Deep Evolutionary Drivers of Cooperation (Loss)

Gijsbert Werner

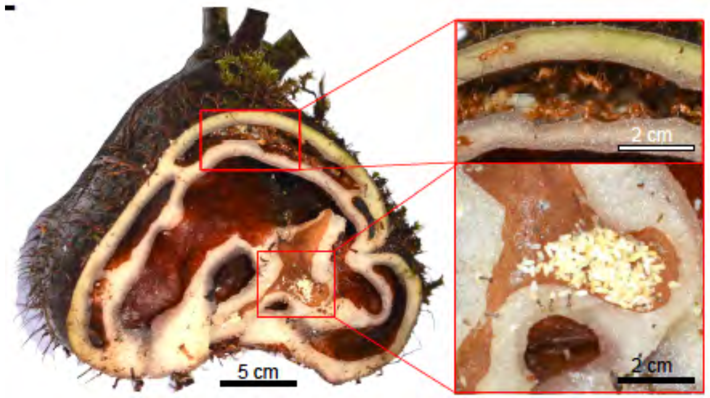
Leiden University, 17 May 2018

UNIVERSITY OF OXFORD

Mutualisms: cooperation between species

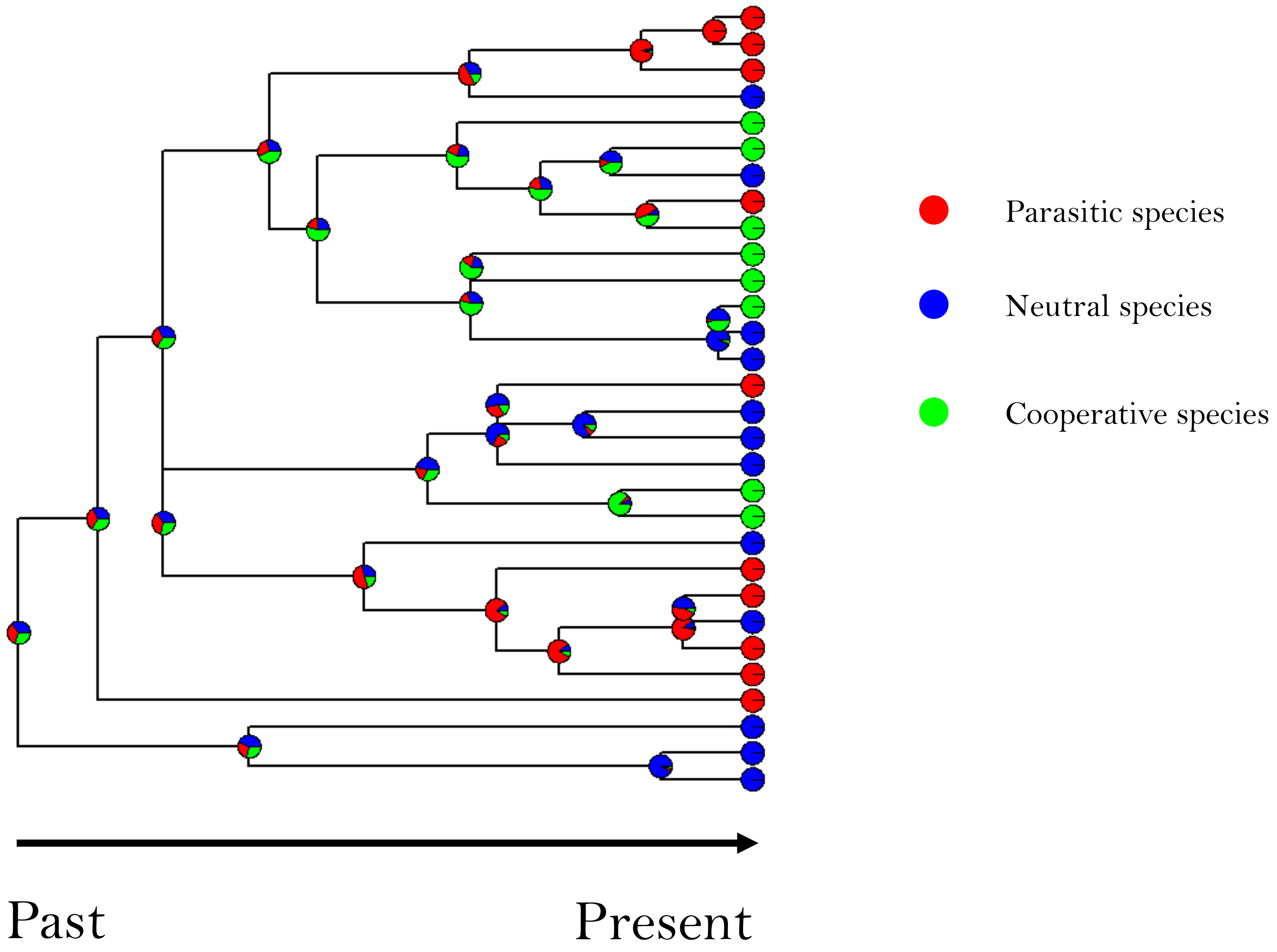
1. Cheating can undermine cooperation

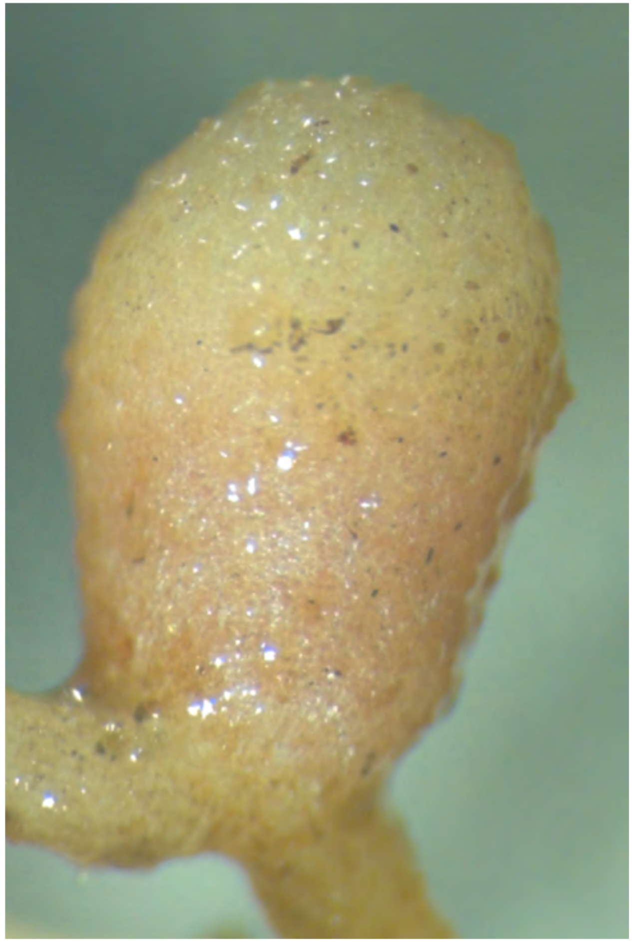
2. Mutualisms require complex adaptations



Picture Guillaume Chomicki, University of Oxford

Phylogenetic comparative reconstruction of cooperation



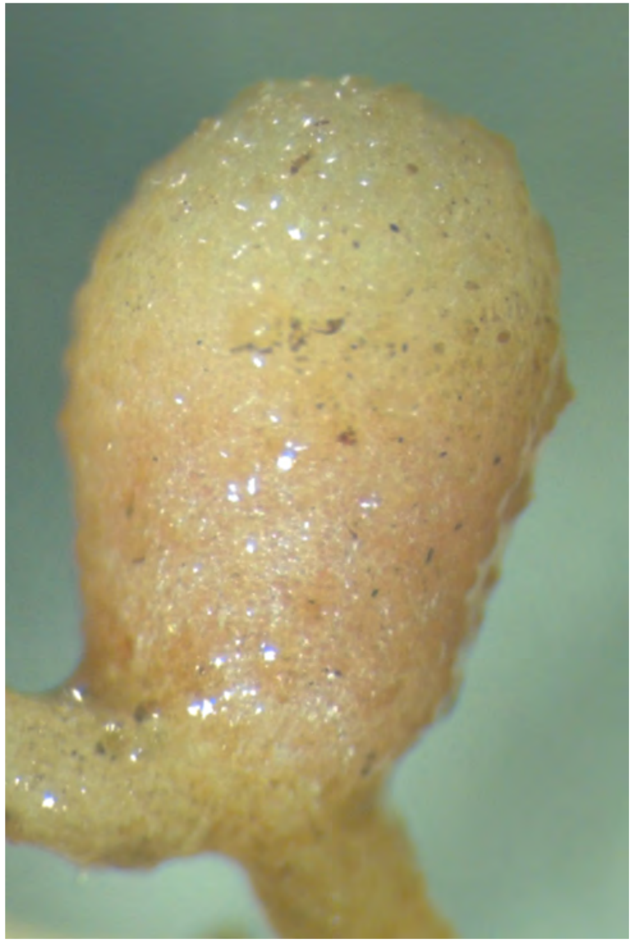


Symbiotic N_2-fixation

Gain of cooperation

Arbuscular mycorrhizal fungi (AMF)

Loss of cooperation



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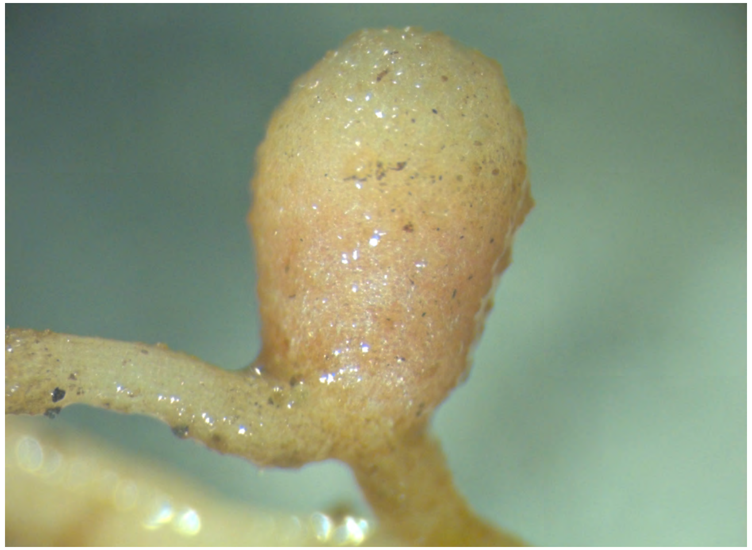

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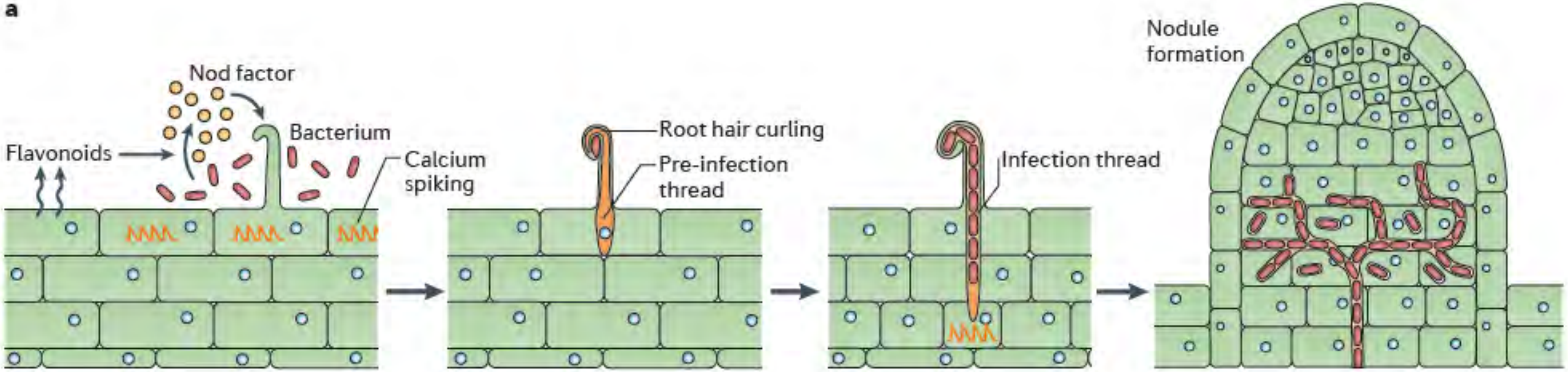


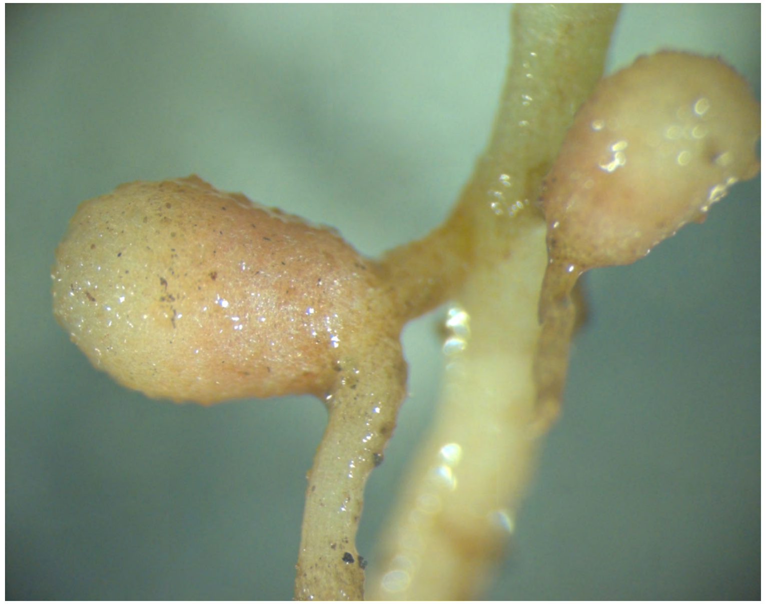
Nod factor
Flavonoids
Bacterium
Calcium spiking
Root hair curling
Pre-infection thread
Infection thread
Nodule formation

Fabaceae (legumes)

Betulaceae

Cannabaceae

Nodulation found in ten plant families, four orders

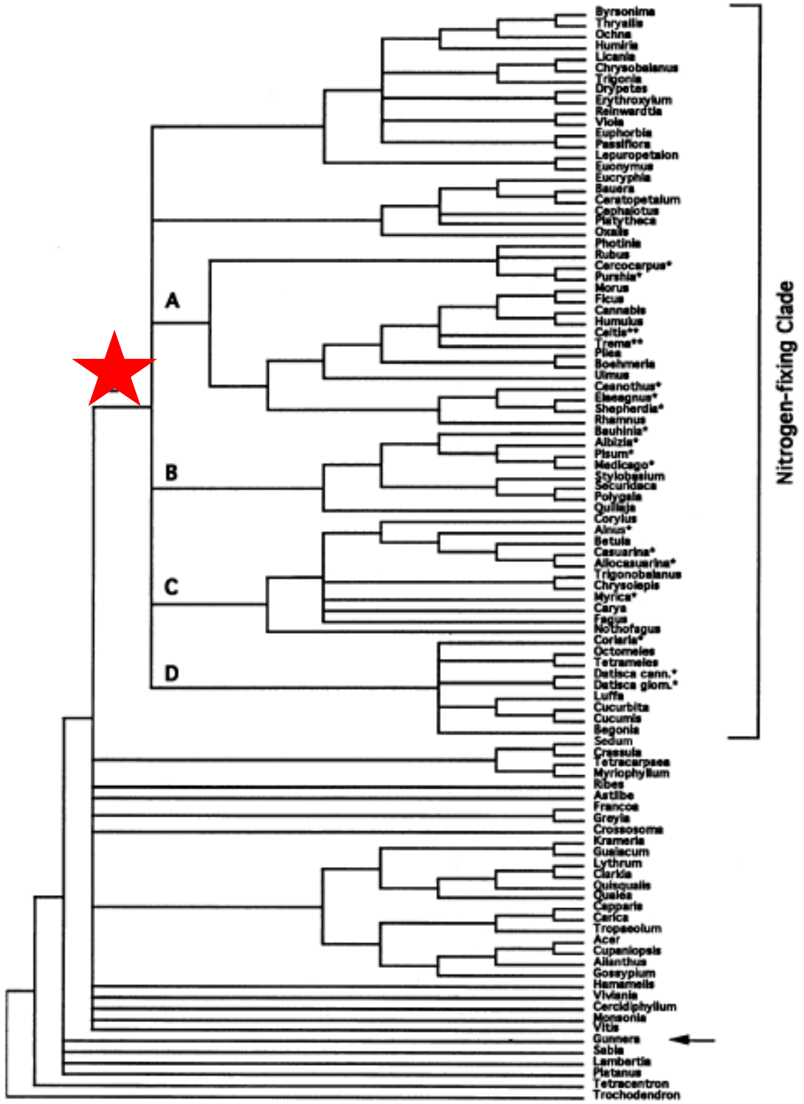



©2011 Julie Gomez

Ten families, lots of origins.

Nodulation is easy to evolve, mutualism arises commonly?

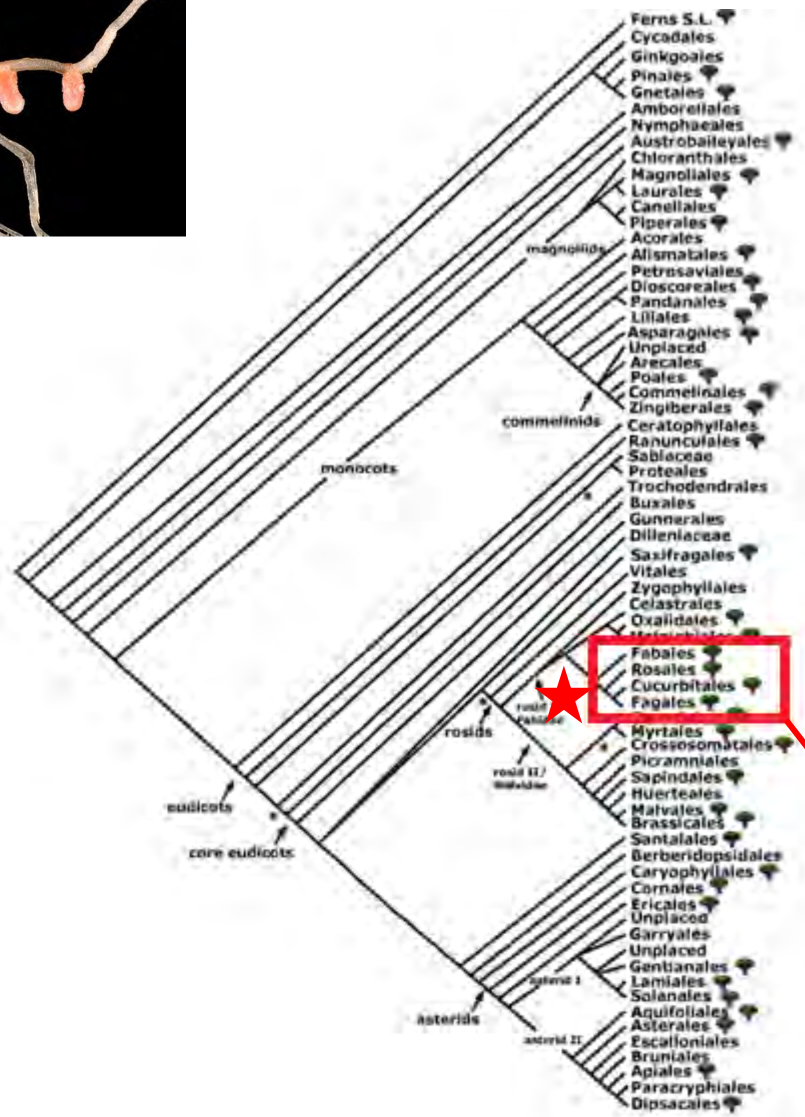
Good news for transfer of symbiosis to crops?

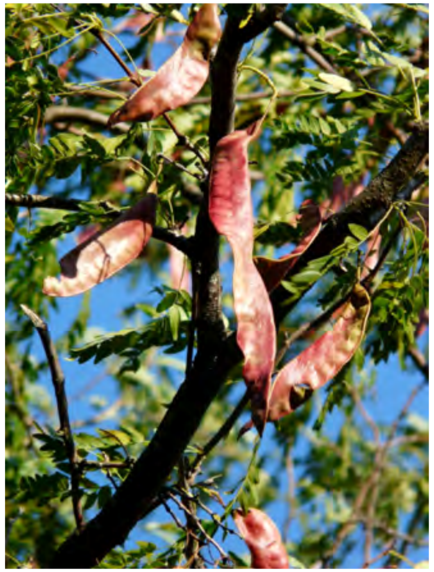


A (single) predisposition for symbiotic N-fixation?

Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms

DOUGLAS E. SOLTIS*, PAMELA S. SOLTIS*, DAVID R. MORGAN†, SUSAN M. SWENSEN‡, BETH C. MULLIN§, JULIE M. DOWD¶, AND PETER G. MARTIN¶||

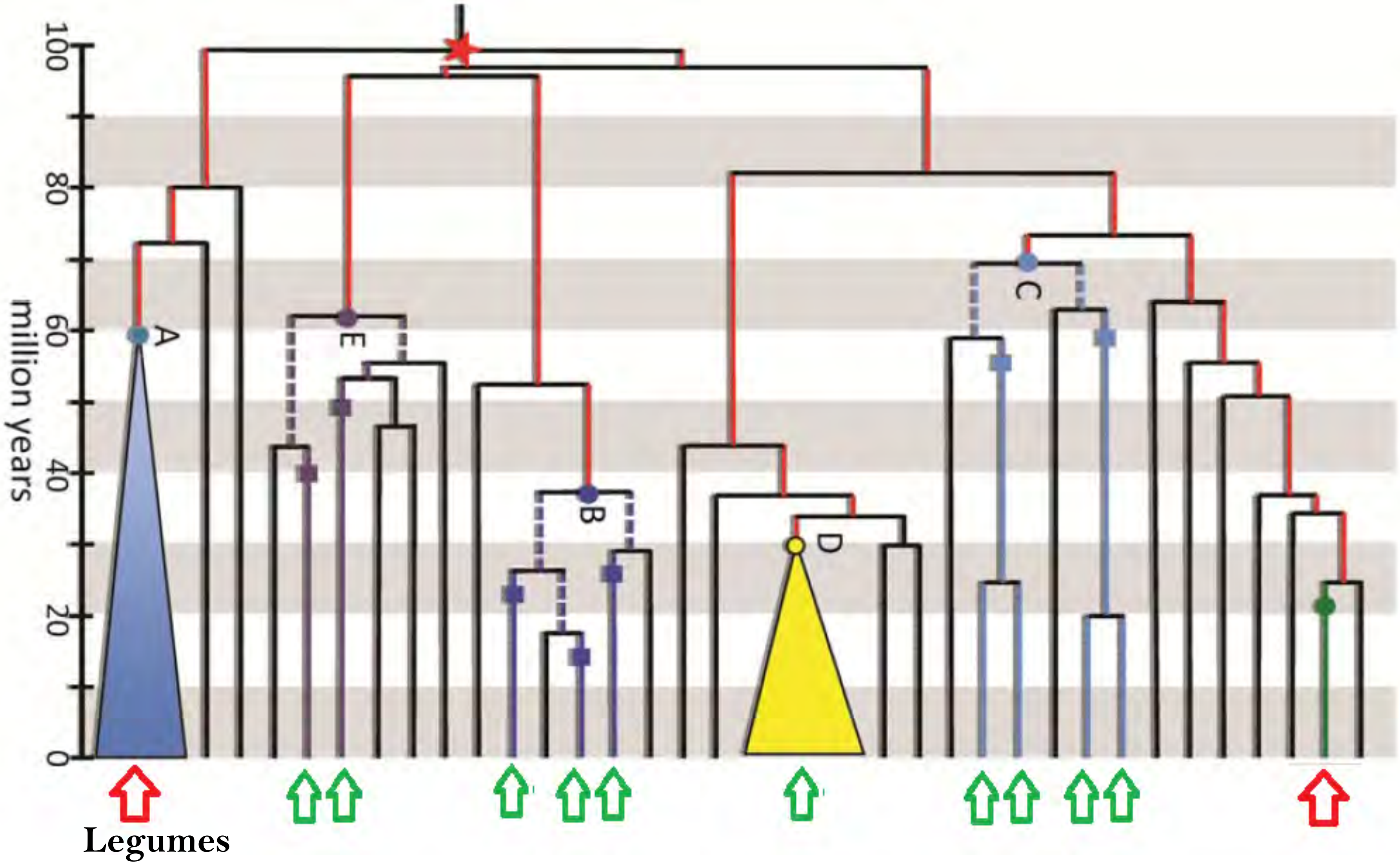




Nitrogen-fixing clade

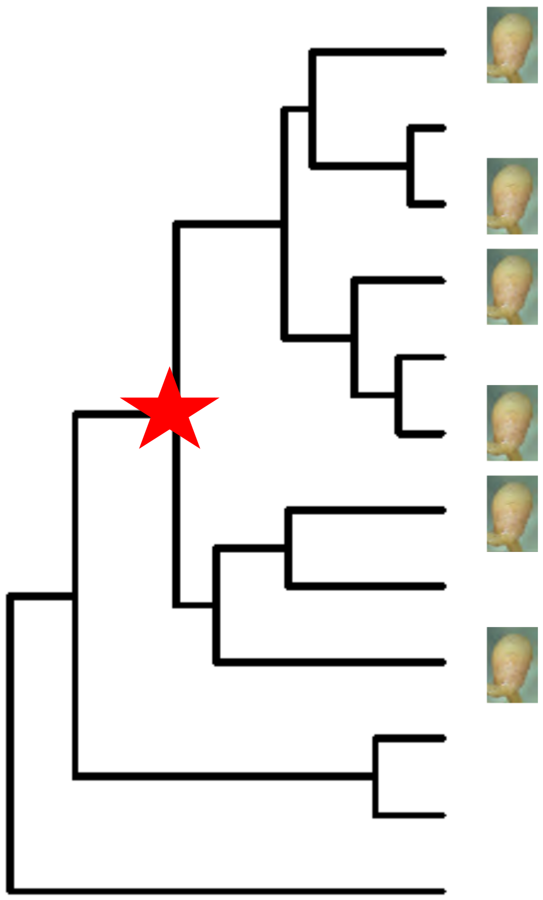
Symbiotic N_2-fixation in angiosperms clustered in NFC...

Stevens, P. F. (2001). Angiosperm Phylogeny Website



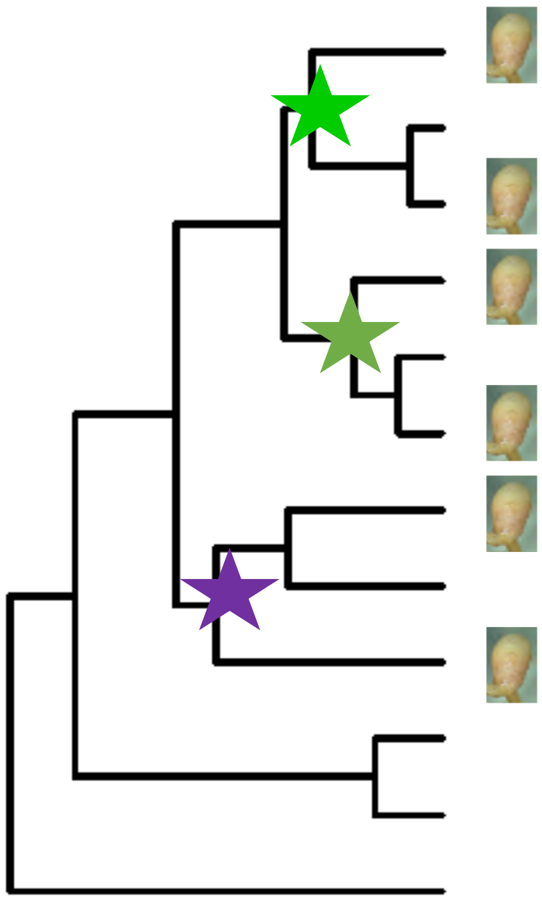
…and has a complicated distribution

Adapted from: Doyle 2011 *MPMI*



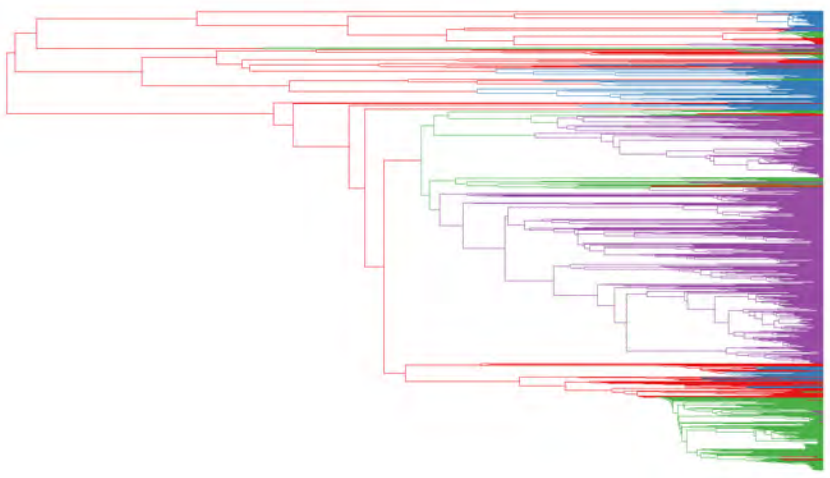
Shared evolutionary innovation..

or



..independent pathways?

From verbal accounts to quantitative phylogenetic reconstruction



Part 1: Database

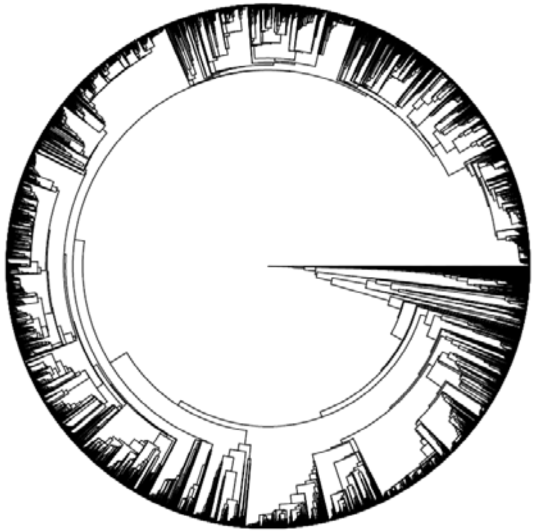
Trifolium alexandrinum	Yes
Solanum tuberosum	No
Phaseolus vulgaris	Yes
Alnus rubra	Yes
Lupinus angustifolius	Yes

DRYAD

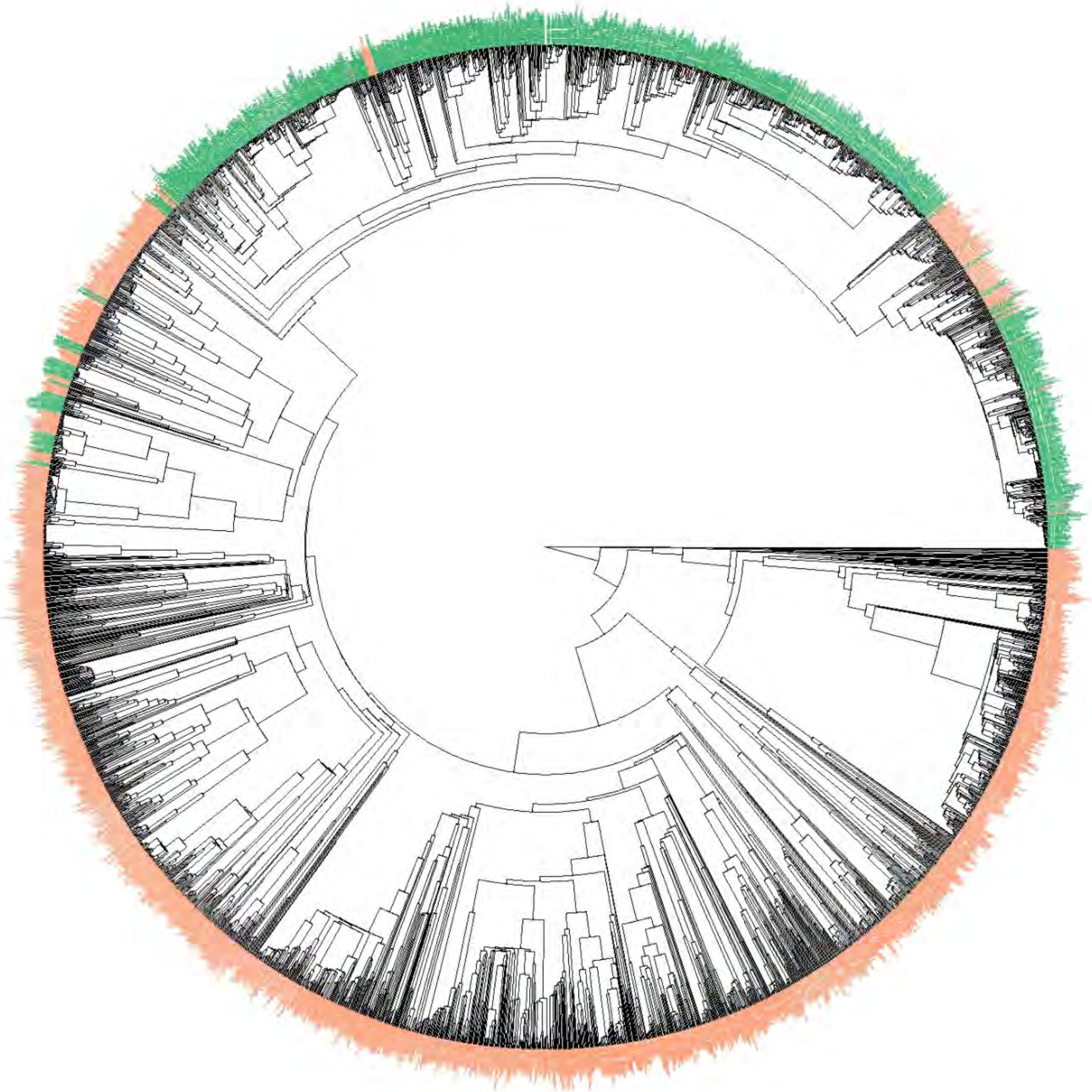
Prof. Janet Sprent, University of Dundee
N2-fixation database, Legume phylogenetics

Dr. Jens Kattge, Max Planck
N2-fixation database, TRY

Part 2: Phylogeny



Zanne et al., 2014. Nature



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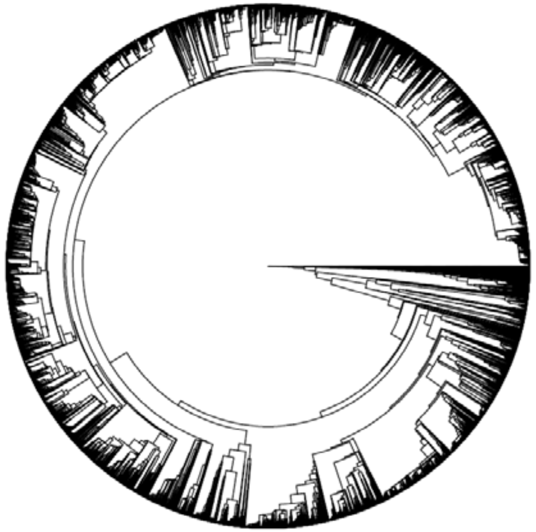

Zanne et al., 2014. Nature

Reconstruction Method

Non-fixing $\underset{\text{Loss}}{\overset{\text{Gain}}{\rightleftarrows}}$ Fixing

Beaulieu et al., 2013. Syst Biol

Dr. William Cornwell, UNSW

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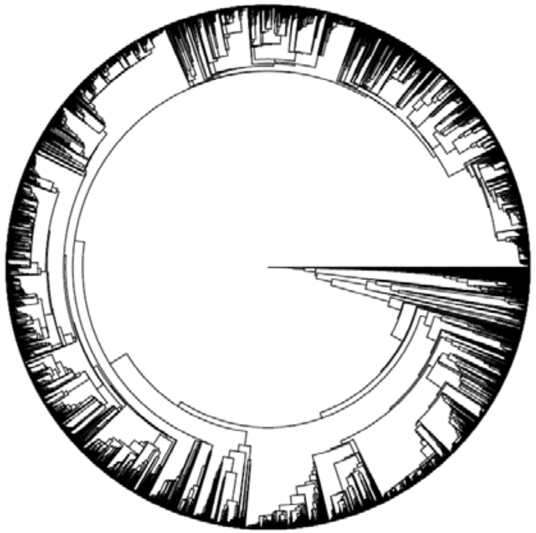

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Deep time (>200 MYA) & thousands of species → single speed of evolution unlikely

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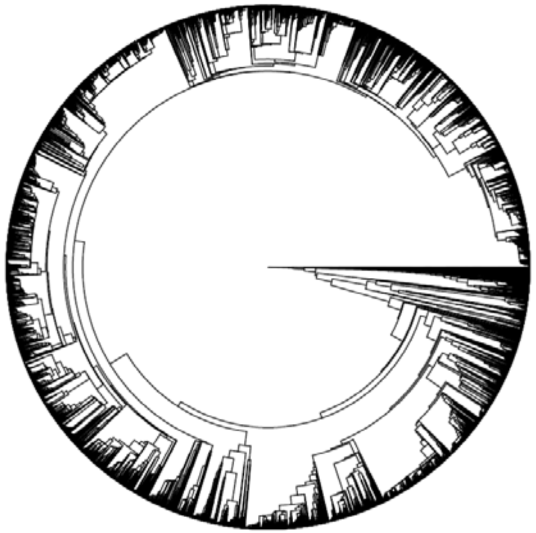

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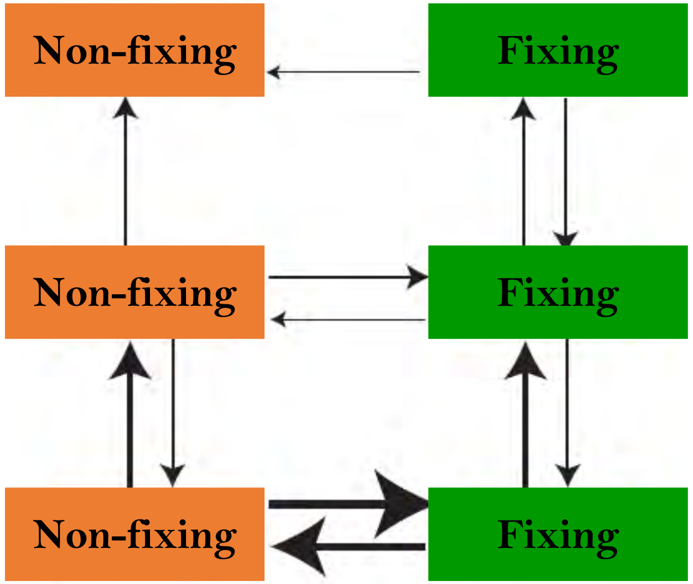

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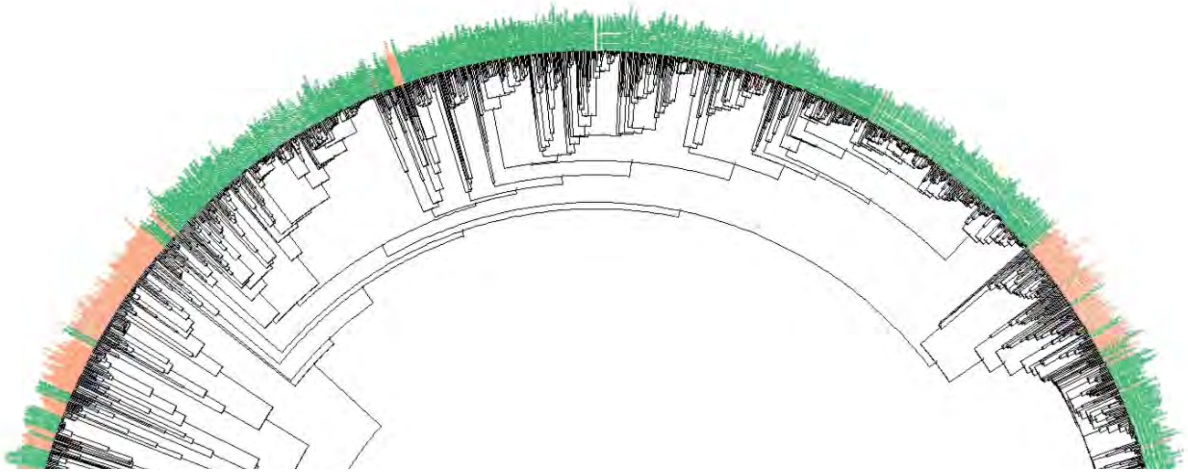
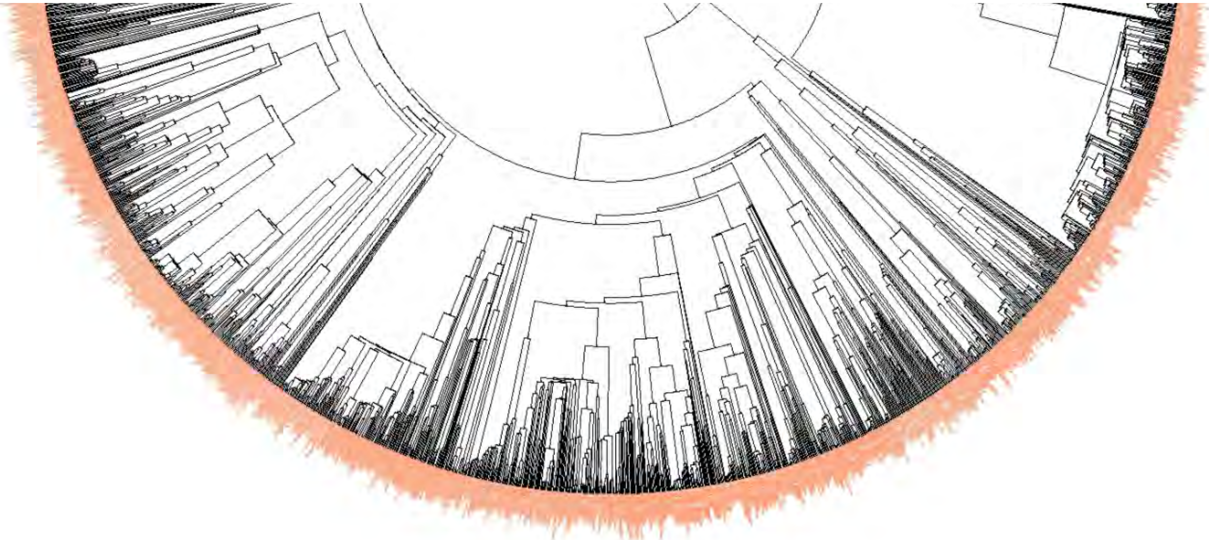
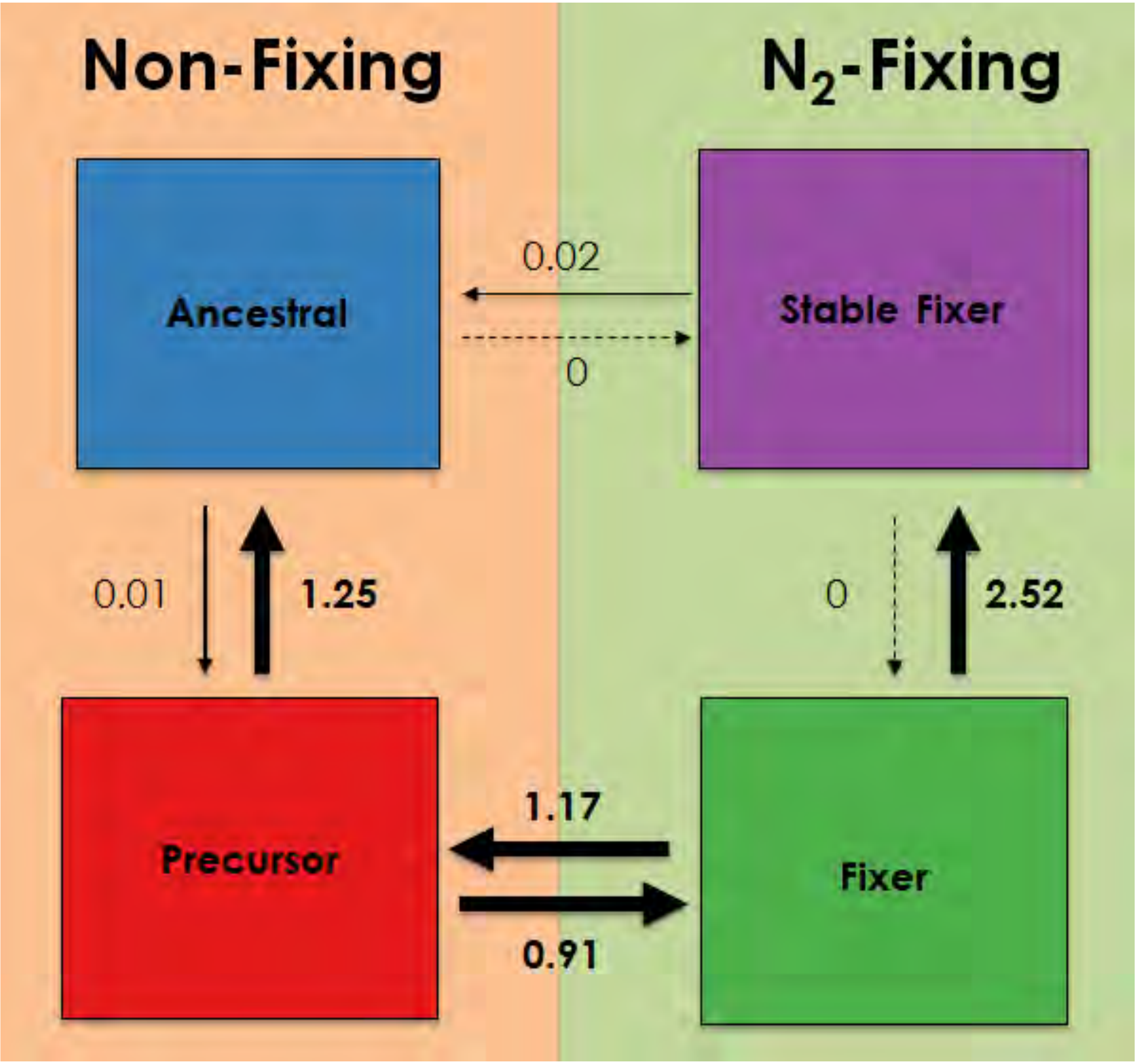


