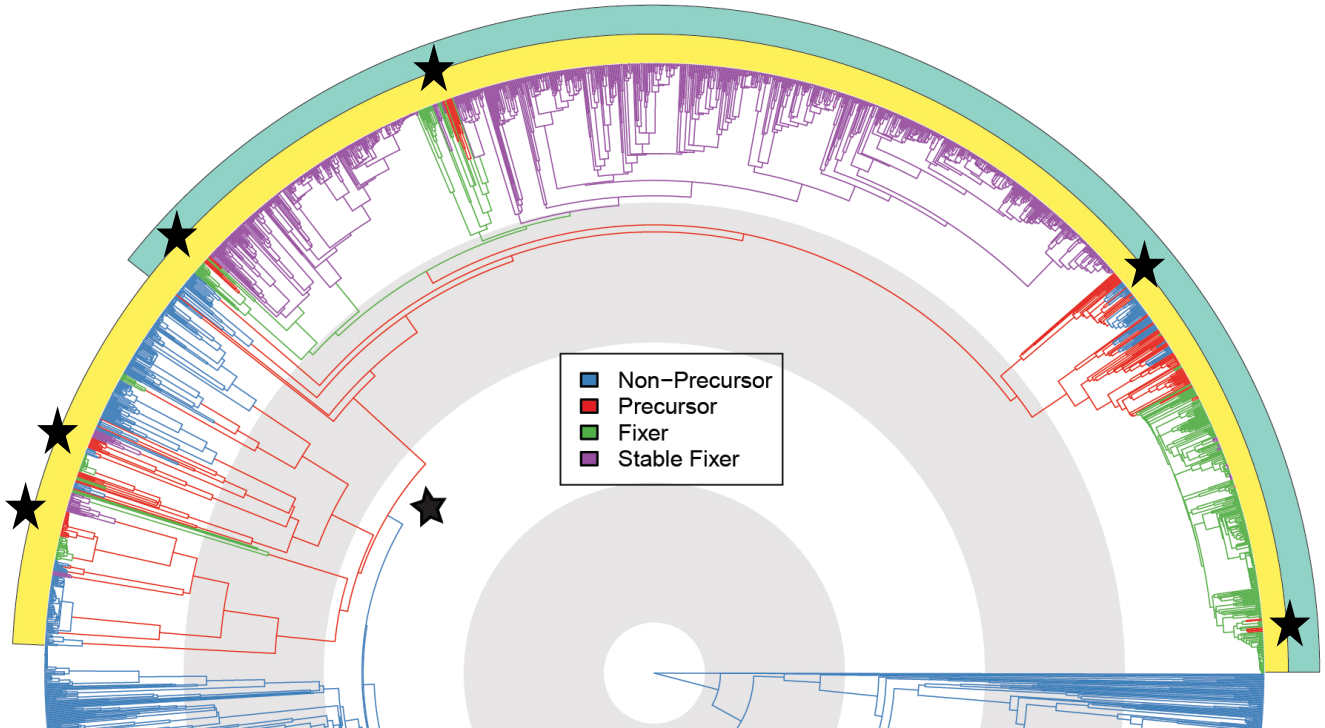


Table 2 | Phylogenetically diverse subset of probable extant precursors

Precursor species (non-fixing)	%
*Acacia eriocarpa** (*Mimosoideae*)	97.1
Trema orientalis (*Cannabaceae*)	91.6
*Mora excelsa** (*Caesalpinioideae*)	89.8
*Parkia speciosa** (*Mimosoideae*)	85.0
Betula pendula (*Betulaceae*)	80.7
*Vouacapoua macropetala** (*Caesalpinioideae*)	73.2
*Cladrastis sikokiana** (*Papilionoideae*)	67.5
Celtis occidentalis (*Cannabaceae*)	62.7
*Nissolia schottii** (*Papilionoideae*)	60.0
Ziziphus mucronata (*Rhamnaceae*)	54.9
*Gleditsia triacanthos** (*Caesalpinioideae*)	54.3