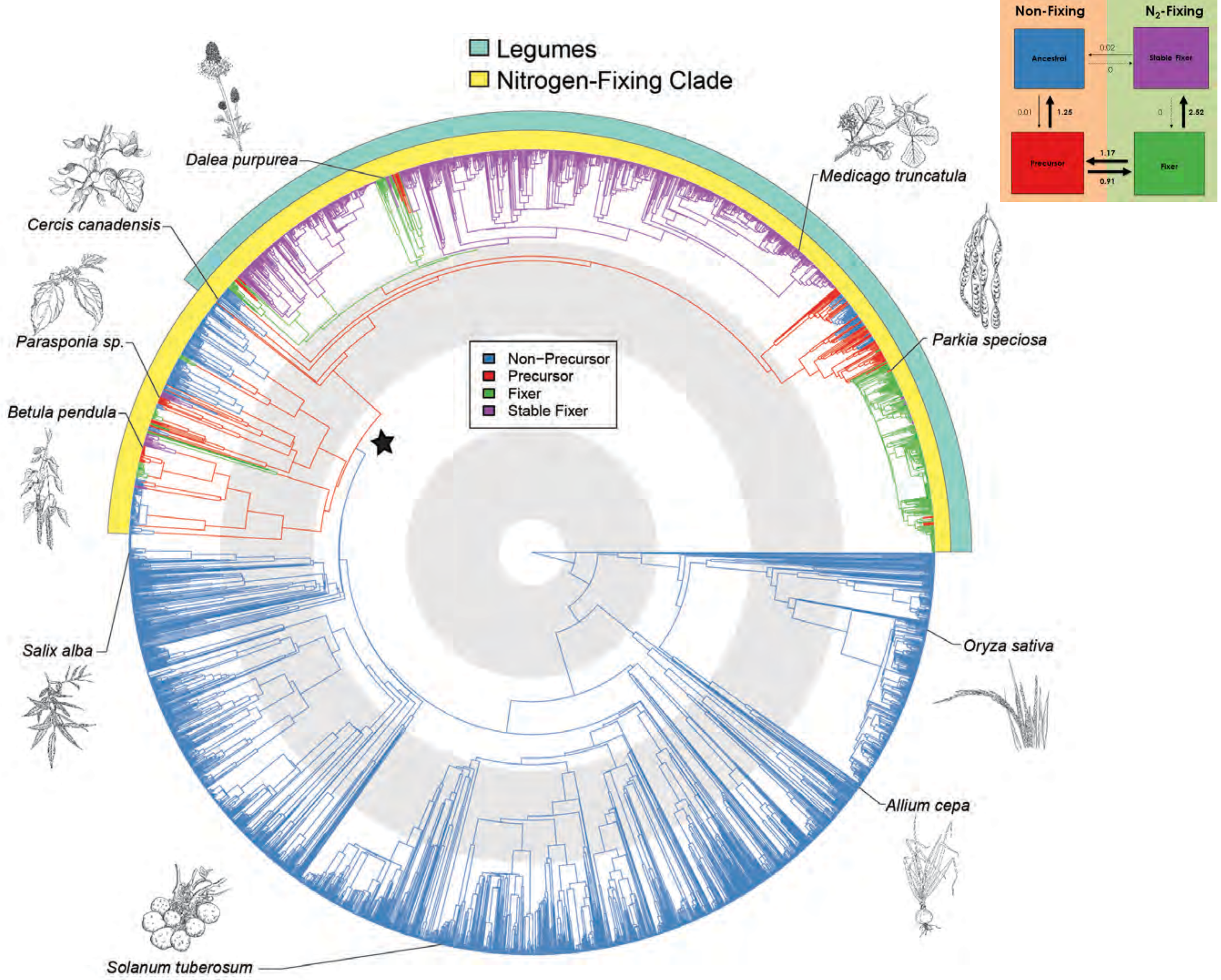
Single Speed Model: Very bad fit (AIC-weight <0.01%)

Best: Model with 2 Rate Classes (AIC-weight 55%)





Werner, Cornwell, Sprent, Kattge & Kiers (2015) *Nature Communications*



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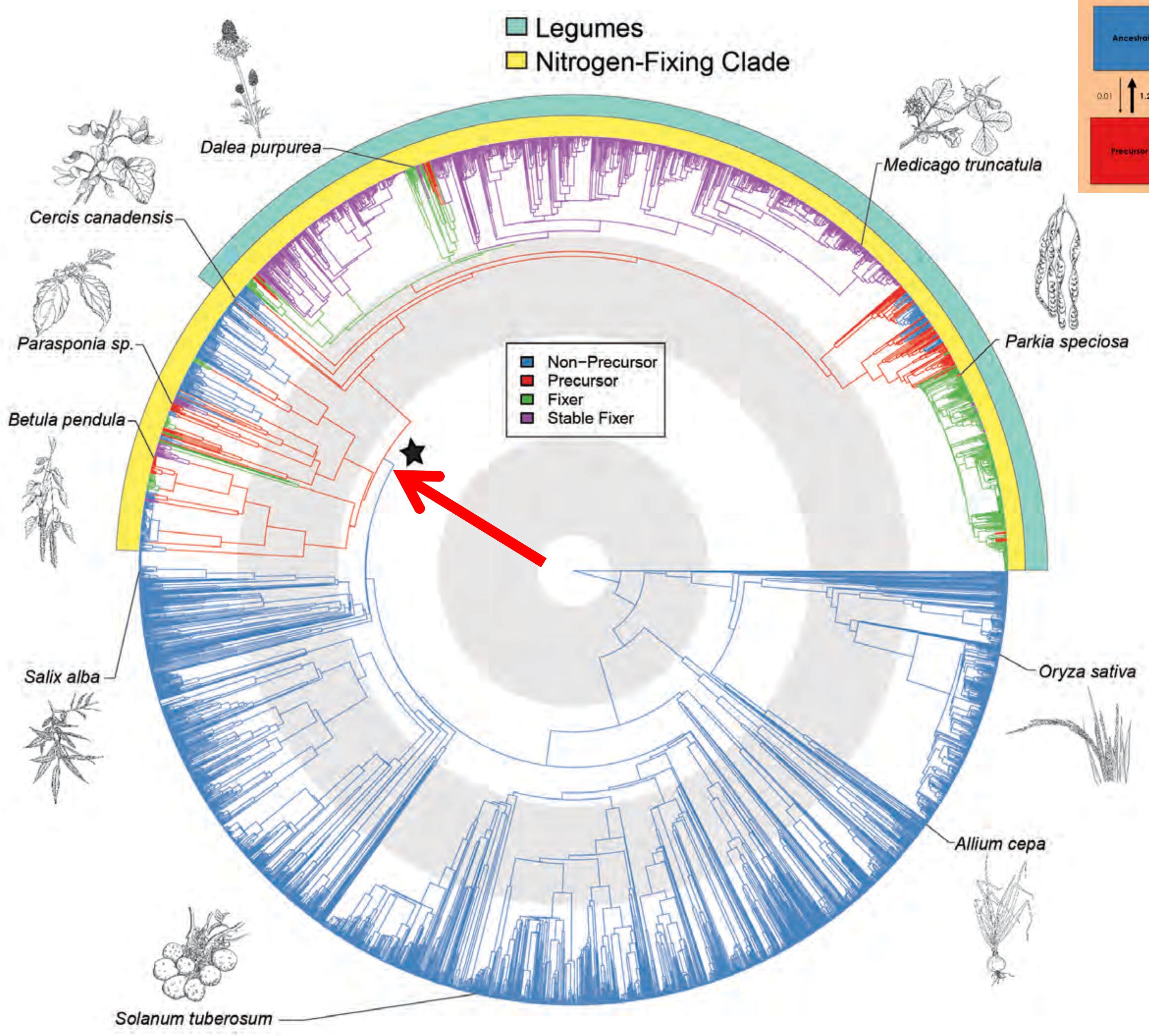
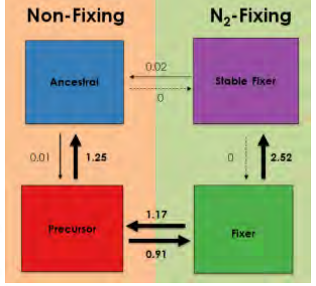


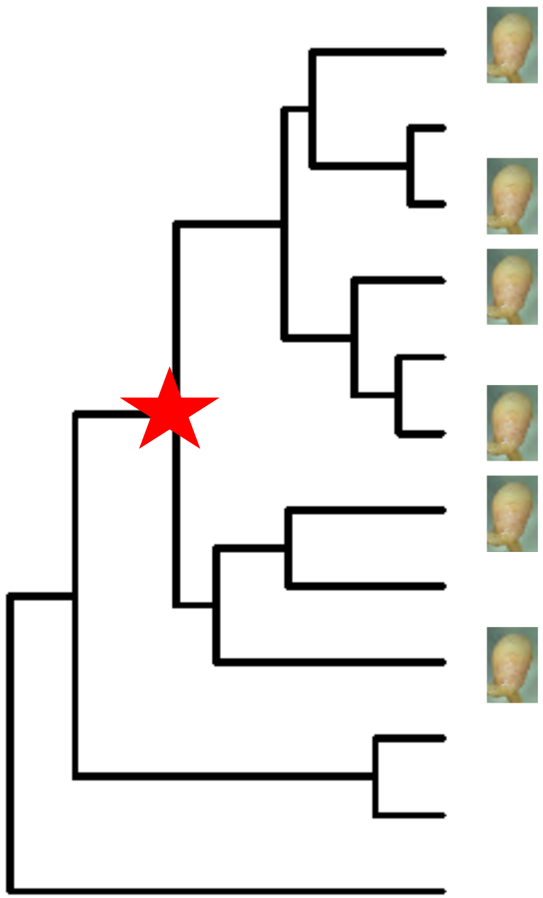


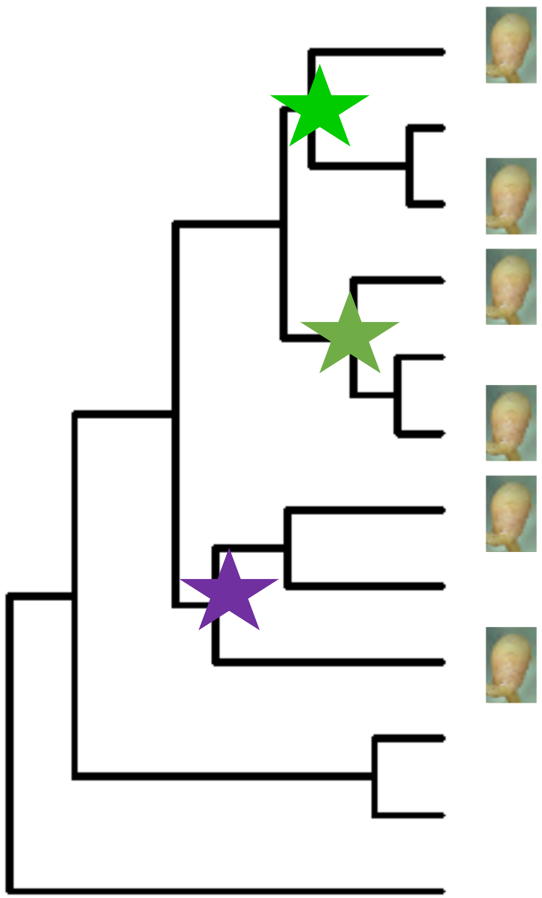
Werner, Cornwell, Sprent, Kattge & Kiers (2015) *Nature Communications*

Number of evolutionary events

Event	Number	SD
Evolution of Precursor	1.01	0.65
Loss of Precursor	16.71	3.21
Evolution of Fixing	8.15	2.47
Loss of Fixing	9.93	2.80

Werner, Cornwell, Sprent, Kattge & Kiers (2015) *Nature Communications*



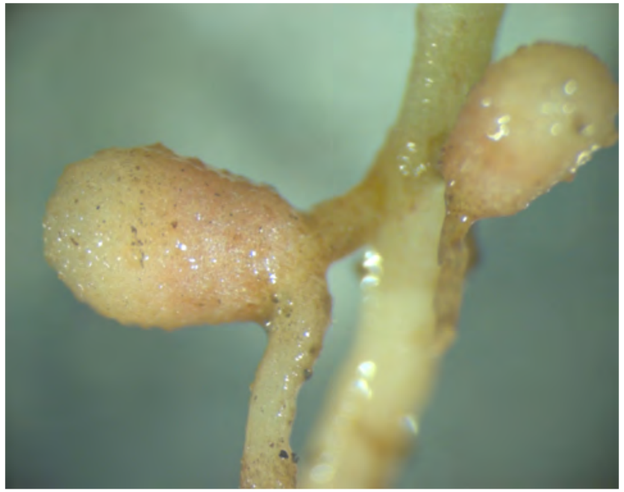


Shared evolutionary innovation..

or

..independent pathways?

1. Precursor → 2. Symbiotic N2-fixation → 3. Stable Fixer



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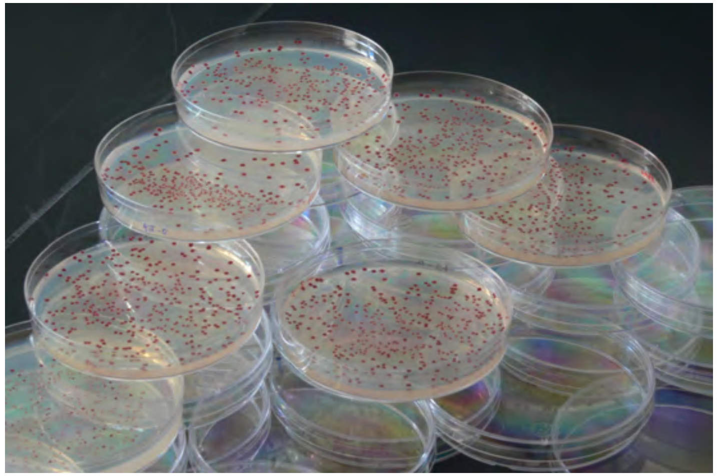
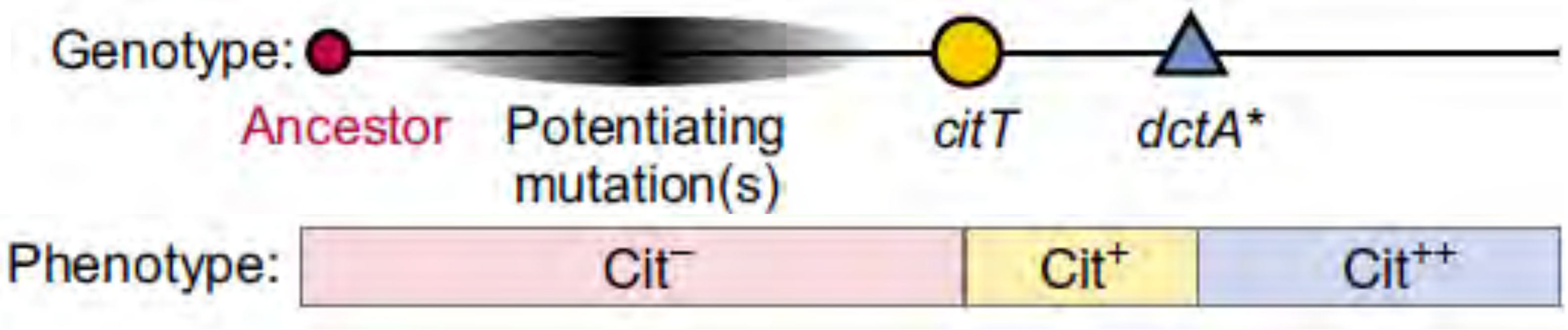


Experimental evolution of complex traits:

1. Potentiation → 2. Actualization → 3. Refinement



Blount et al. 2012, Nature; Quandt et al. 2014, PNAS

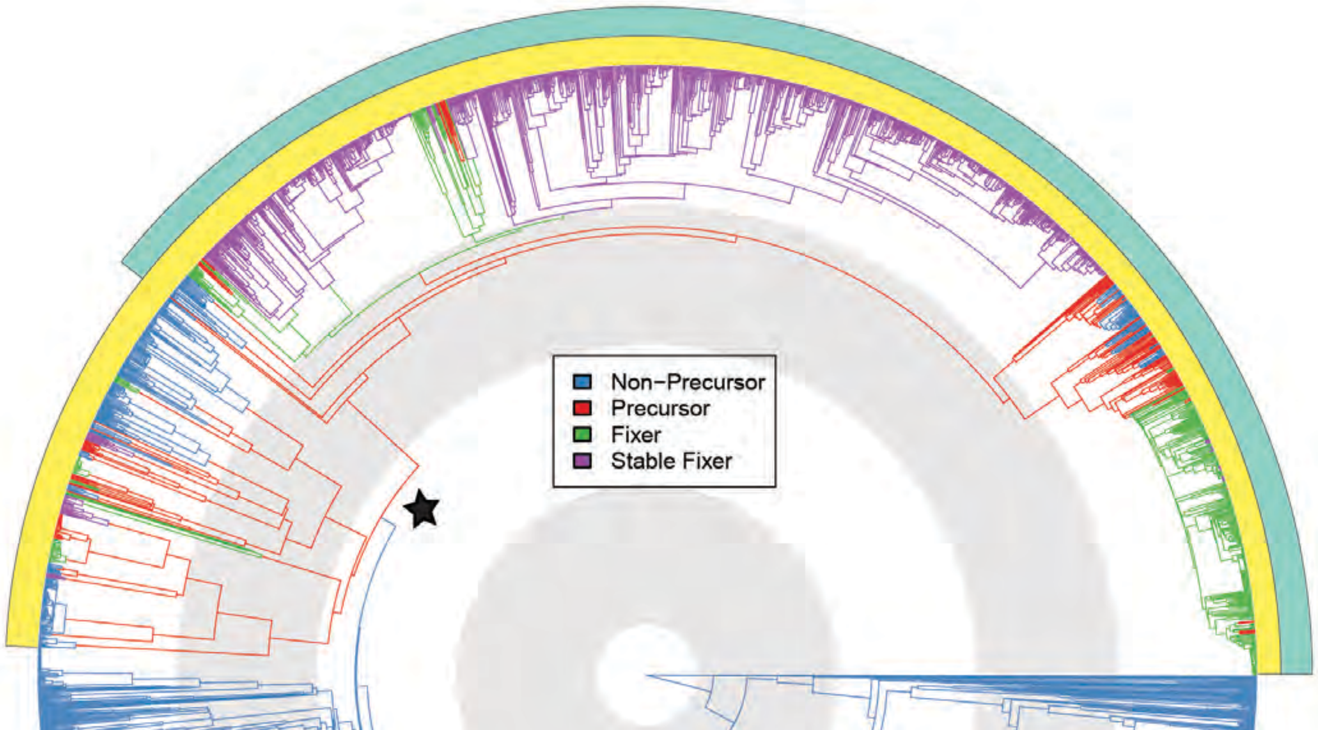
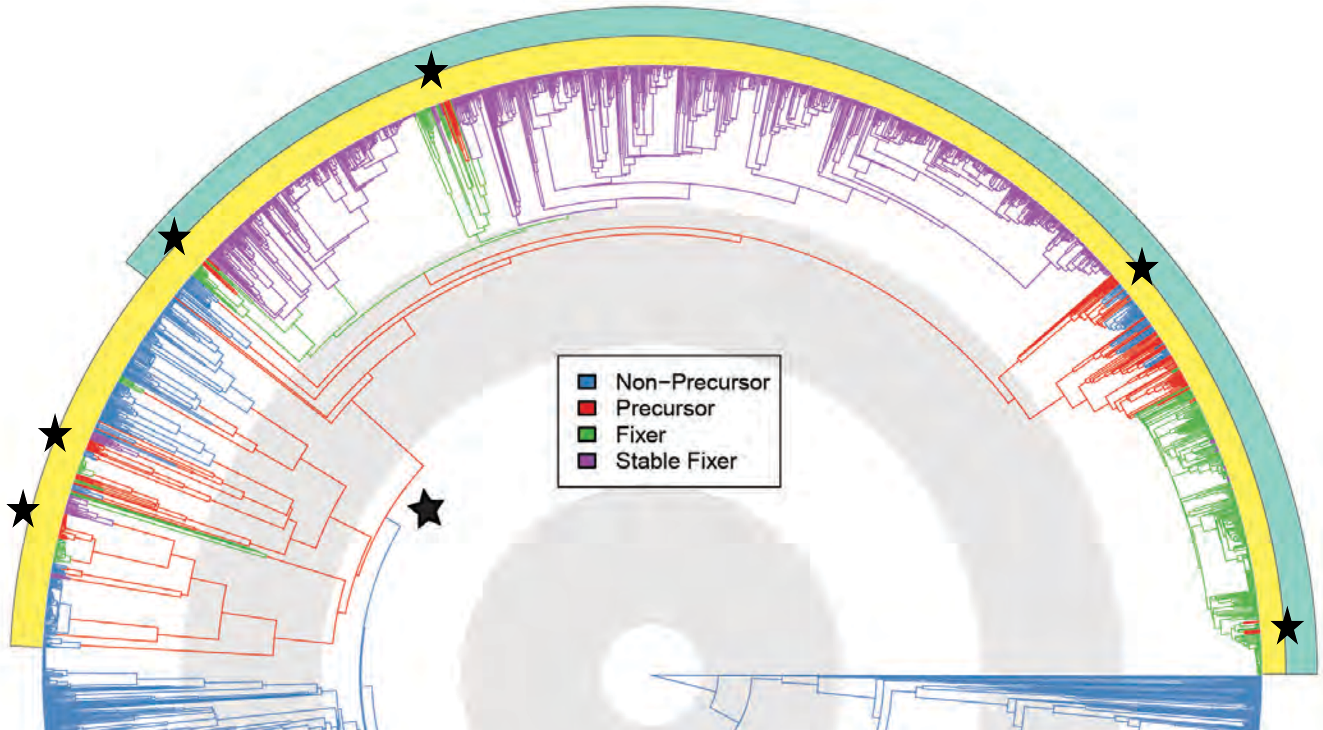
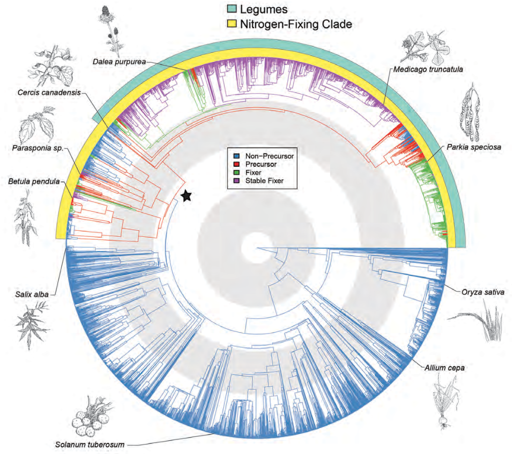

Non−Precursor
Precursor
Fixer
Stable Fixer

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

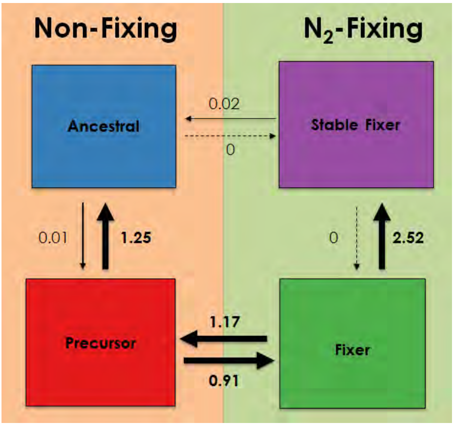


Key events identified



Novel states found

Precursor well supported



Identified current precursor species

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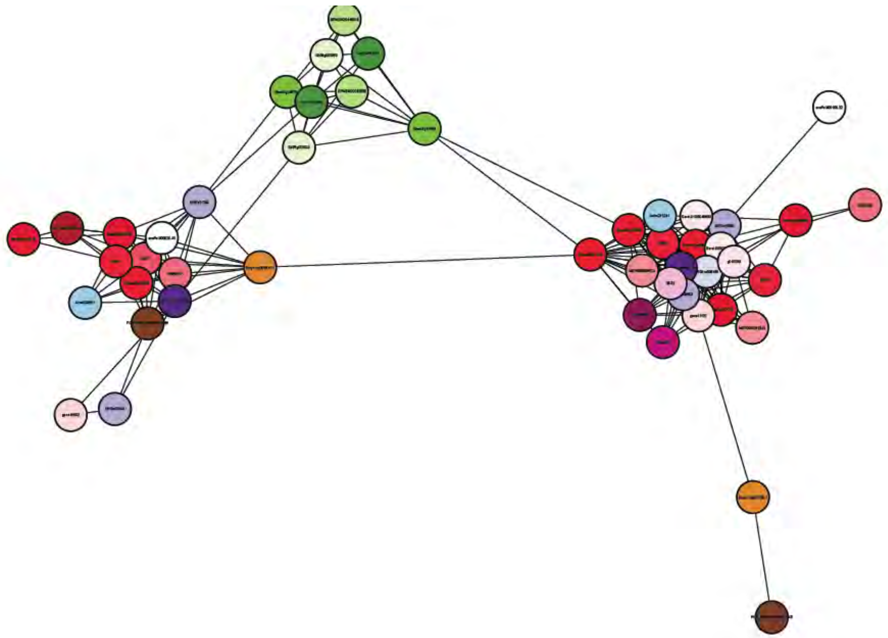
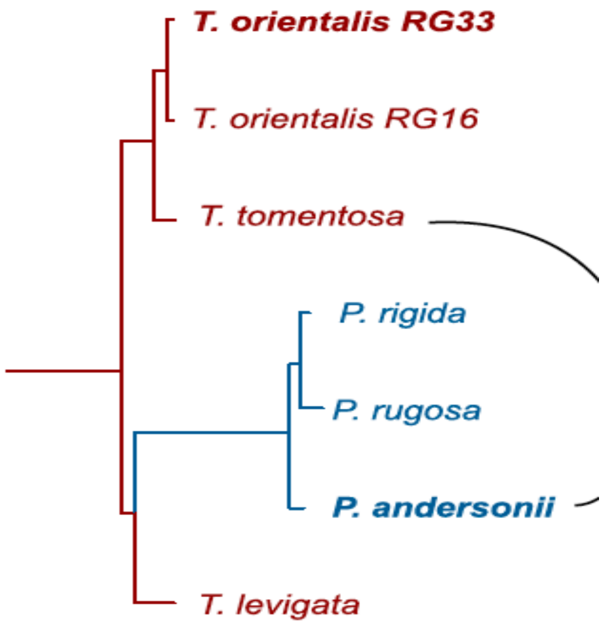


Phylogenomics & mapping gene (families)

Evolution of Nodulation Consortium

华大基因
BGI

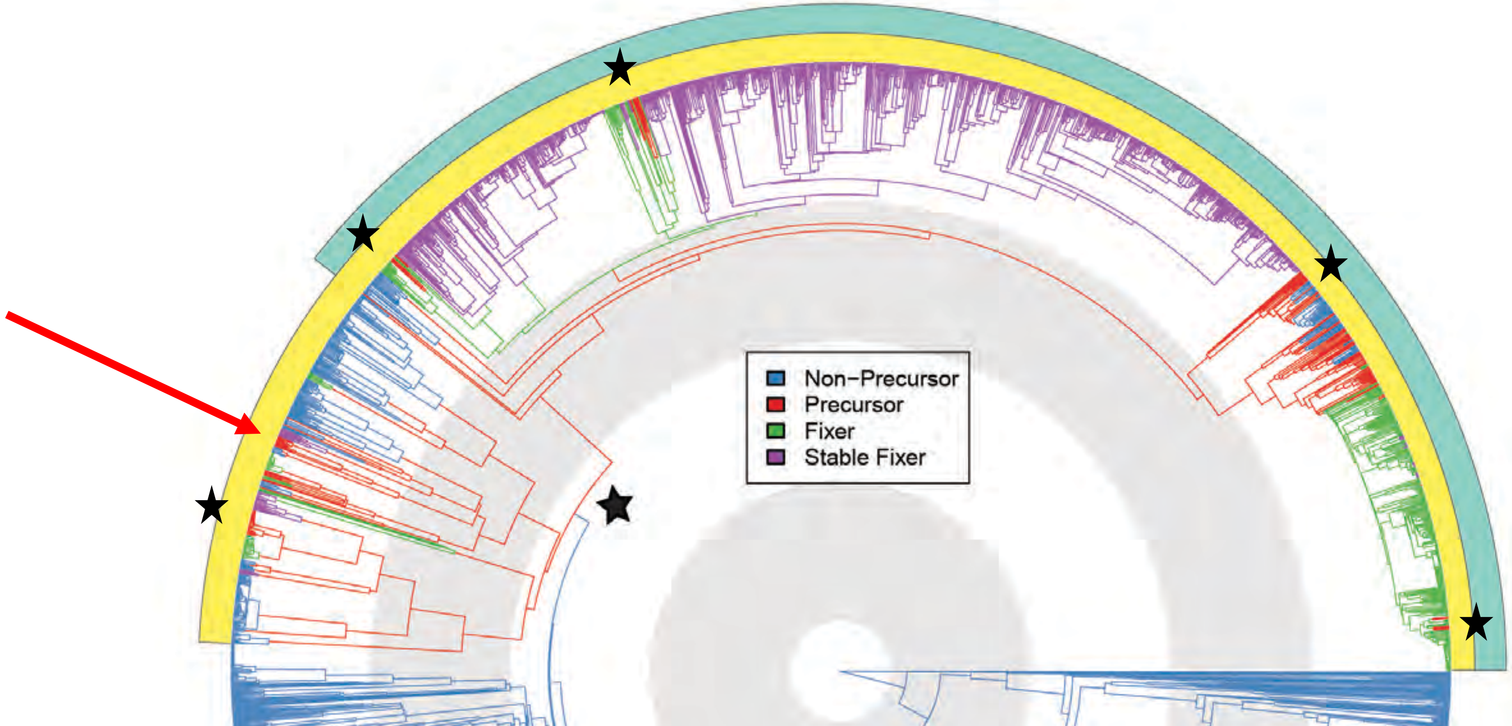


Rene Geurts, Wageningen

Parasponia/Trema-Cluster

Parasponia fixes, Trema does not

Only one outside the legumes using rhizobial bacteria


Non−Precursor
Precursor
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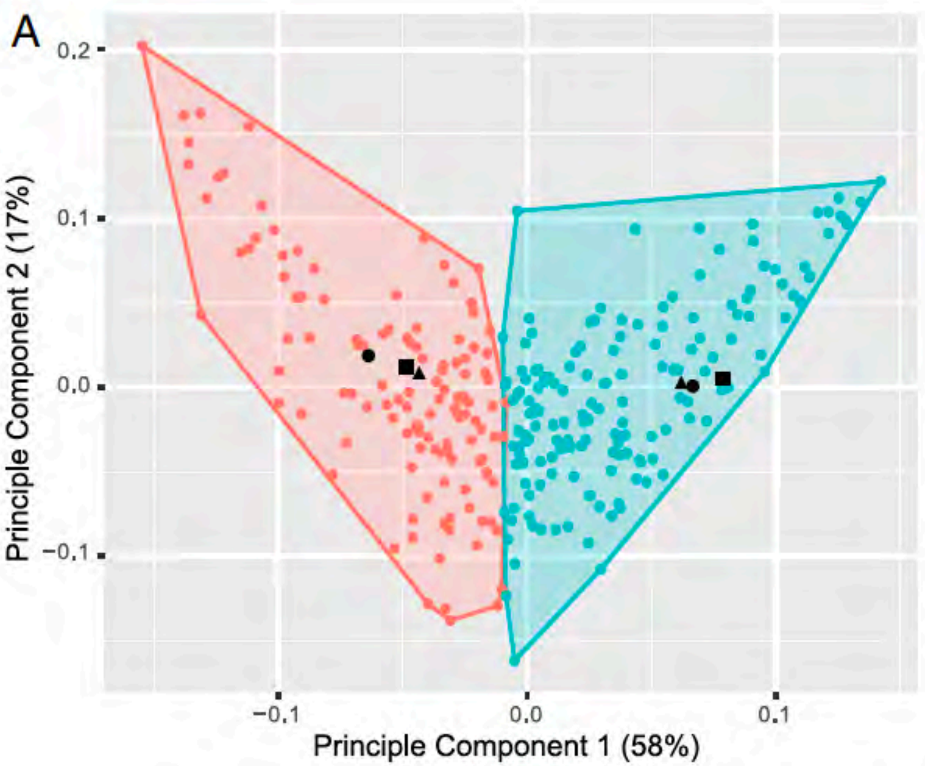
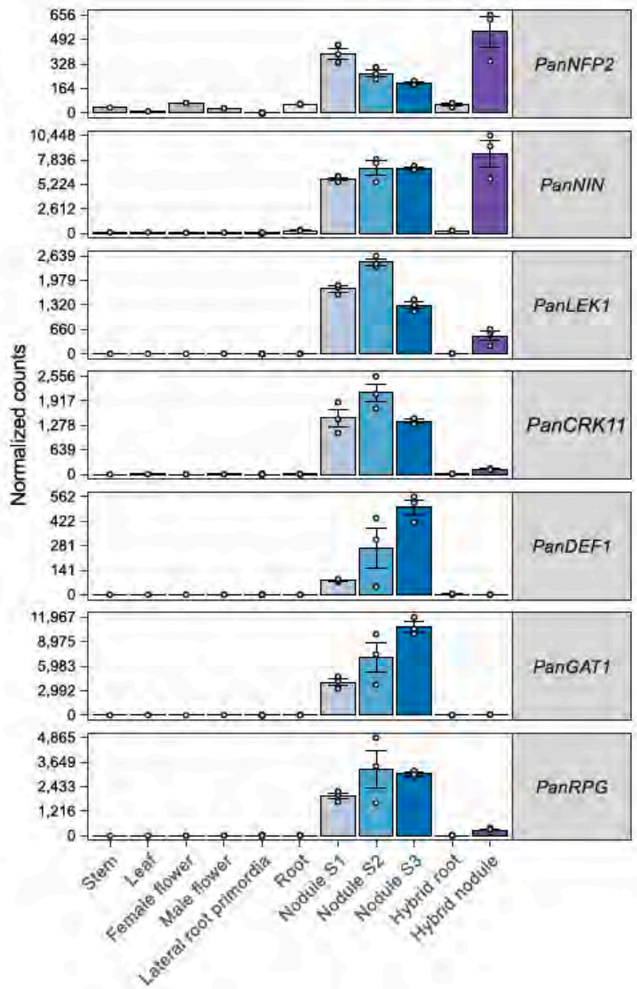


Parasponia and legumes share 290 nodulation genes
- Including some with only known functions in nodulation



7 key nodulation genes lost in Trema (and close relatives).

Comparative genomics of the nonlegume *Parasponia* reveals insights into evolution of nitrogen-fixing rhizobium symbioses

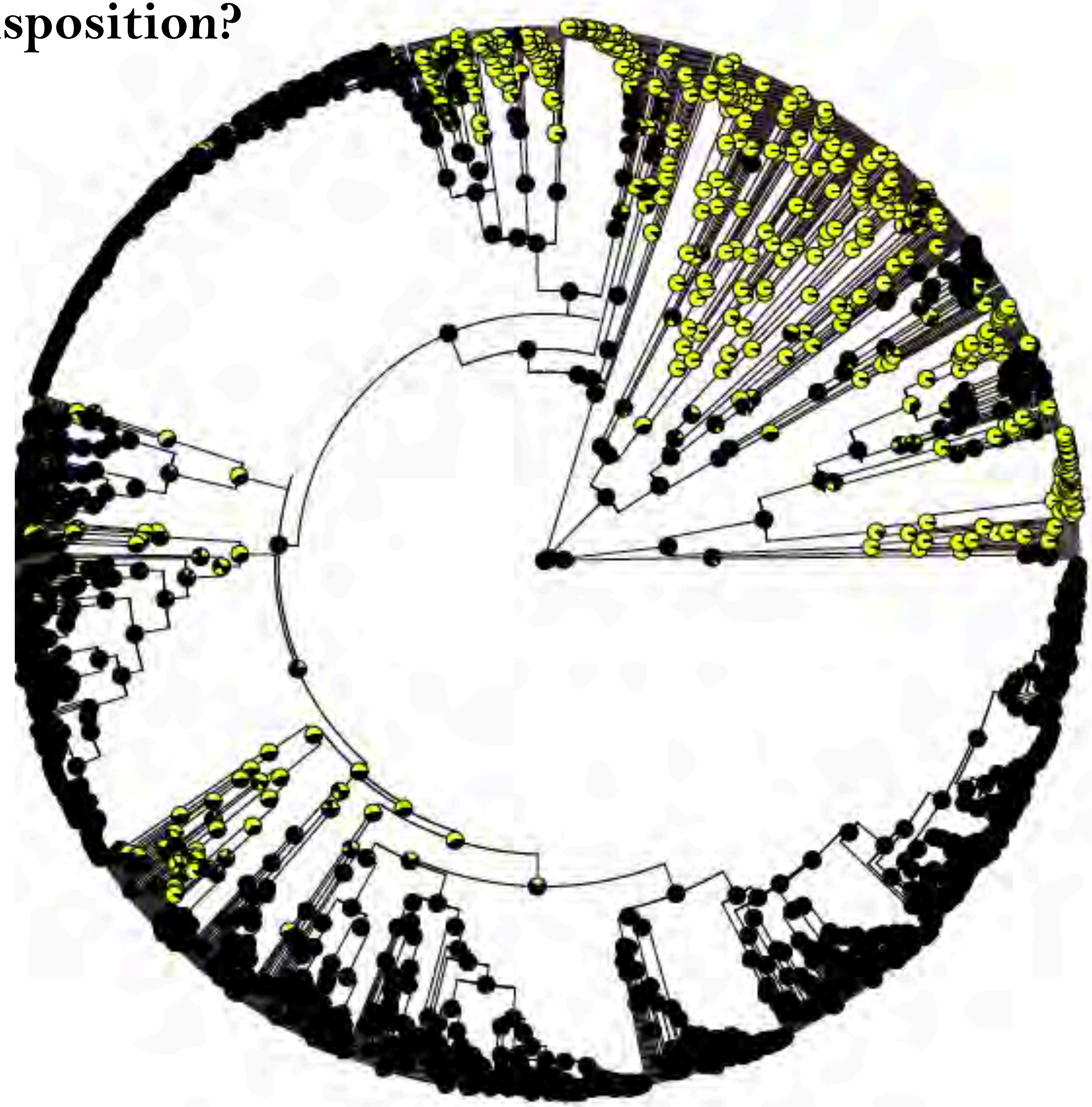
A single origin, rather than 1 predisposition?

- **Requires symbionts switching**
- **And many losses**

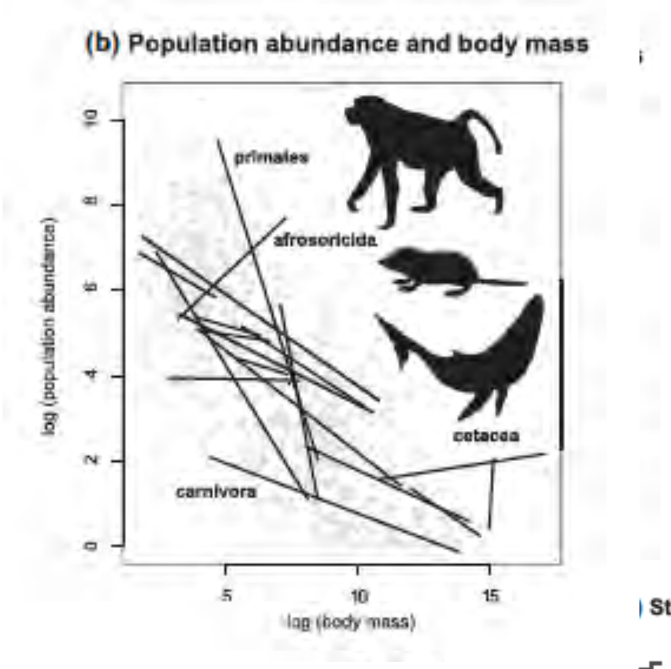
A single origin, rather than 1 predisposition?

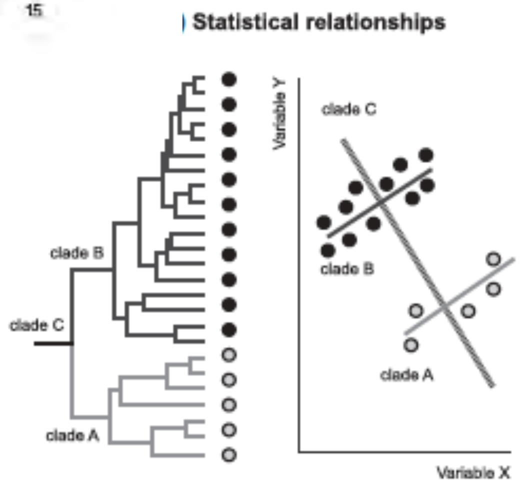
- Requires symbionts switching
- And many losses
    - >25 in the NFC
    - Particularly early

    - Complex traits easier to lose than gain?