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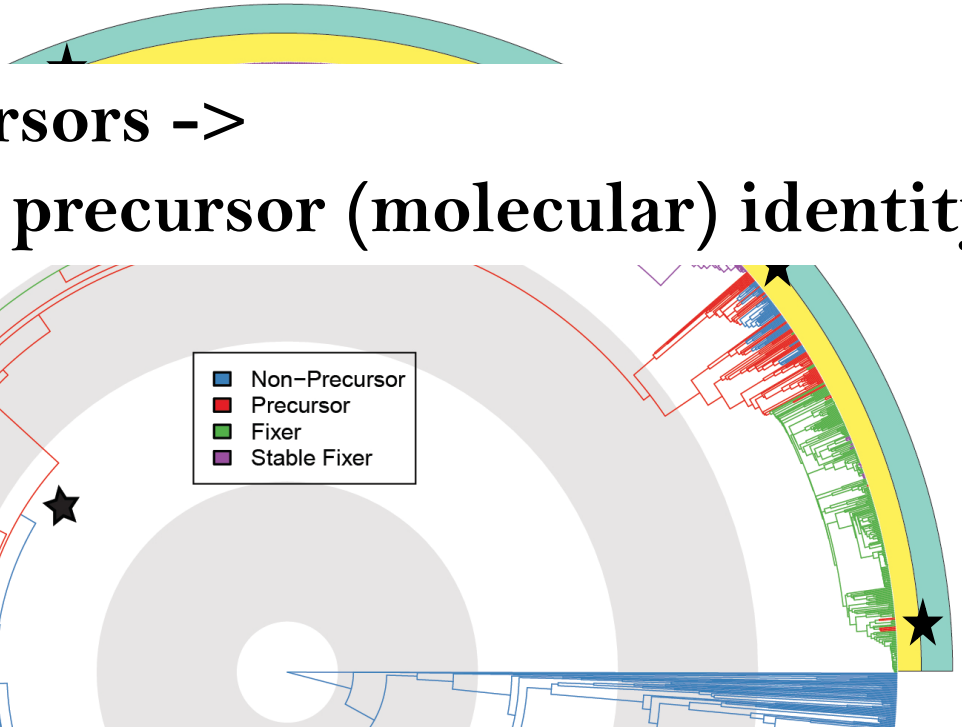


High % precursors ->
Useful to find precursor (molecular) identity

Evolution of Nodulation Consortium

Martin Parniske
(LMU, Munich)
Max Griesman

Katharina Pawlowski
(Stockholm University)

Rene Geurts
(Wageningen UR)

Klaus Mayer
(LMU, Munich)

Giles Oldroyd
(JIC)

Jean-Michel Ane
(UW Madison)

Janet Sprent
(Univ. Dundee)

Gijsbert Werner
(Univ. Oxford)

Shifeng Cheng
(BGI-Shenzhen)

Gane KS Wong
(Univ. Alberta)

Valerie Hocher
(IRD, Montpellier)

Alison Bery
(UC Davis)

Luis Wall
(Quilmes University)

Philippe Normand
(Univ. Lyon)