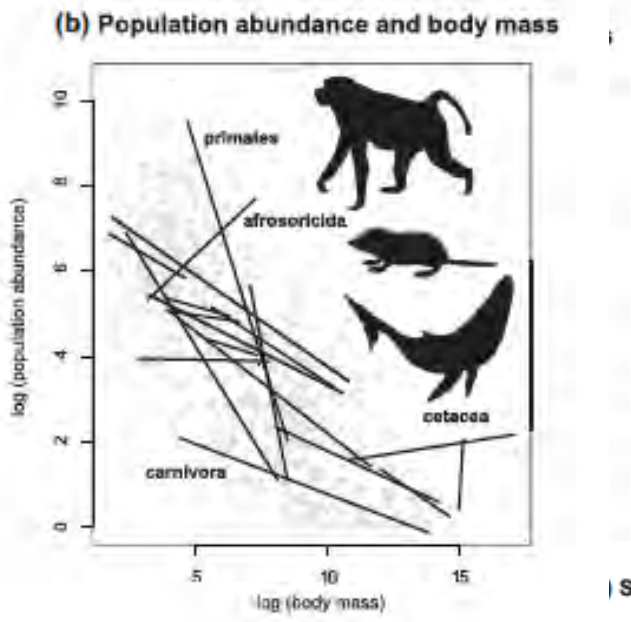
Phylogenetic scale is key

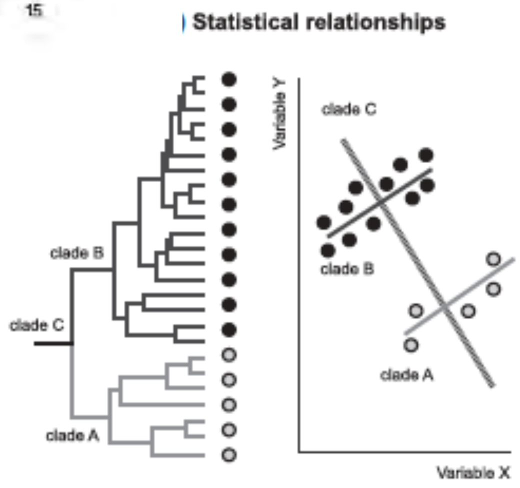


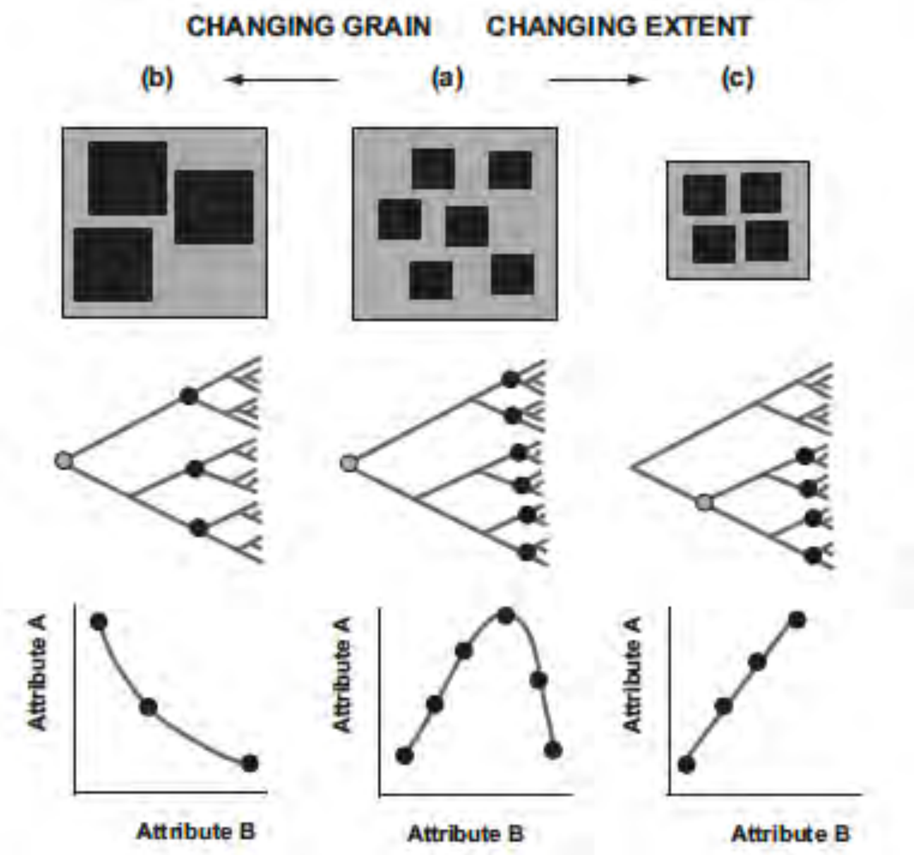


Graham et al. 2018 Phylogenetic scale in ecology and evolution

Phylogenetic scale is key



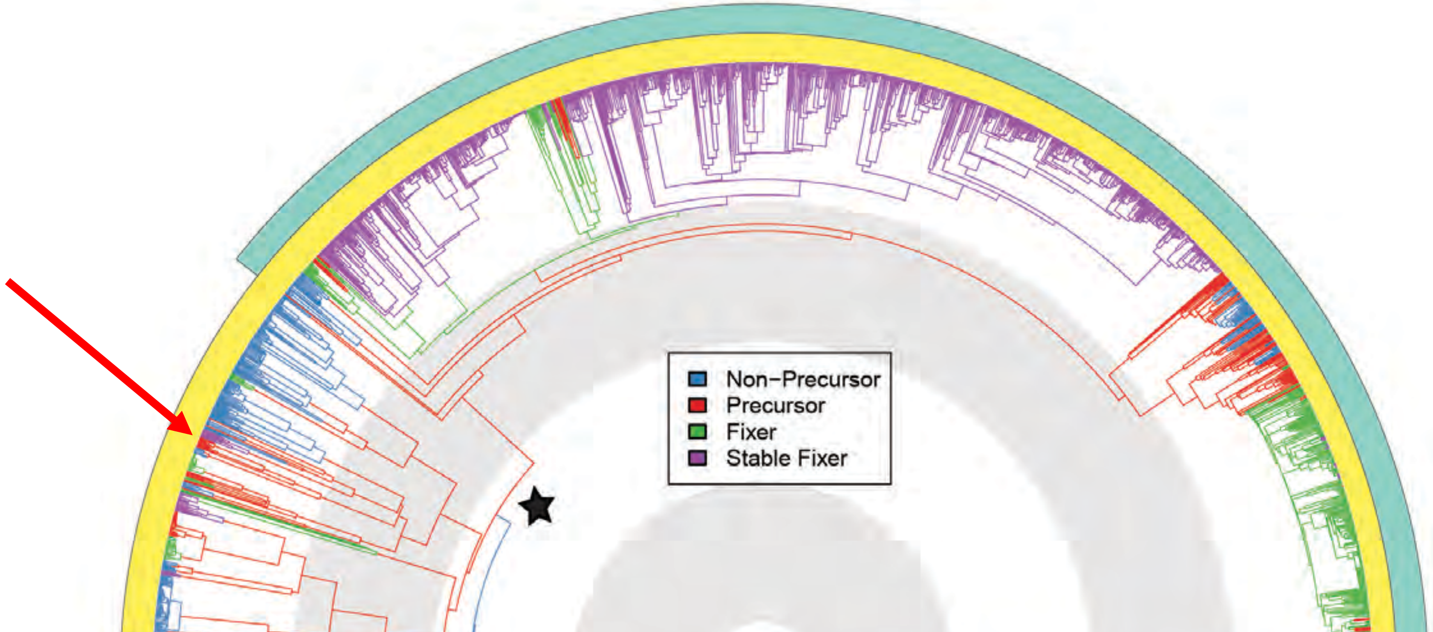




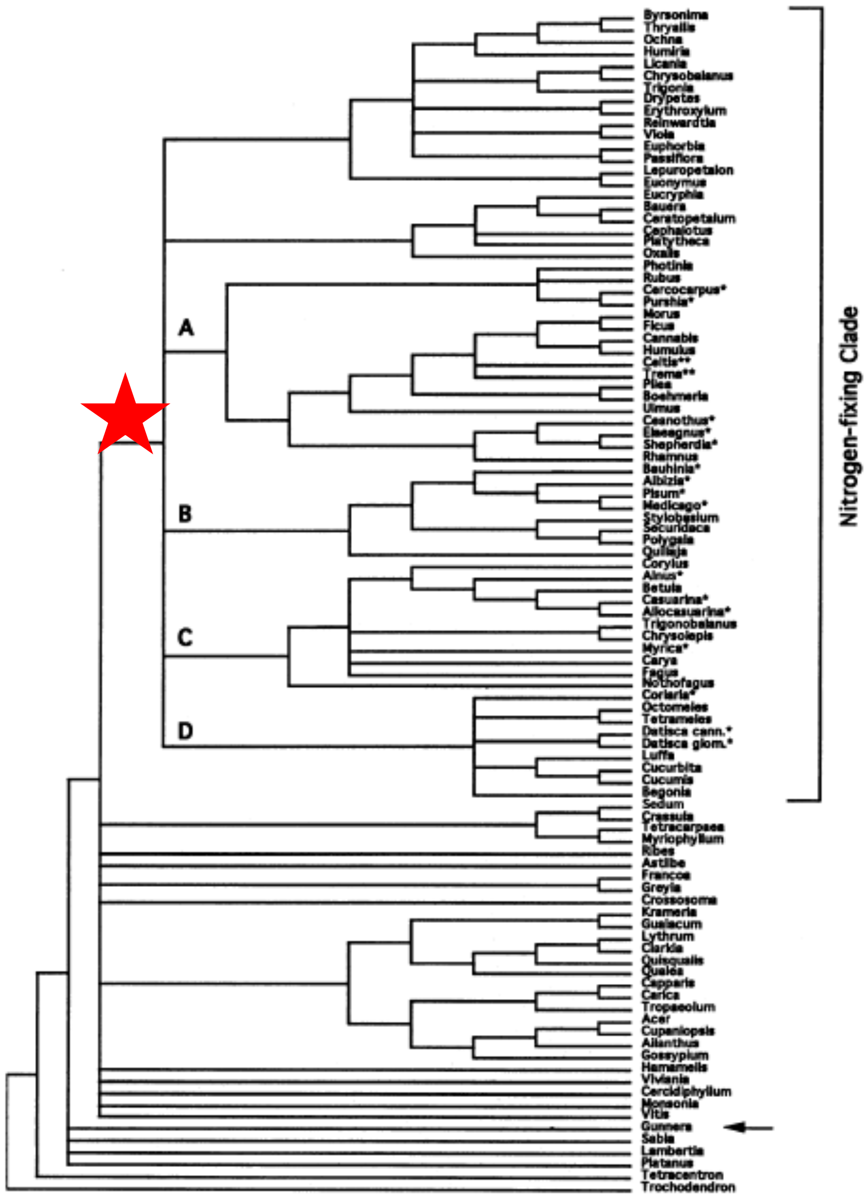
Graham et al. 2018 Phylogenetic scale in ecology and evolution

What is your trait of interest?

Nodulation per se? Type of nodule?



Or, symbiotic
N2-fixation generally?



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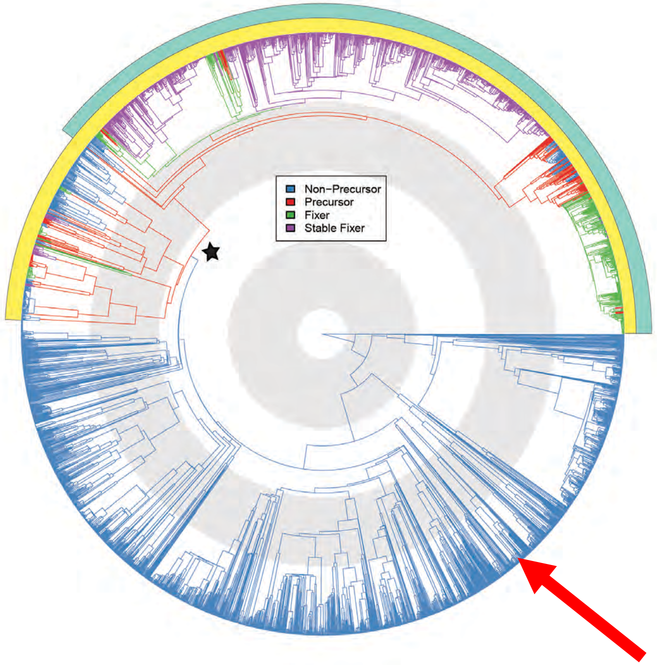
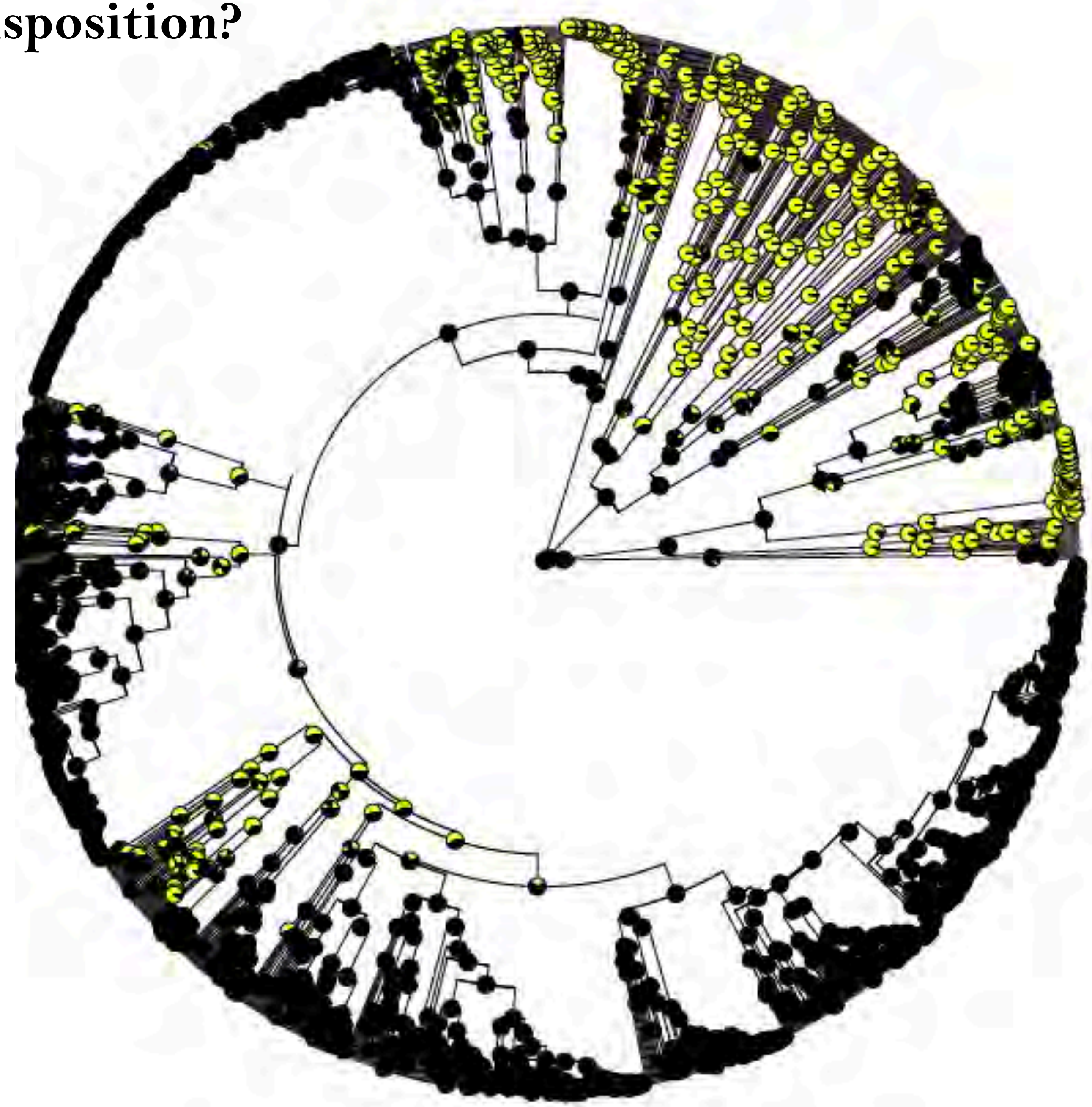


Gunnera – Nostoc

A single origin, rather than 1 predisposition?

- Requires symbionts switching
- And many losses
  - >25 in the NFC
  - Particularly early

New question:
Why mutualism losses?



Sometimes mutualistic cooperation breaks down

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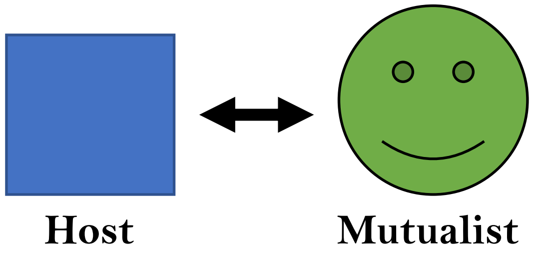
Why mutualism breakdown?
What are the evolutionary drivers?

Pathways to mutualism breakdown

Joel L. Sachs and Ellen L. Simms

University of California – Berkeley, Department of Integrative Biology, 3060 Valley Life Sciences Building, #3140, Berkeley, CA 94720, USA



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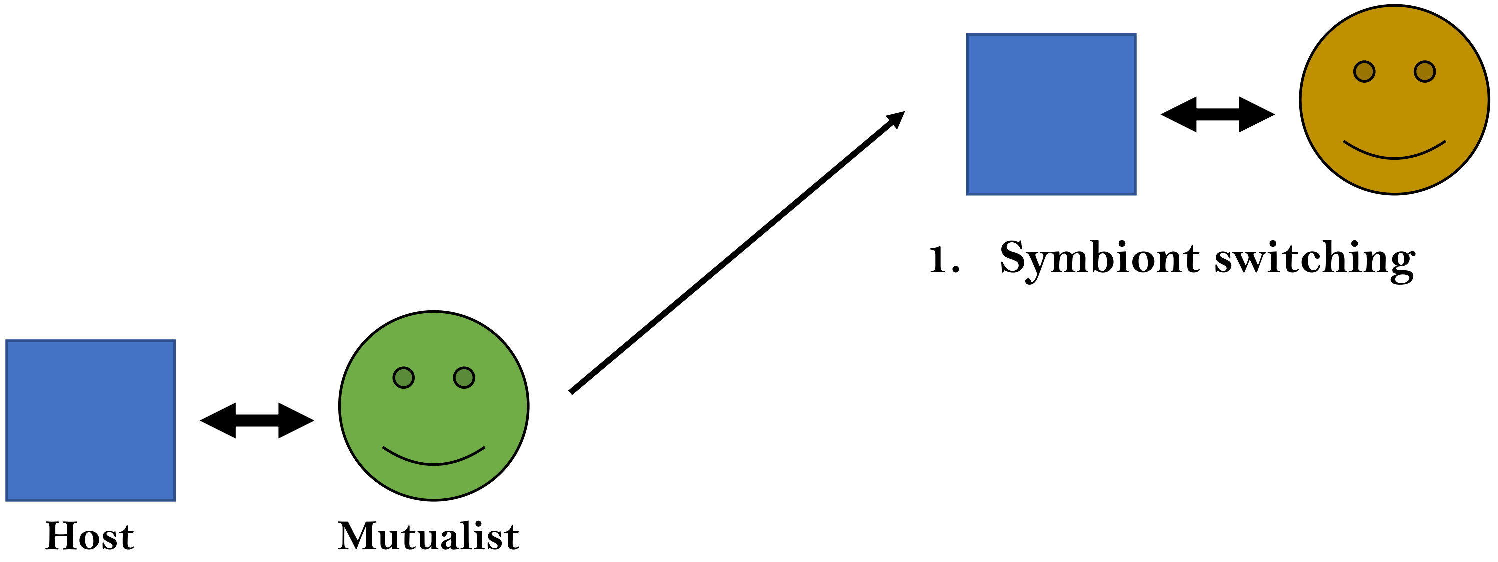

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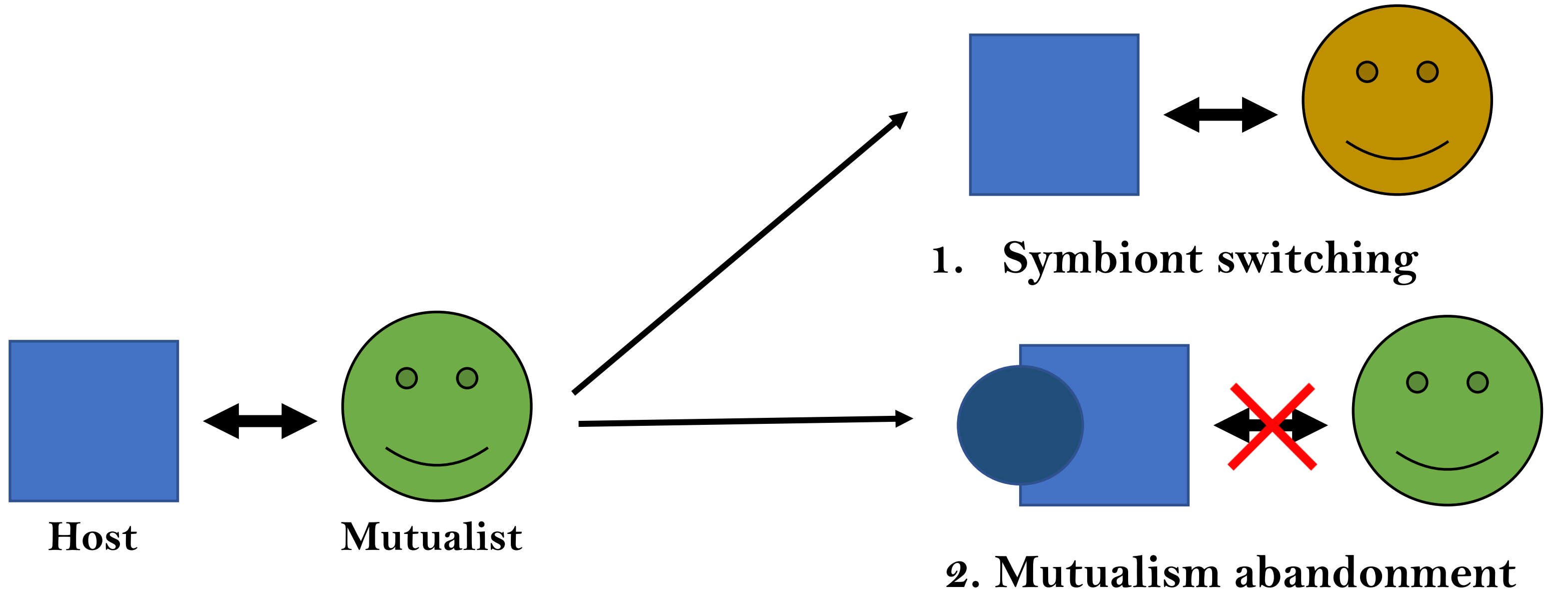
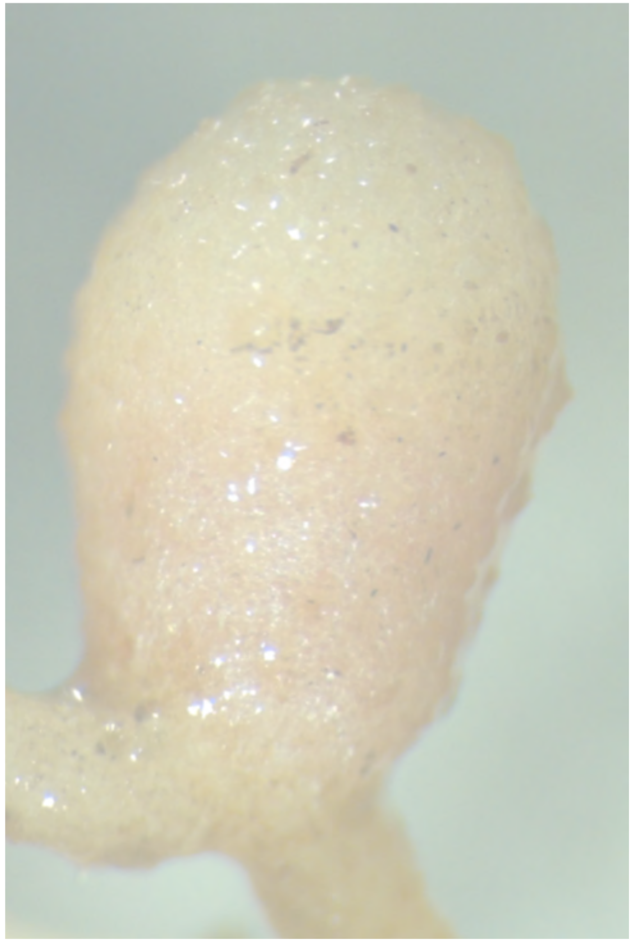


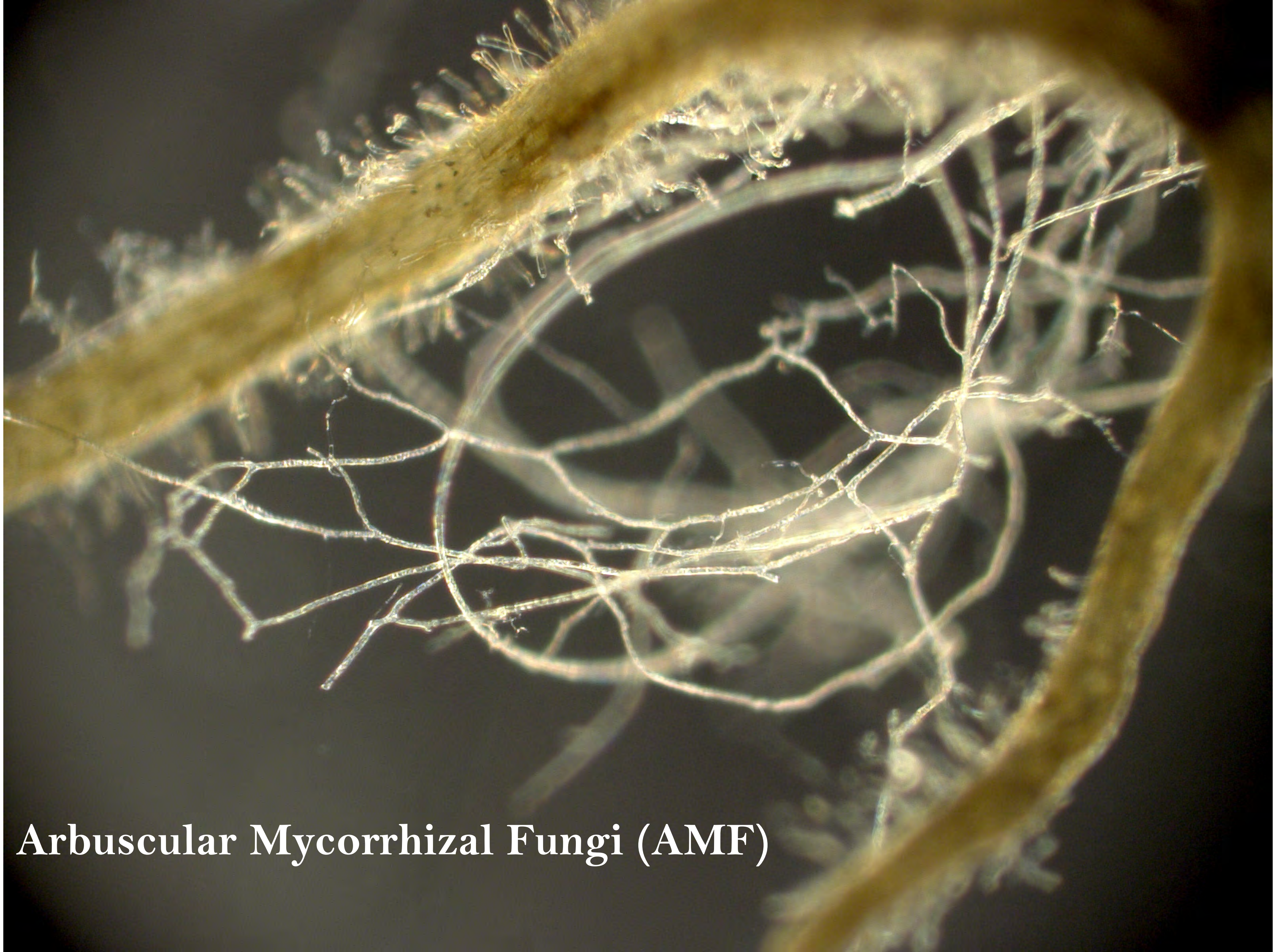


Symbiotic
N_2-fixation

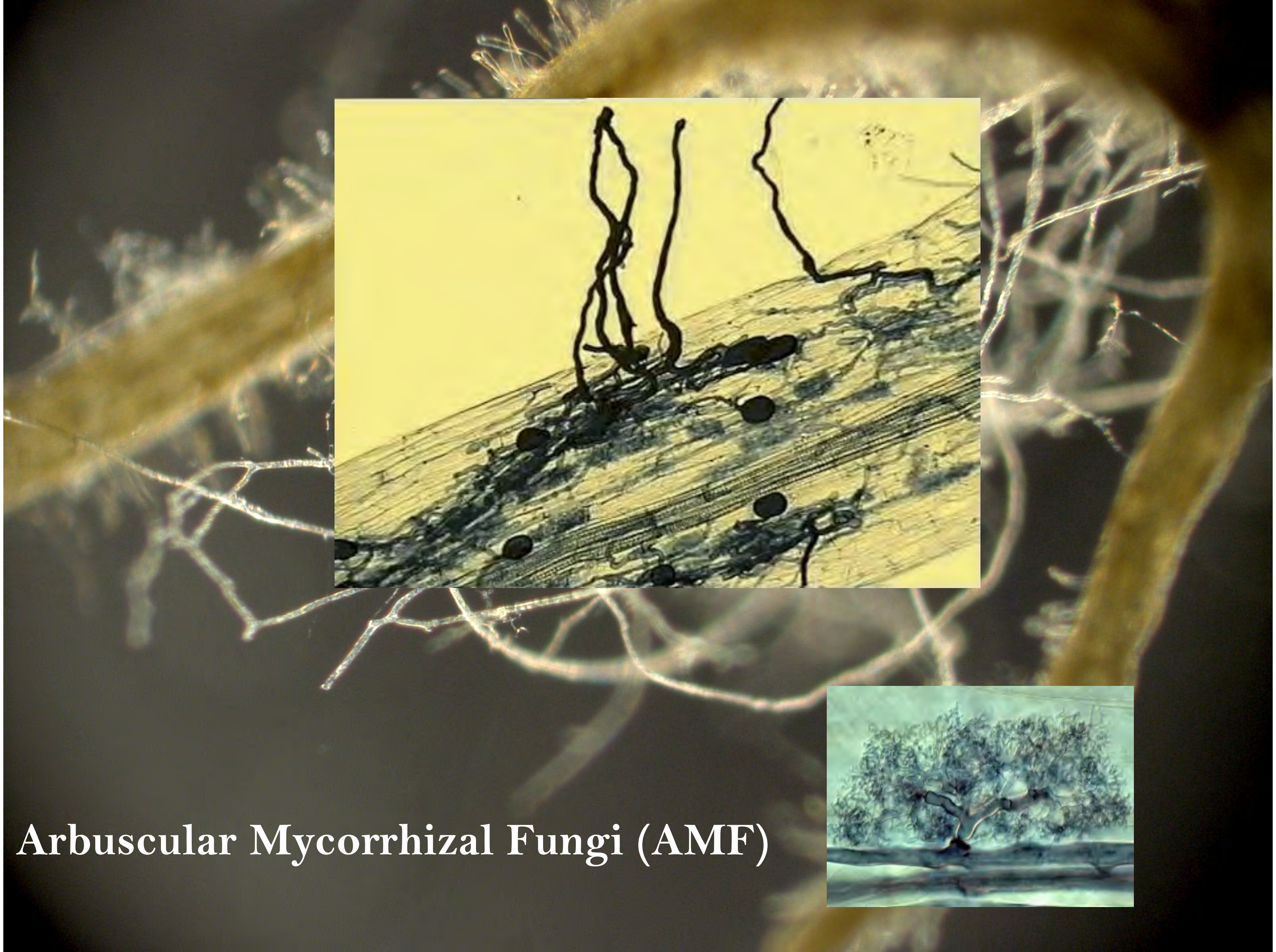
~~Gain~~ Loss of cooperation

Arbuscular mycorrhizal fungi (AMF)

Loss of cooperation

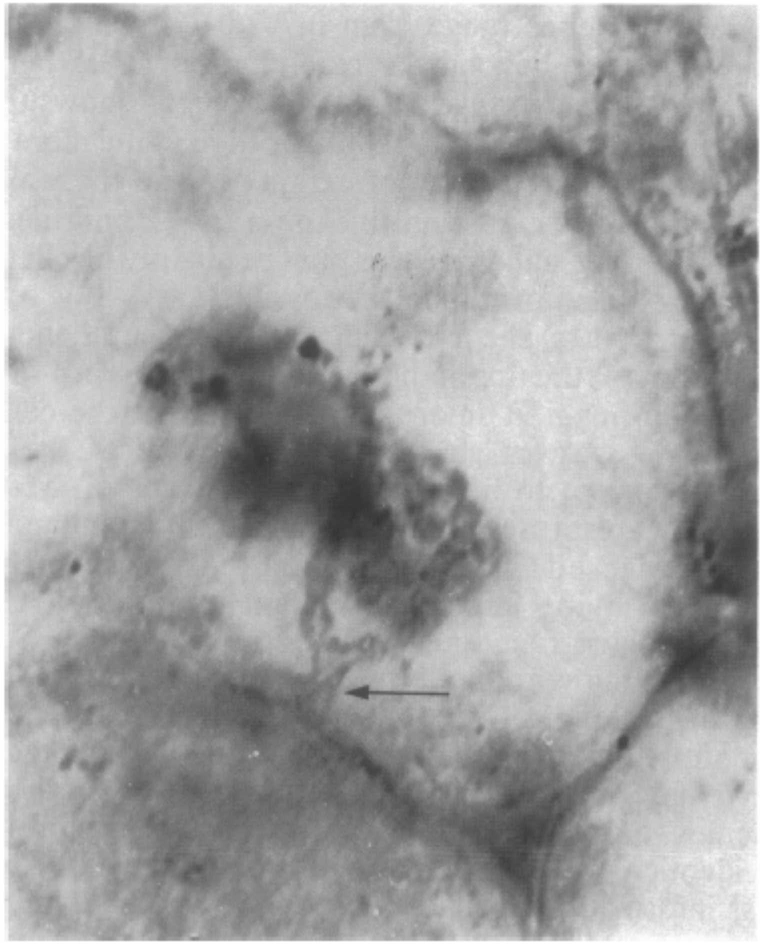


Arbuscular Mycorrhizal Fungi (AMF)



Arbuscular Mycorrhizal Fungi (AMF)

AMF predate colonisation of the land

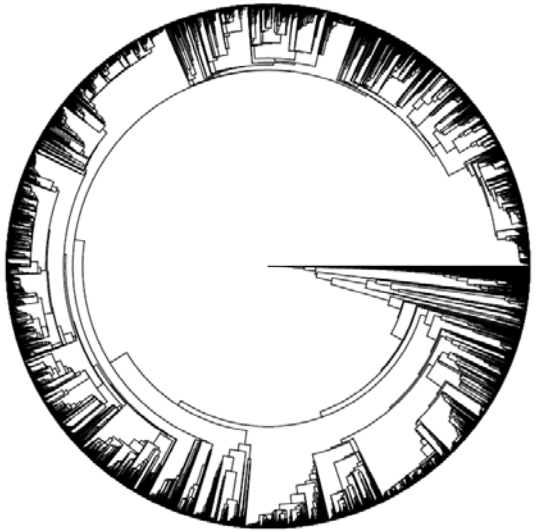


Remy et al. (1994) PNAS

Yet, some plant species do not have AMF

What are pathways towards (stable) AM Loss?

1. Phylogeny



Zanne et al., 2014. Nature

Dr. Nadia Soudzilovskaia, Leiden

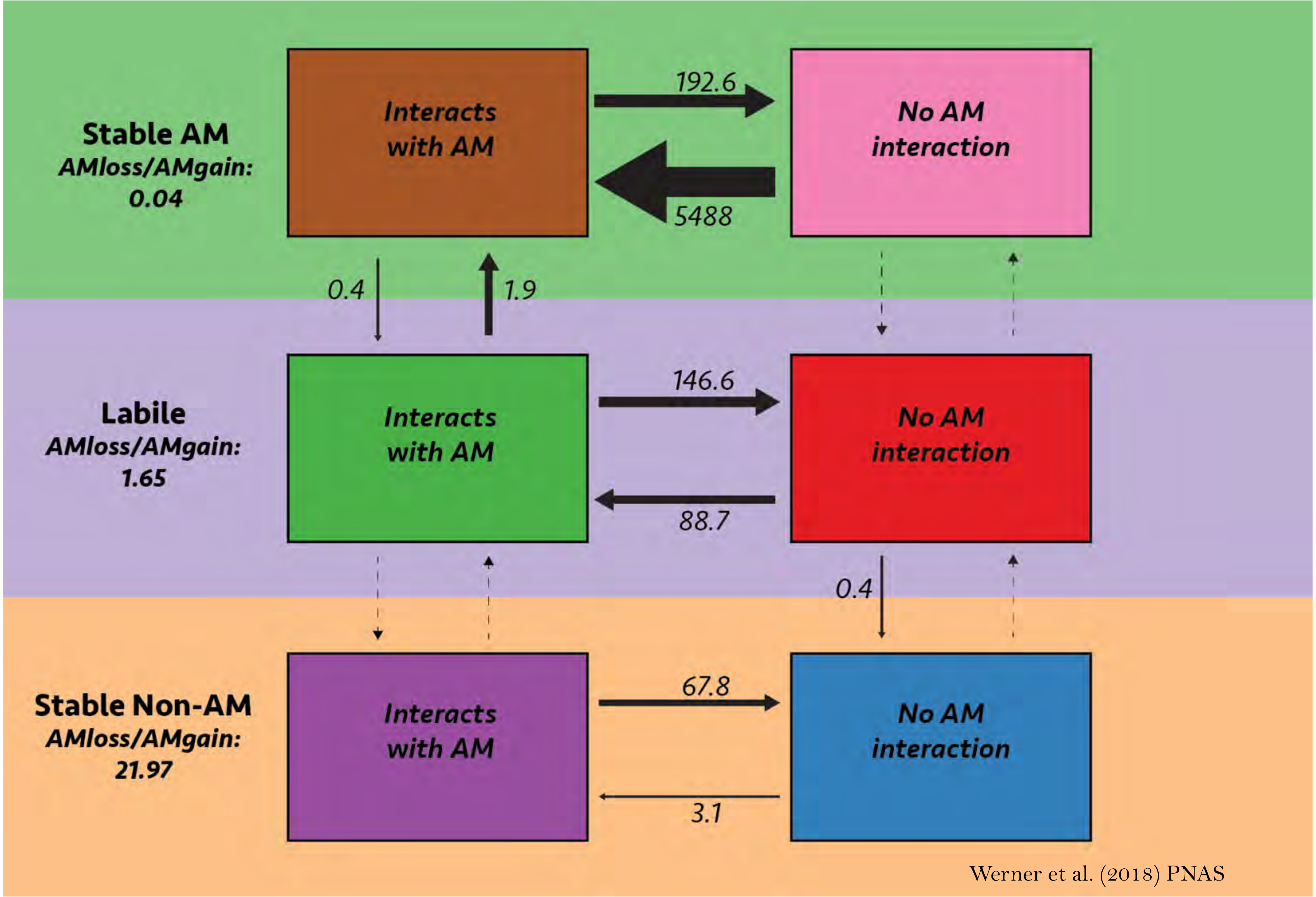
>30k species

Prof. Hans Cornelissen, VU Amsterdam

2. Database

Species	AM	ECM	ER
Abarema jupunba	Yes	No	No
Abies alba	No	Yes	No
Abies amabilis	No	Yes	No
Abronia umbellata	Yes	No	No
Abuta grandifolia	Yes	No	No
Abutilon grandifolium	Yes	No	No
Acacia ampliceps	Yes	No	No

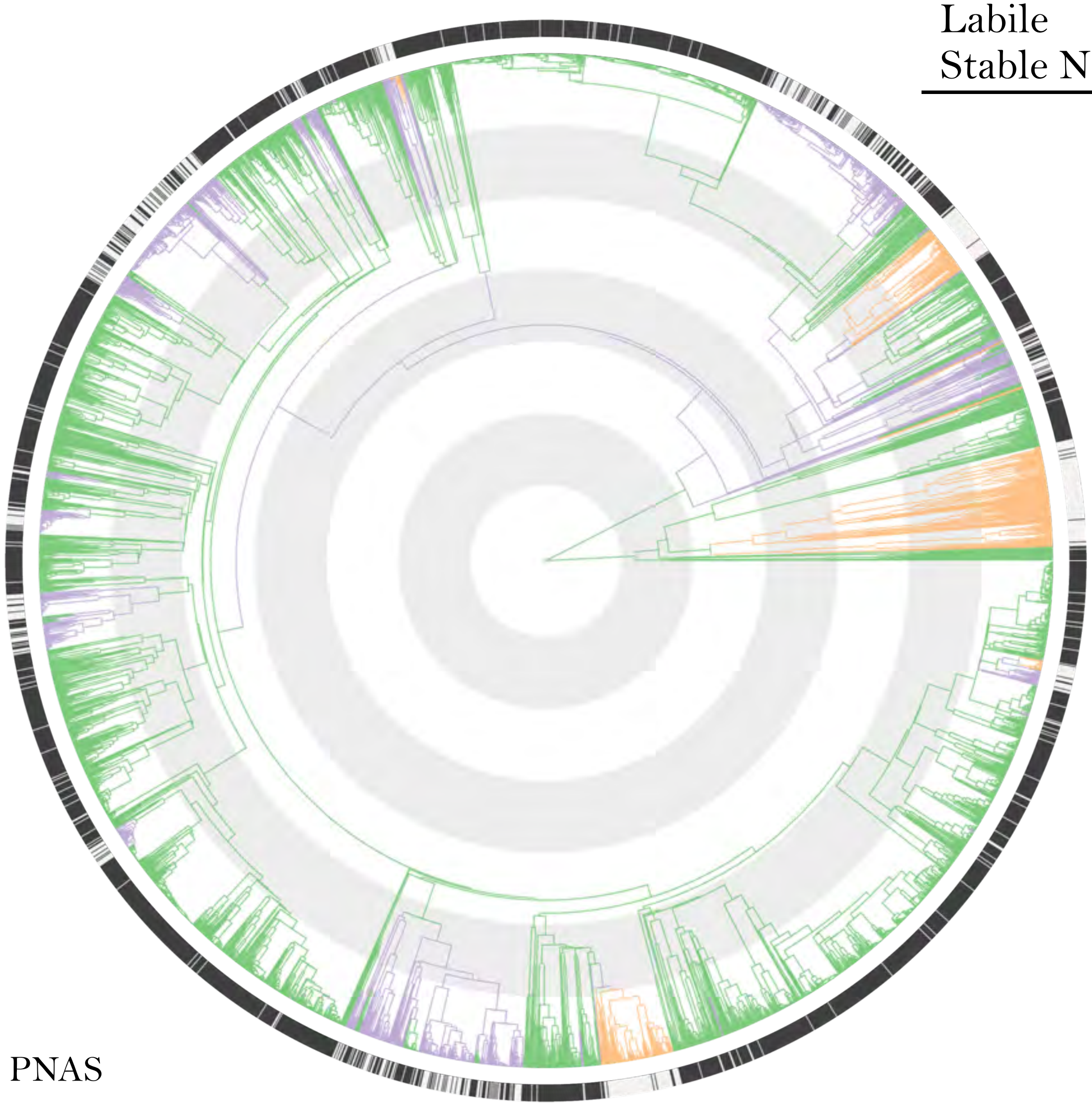
Akhmetzhanova et al. 2012 Ecology;
Wang 2006 Mycorrhiza



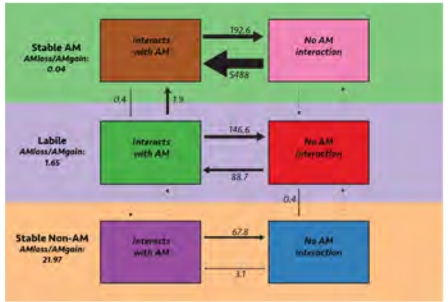
Werner et al. (2018) PNAS

'Stable AM' is ancestral and retained in most plants

Stability Class	# Species	Percentage
Stable AM	2,616	70.0%
Labile	829	22.2%
Stable Non-AM	291	7.8%

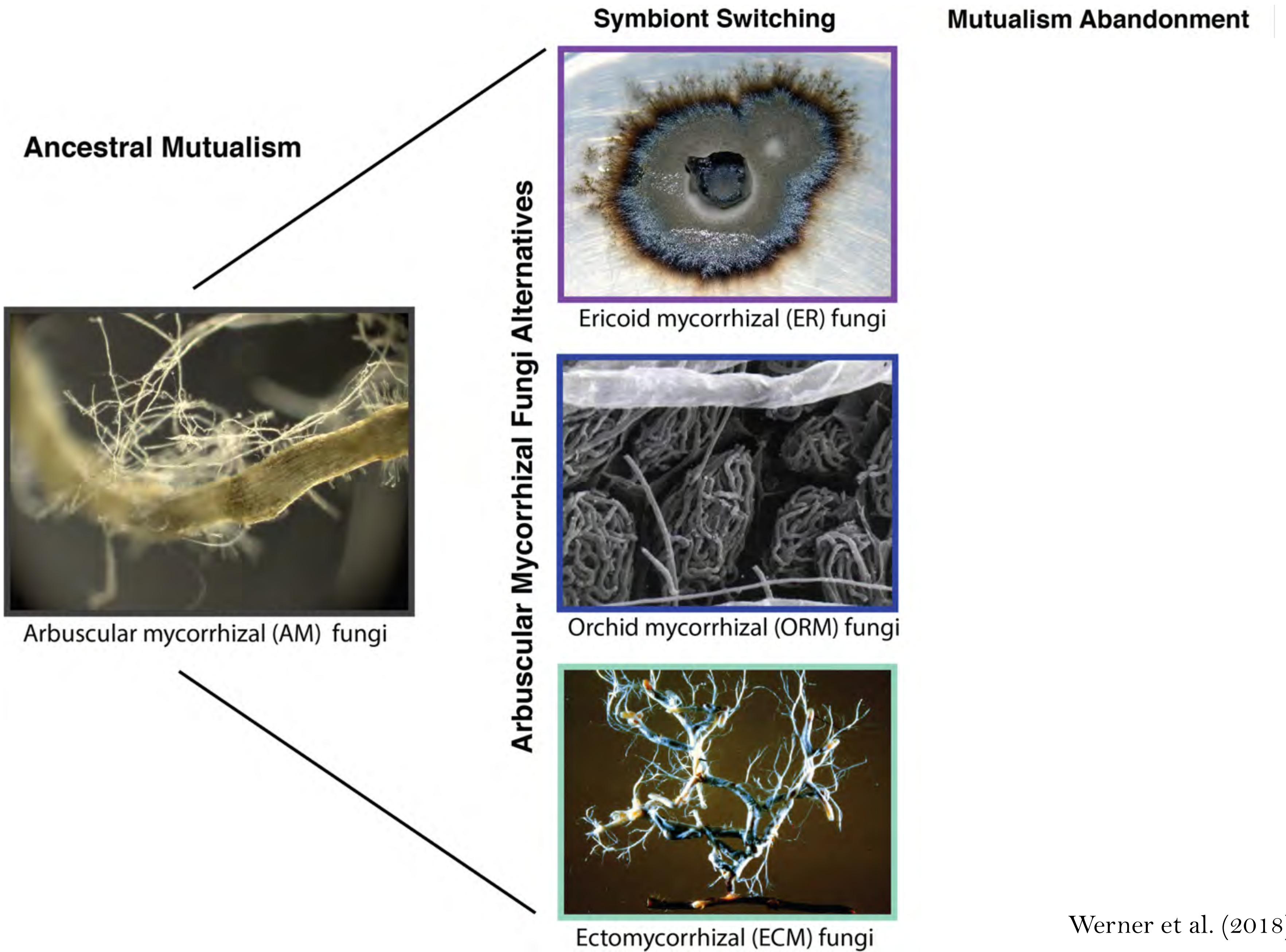


24.6 losses estimated



Werner et al. (2018) PNAS

Is mutualism breakdown driven by symbiont switching and abandonment?