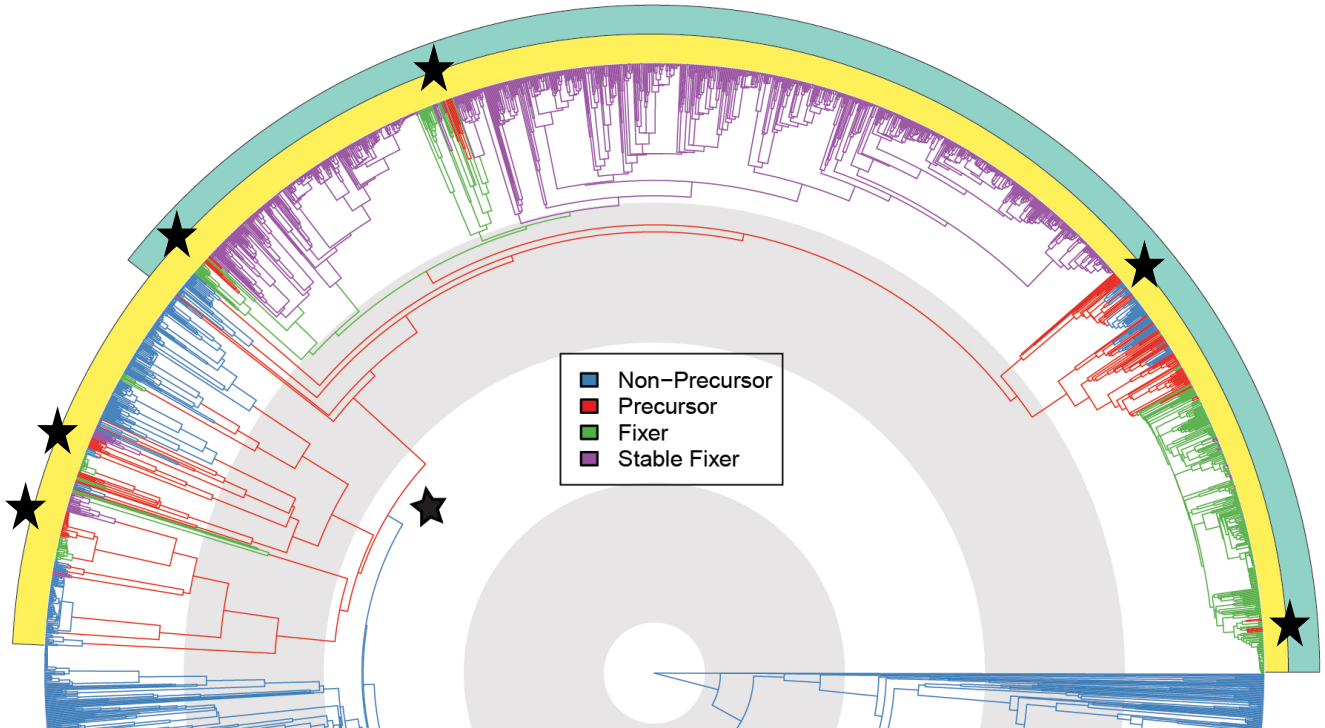
华大基因
BGI

Key Conclusions:

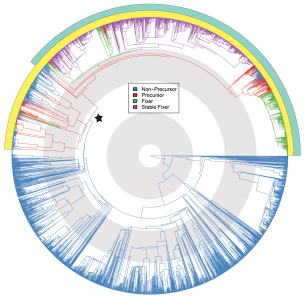
- Ancient cryptic precursors can enable complex traits
- Reconstructions identify practically & scientifically relevant 'hidden' species

Open questions:

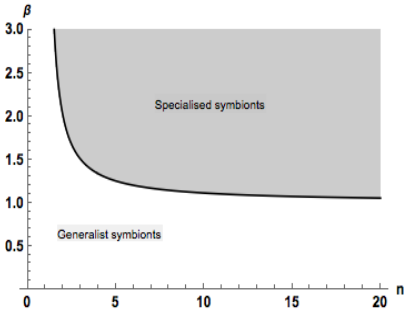
- What is the precursor?
- Further steps towards symbiosis, convergent? Dissimilar?

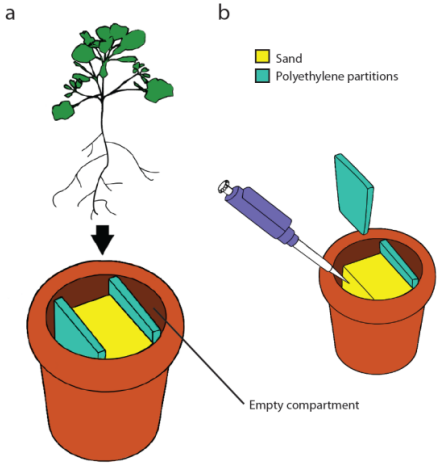


Conclusions & questions



- To understand cooperation
  - Combine: mechanistic, ecological, theoretical & historical perspectives
- Important open questions
  - Relative importance stabilisation mechanisms
  - Effect of context
  - Mechanistic underpinning





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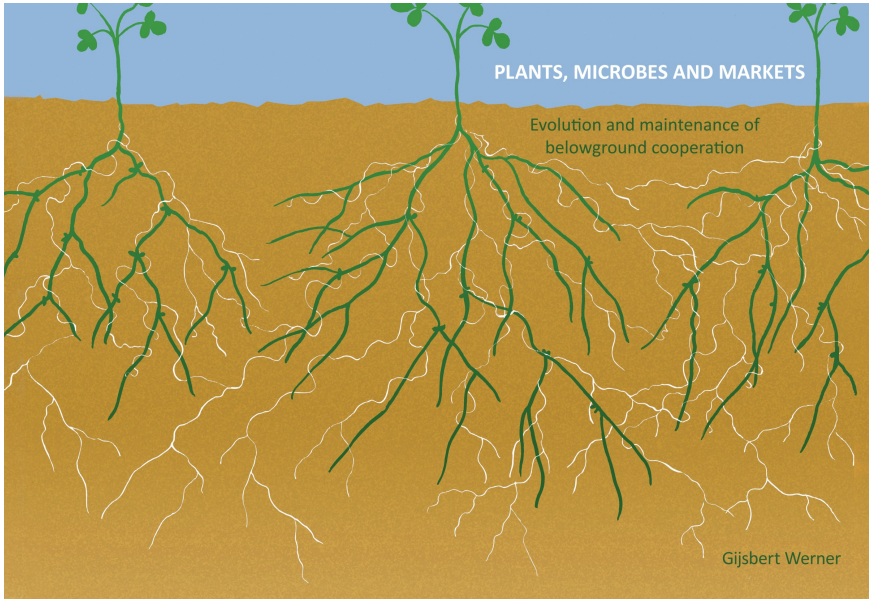

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