Werner et al. (2018) PNAS

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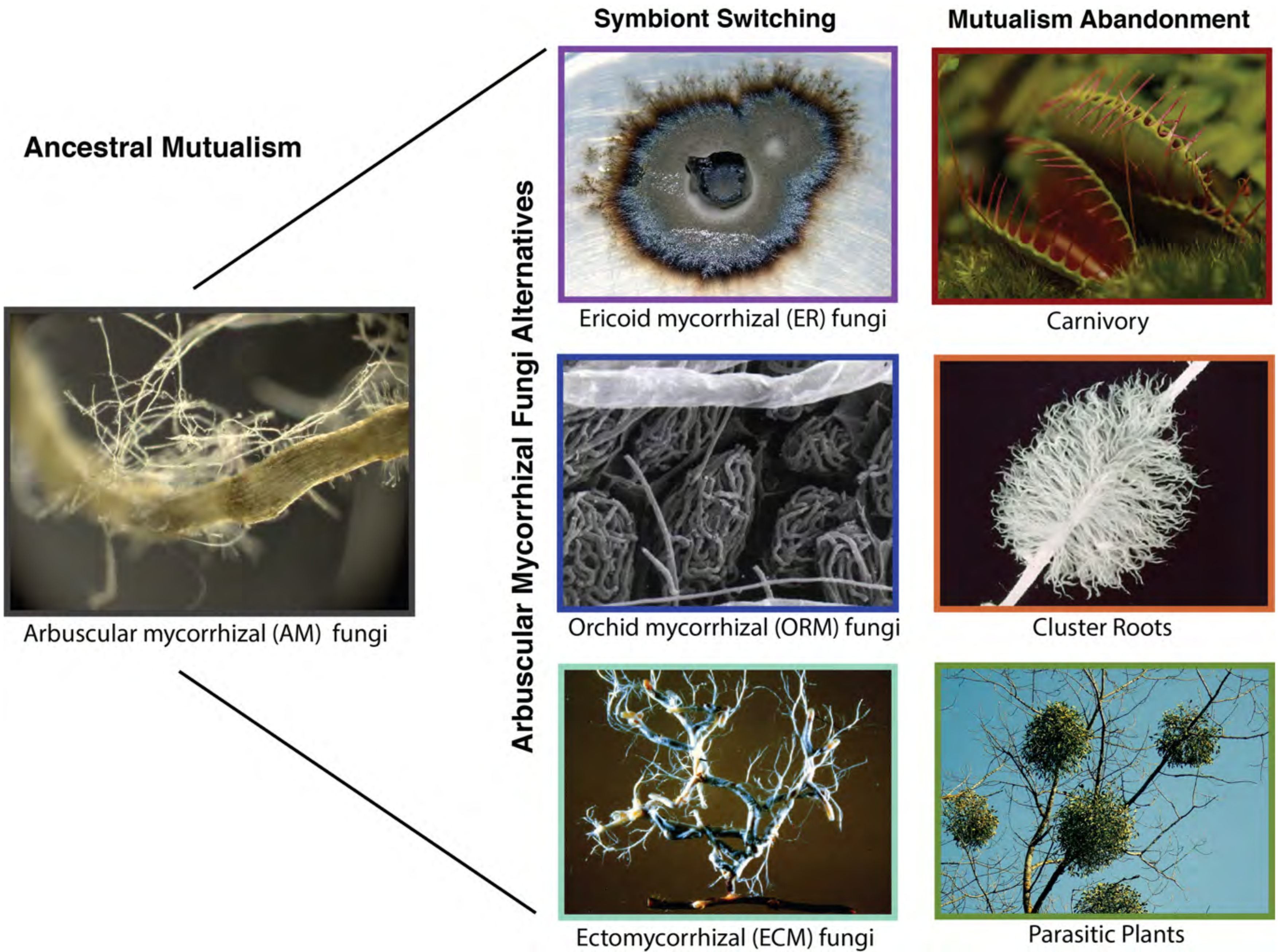


Dependent or independent model of evolution?

Dependent or independent model of evolution?

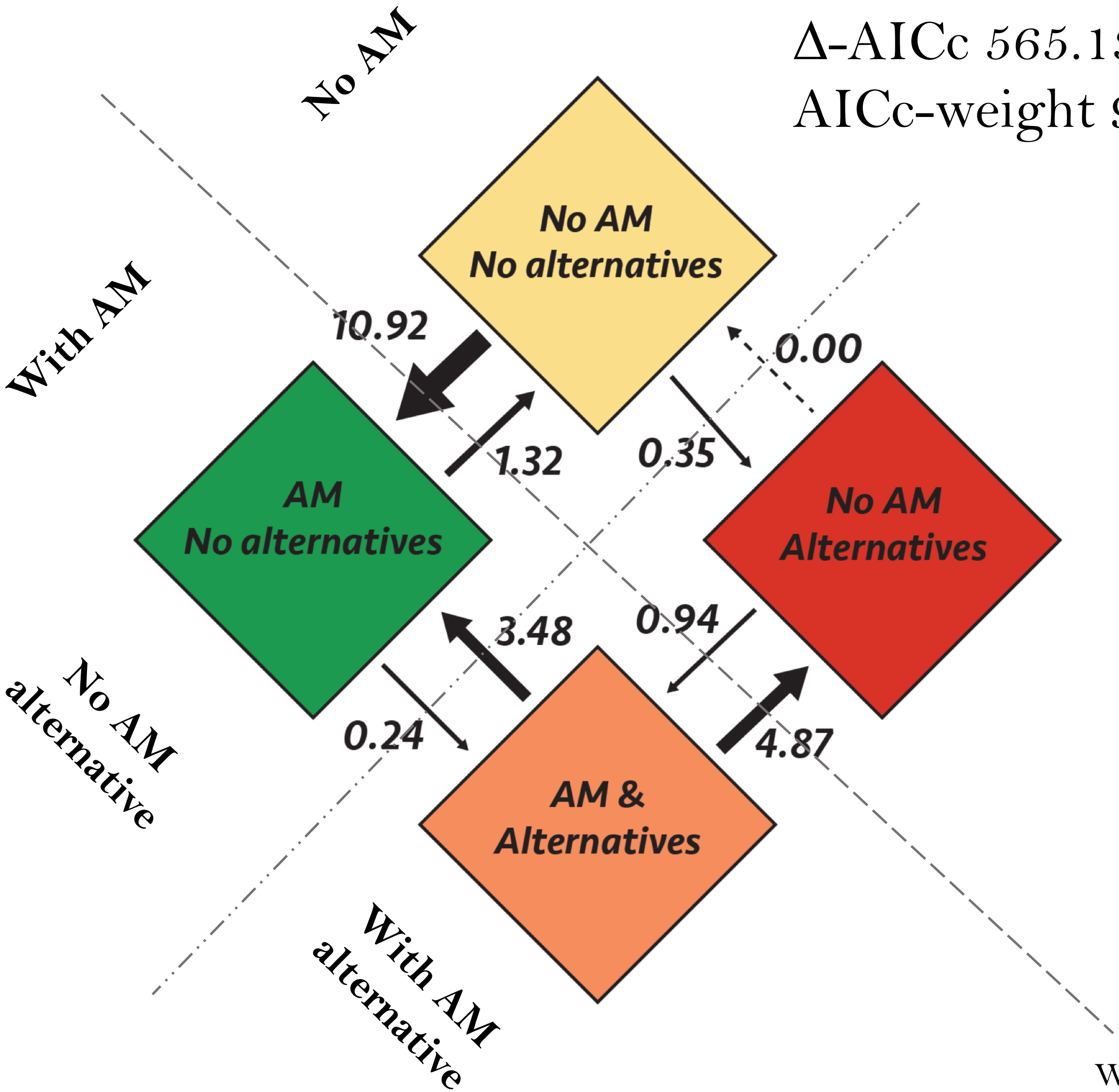
Δ-AICc 565.13
AICc-weight 99.9%

Werner et al. (2018) PNAS

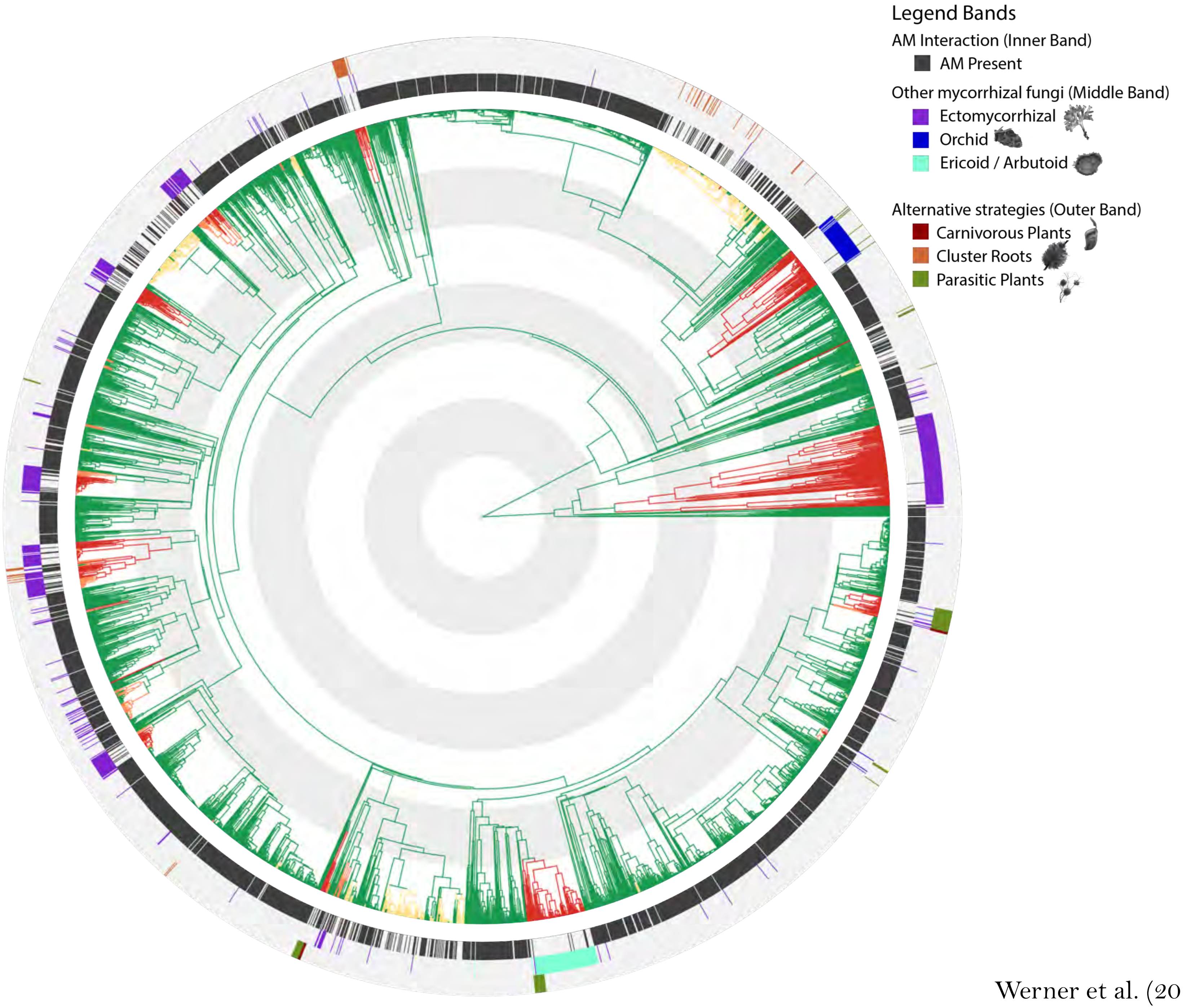
Dependent or independent model of evolution?

Δ-AICc 565.13

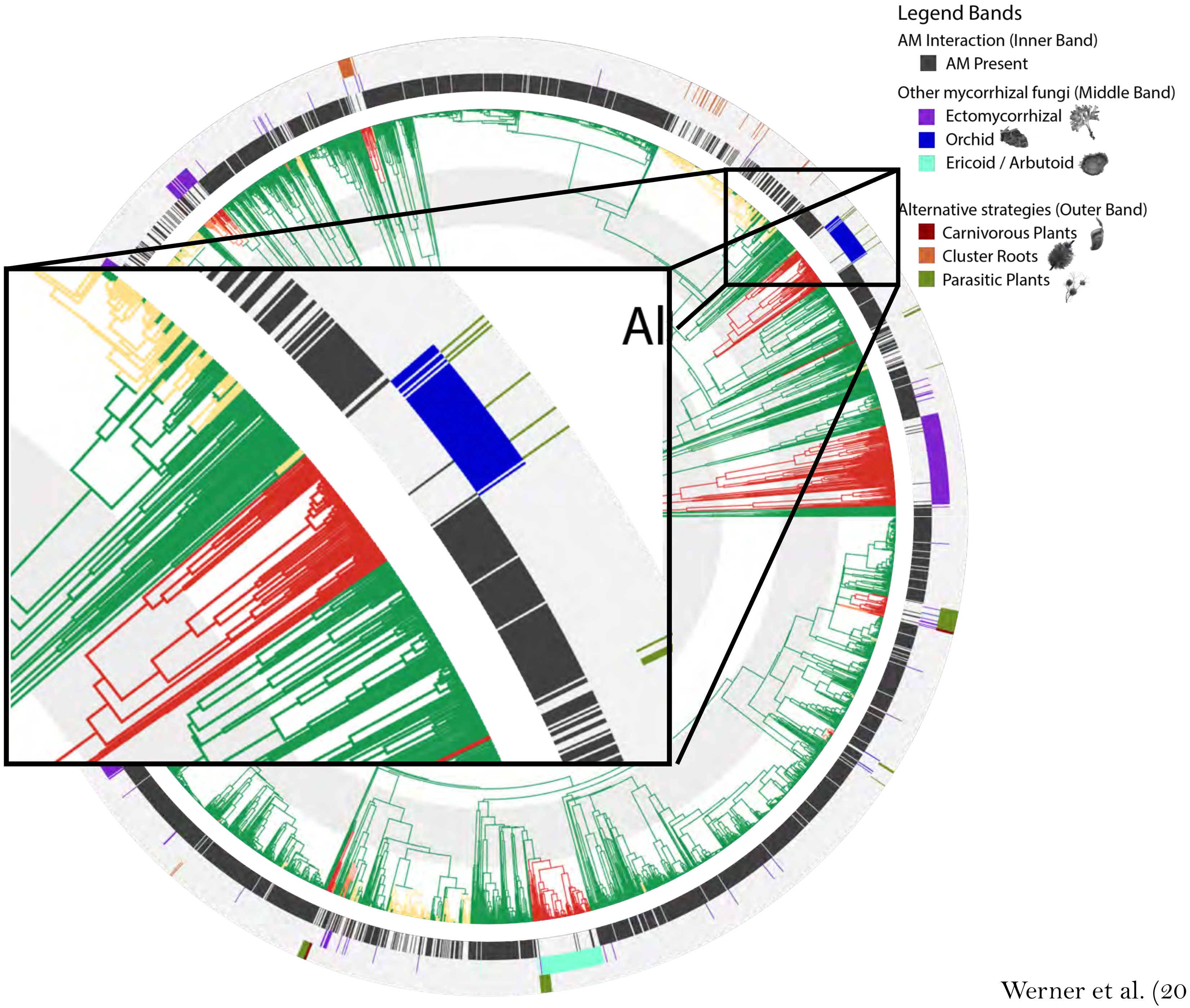
AICc-weight 99.9%



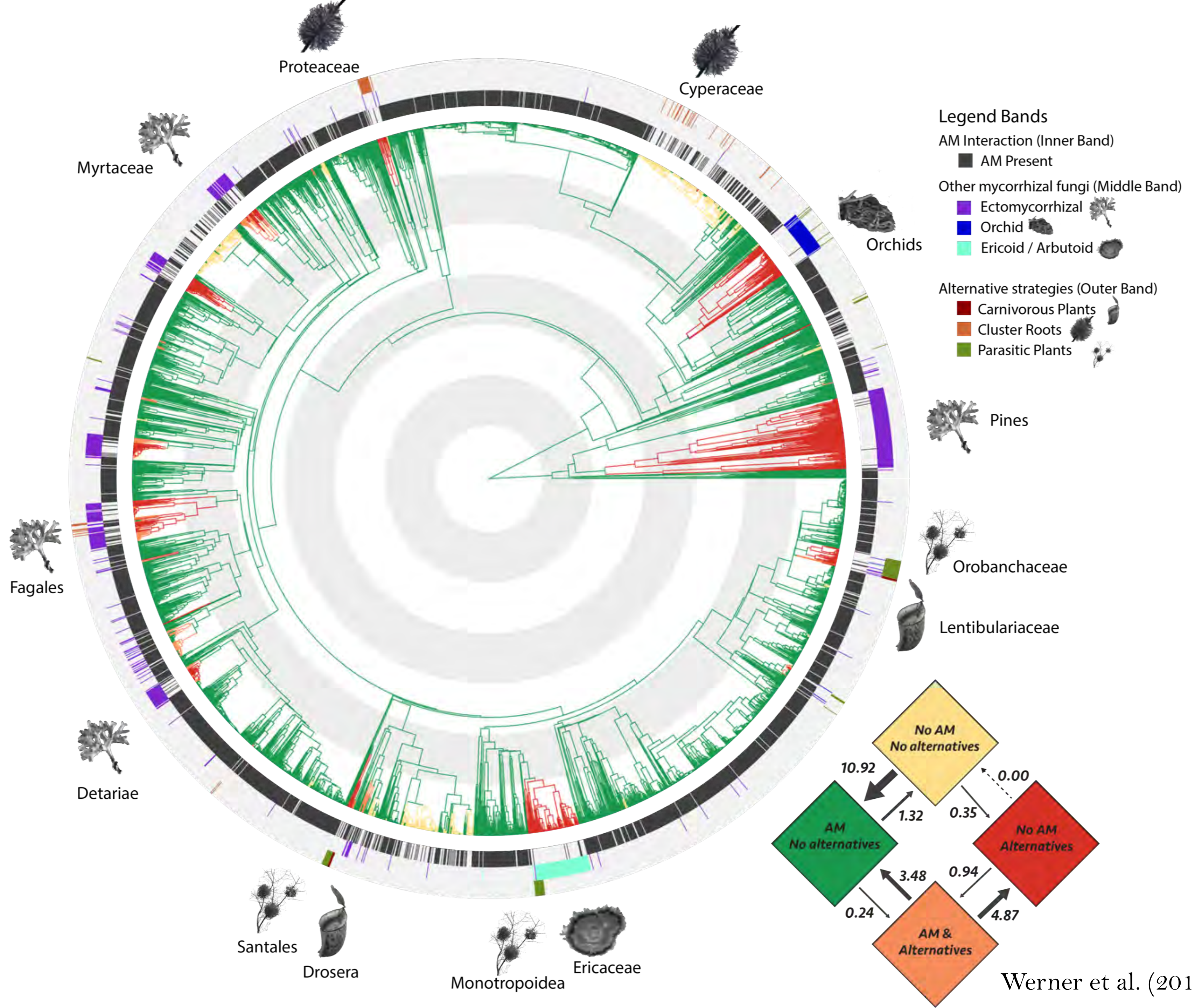
Werner et al. (2018) PNAS



Werner et al. (2018) PNAS



Werner et al. (2018) PNAS

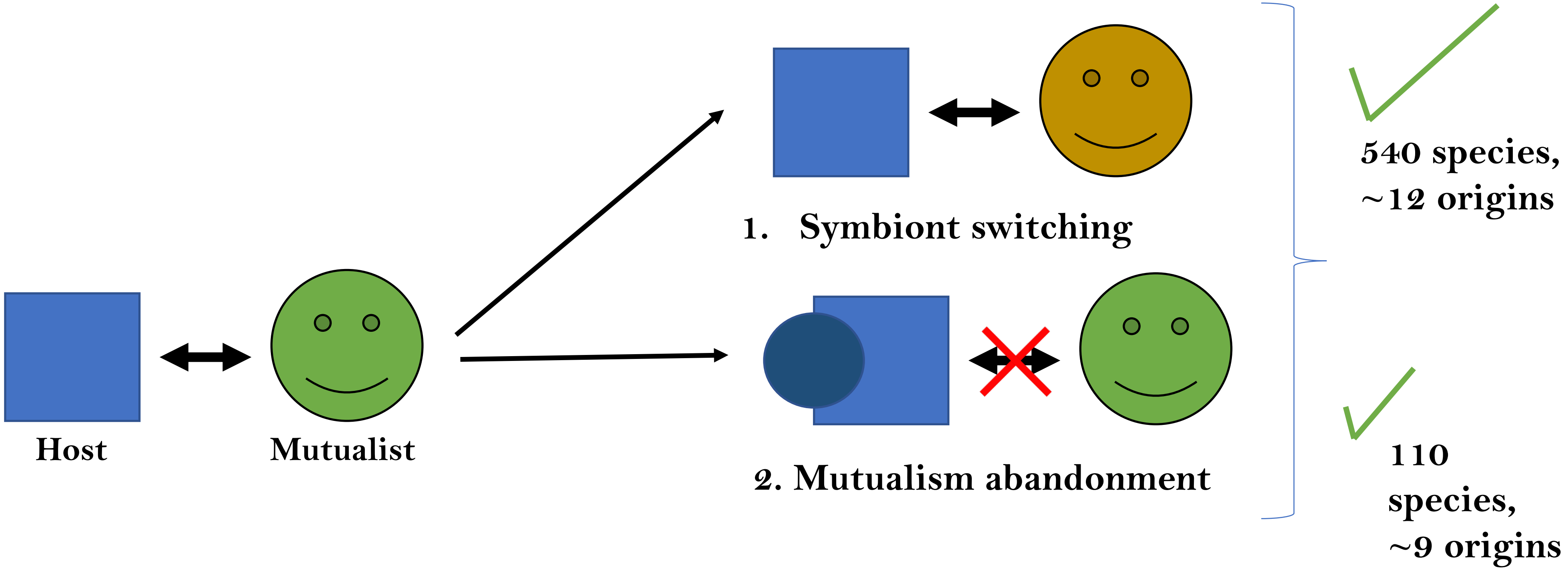


Werner et al. (2018) PNAS

Pathways to mutualism breakdown

Joel L. Sachs and Ellen L. Simms

University of California – Berkeley, Department of Integrative Biology, 3060 Valley Life Sciences Building, #3140, Berkeley, CA 94720, USA



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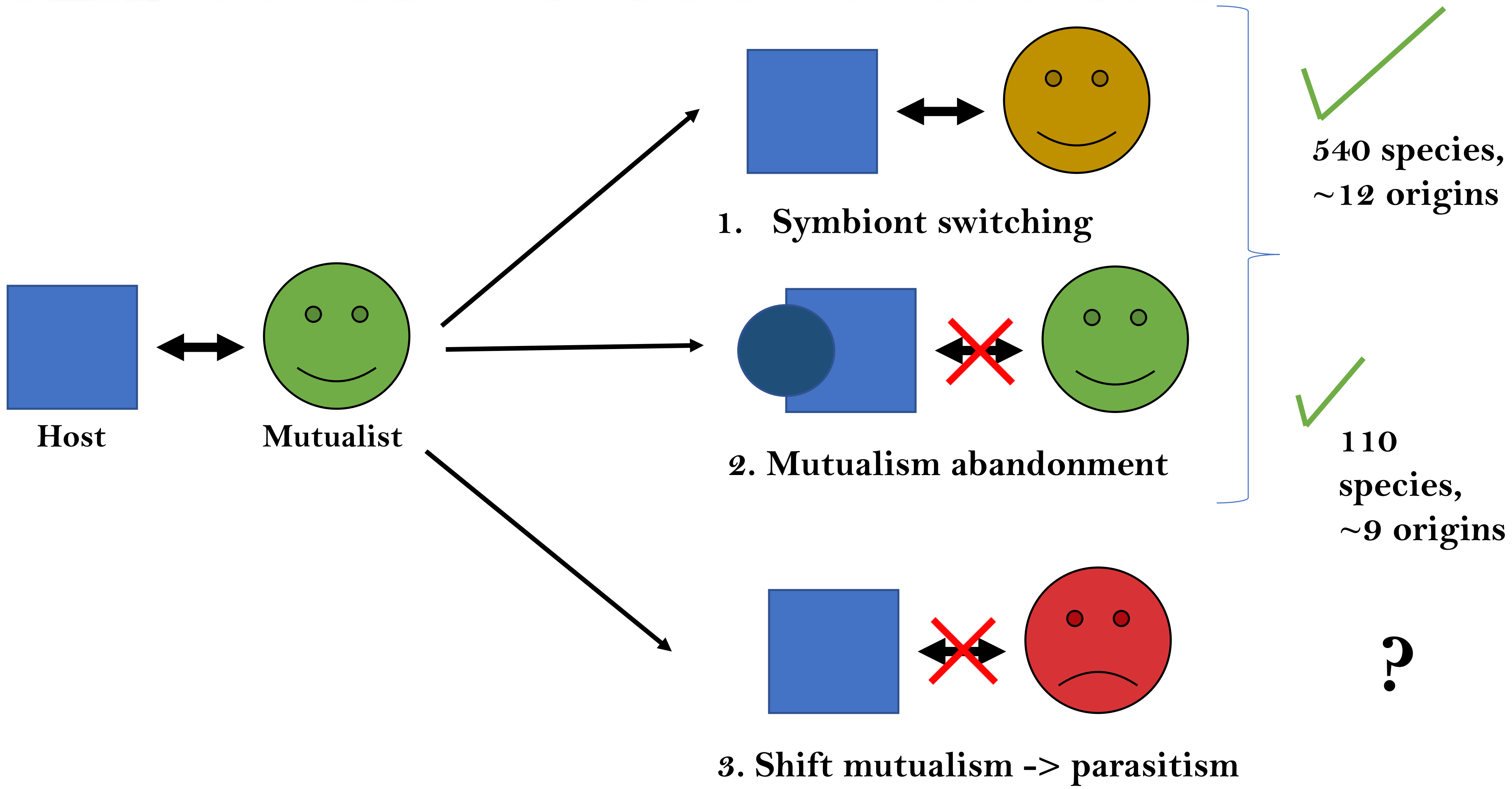


Is mutualism breakdown driven by shifts to AM parasitism?

SCIENTIFIC DATA

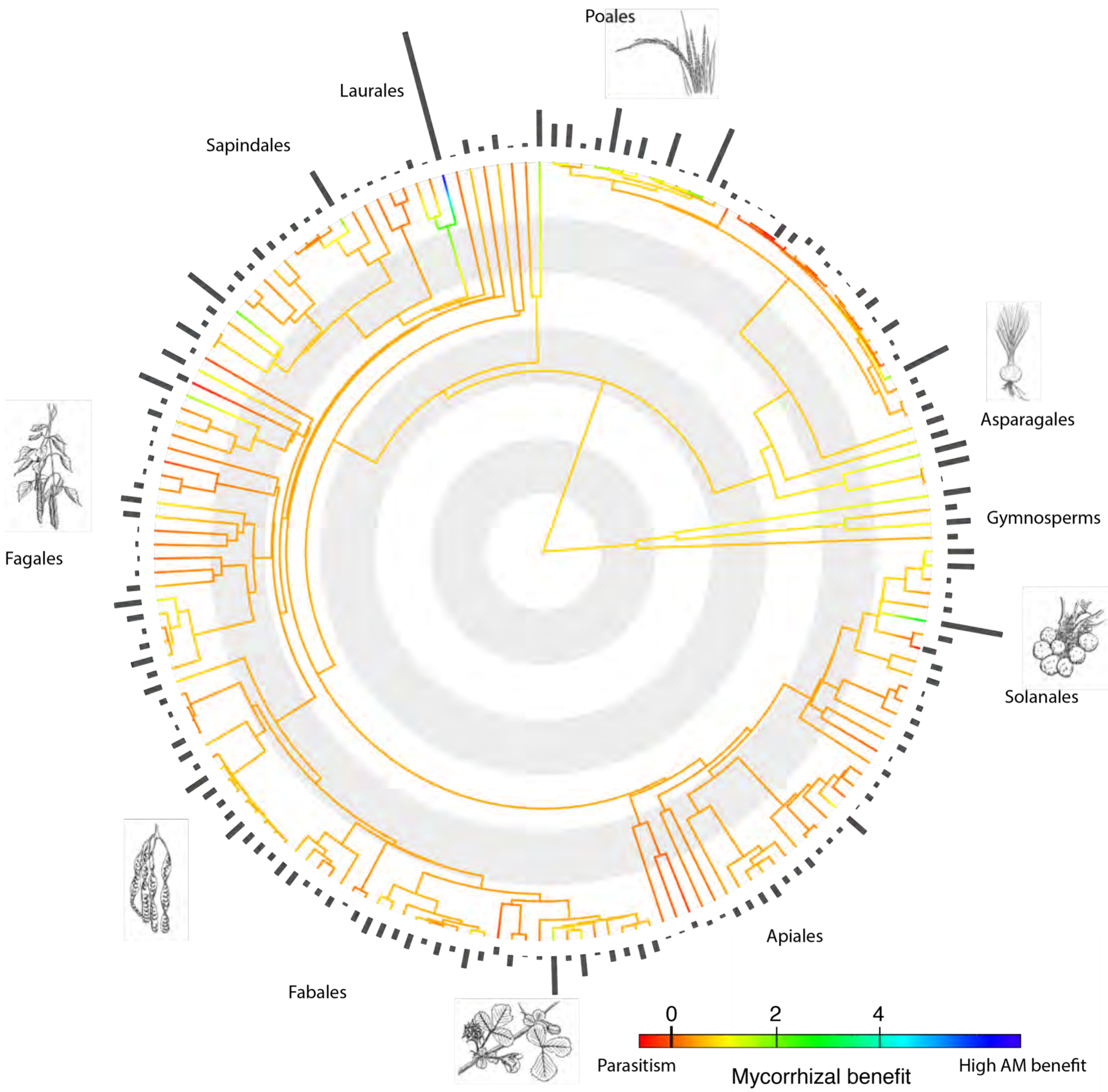
OPEN

SUBJECT CATEGORIES
» Ecology
» Phylogenetics
» Fungal ecology
» Arbuscular mycorrhiza

Data Descriptor: MycoDB, a global database of plant response to mycorrhizal fungi

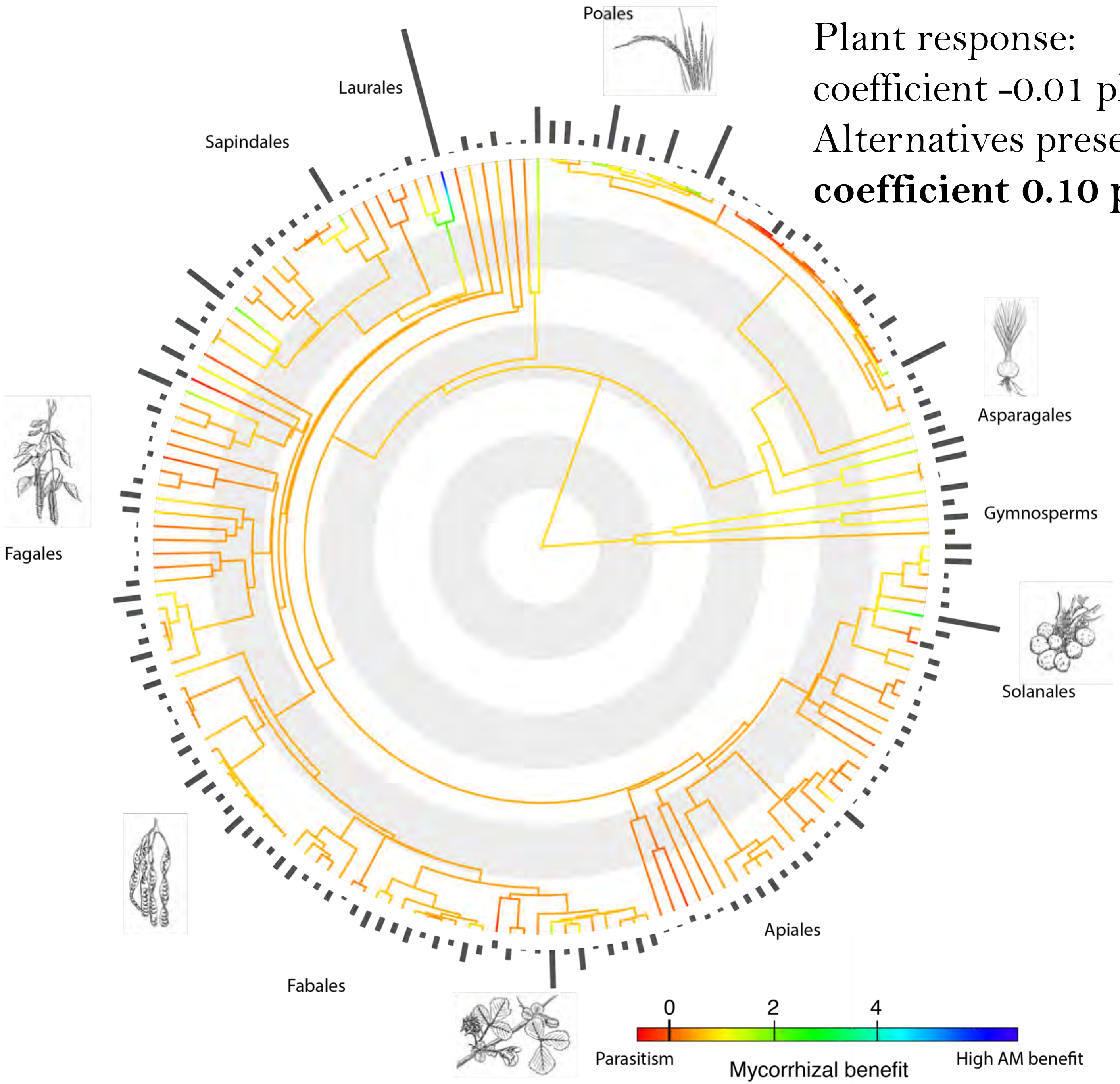
V. Bala Chaudhary *et al.**

No AMF　　　　With AMF



Poales
Laurales
Sapindales
Asparagales
Gymnosperms
Fagales
Solanales
Apiales
Fabales
0
2
4
Parasitism
Mycorrhizal benefit
High AM benefit

Plant response:
coefficient -0.01 pMCMC = 0.49
Alternatives presence:
coefficient 0.10 pMCMC < 0.01**



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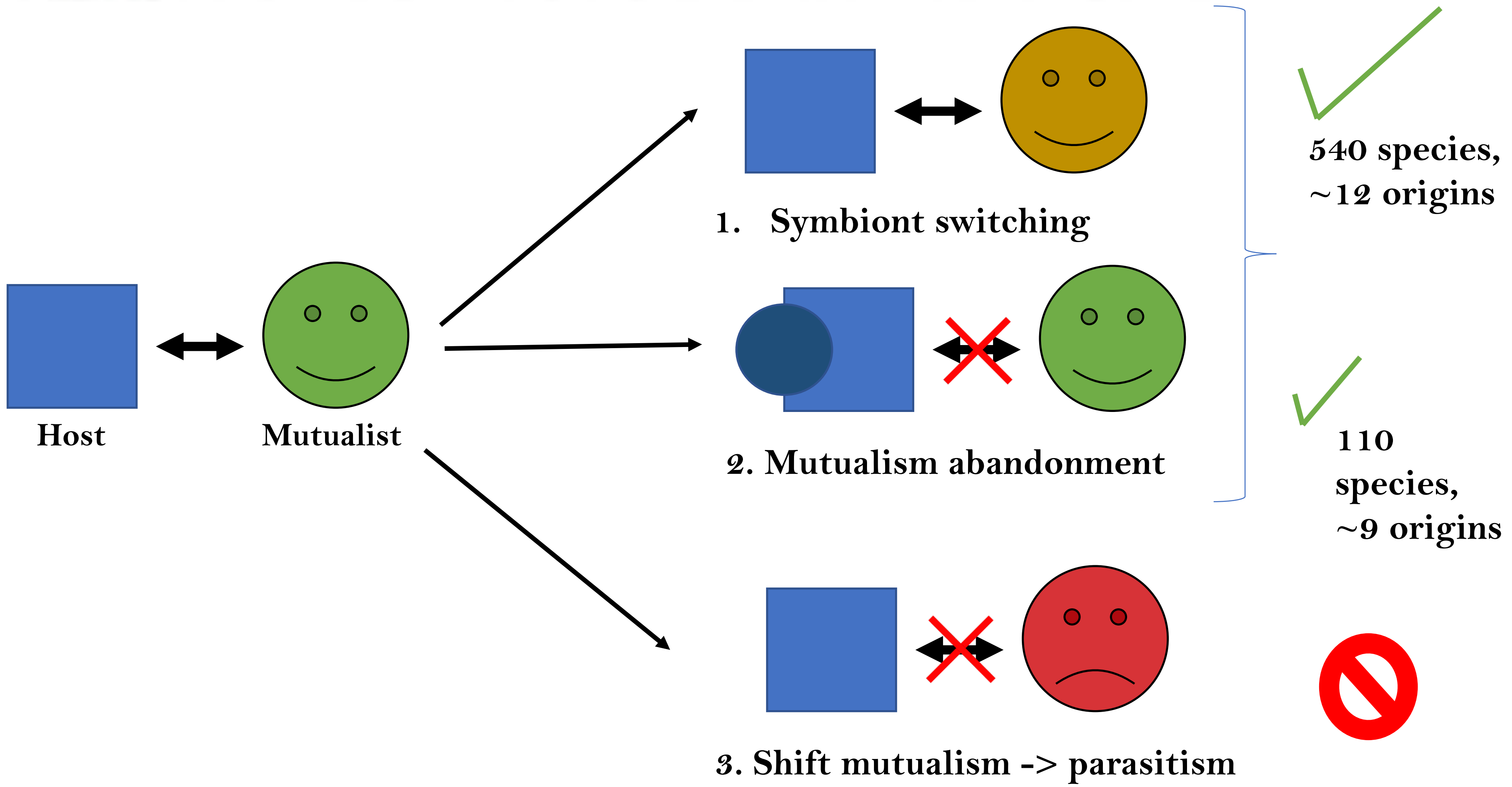
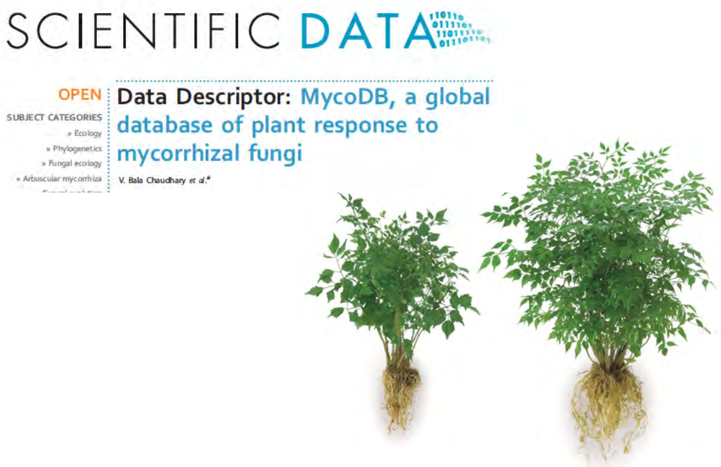
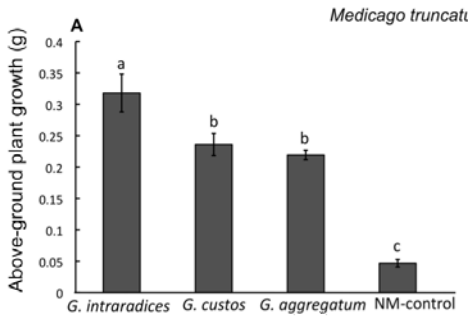


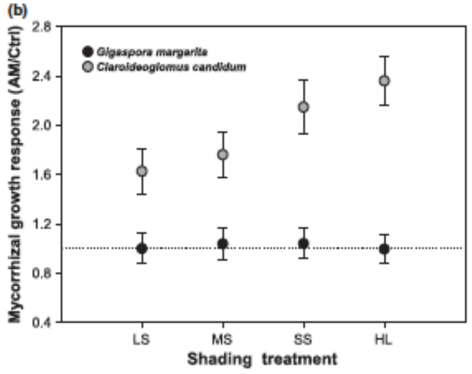


1. Negative growth effects common

In 611 / 2984 AMF studies



Kiers et al. 2011 Science



Zheng et al. (2015) New Phyt.

2. Variation in AMF 'quality'

SCIENTIFIC DATA

OPEN

SUBJECT CATEGORIES
» Ecology
» Phylogenetics
» Fungal ecology
» Arbuscular mycorrhiza

Data Descriptor: MycoDB, a global database of plant response to mycorrhizal fungi

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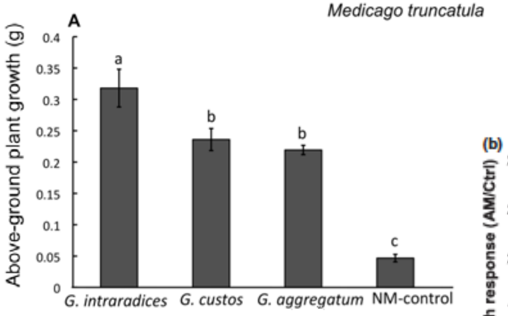
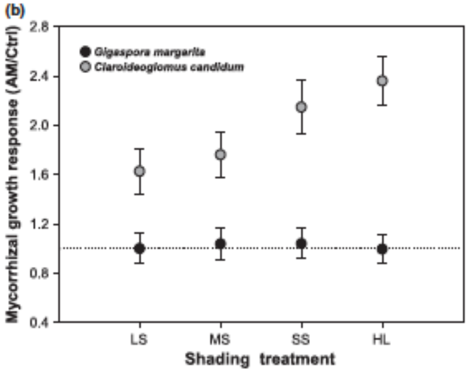


Kiers et al. 2011 Science



Zheng et al. (2015) New Phyt.

2. Variation in AMF 'quality'

Reciprocal Rewards Stabilize Cooperation in the Mycorrhizal Symbiosis

E. Toby Kiers,[1]*† Marie Duhamel,[1,2] Yugandhar Beesetty,[3,4] Jerry A. Mensah,[4] Oscar Franken,[1] Erik Verbruggen,[1] Carl R. Fellbaum,[4] George A. Kowalchuk,[1,5] Miranda M. Hart,[6] Alberto Bago,[7]‡ Todd M. Palmer,[8] Stuart A. West,[9] Philippe Vandenkoornhuyse,[2] Jan Jansa,[10] Heike Bücking[4]†

Ecology Letters, (2009) **12**: 13–21 doi: 10.1111/j.1461-0248.2008.01254.x

Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism

Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist

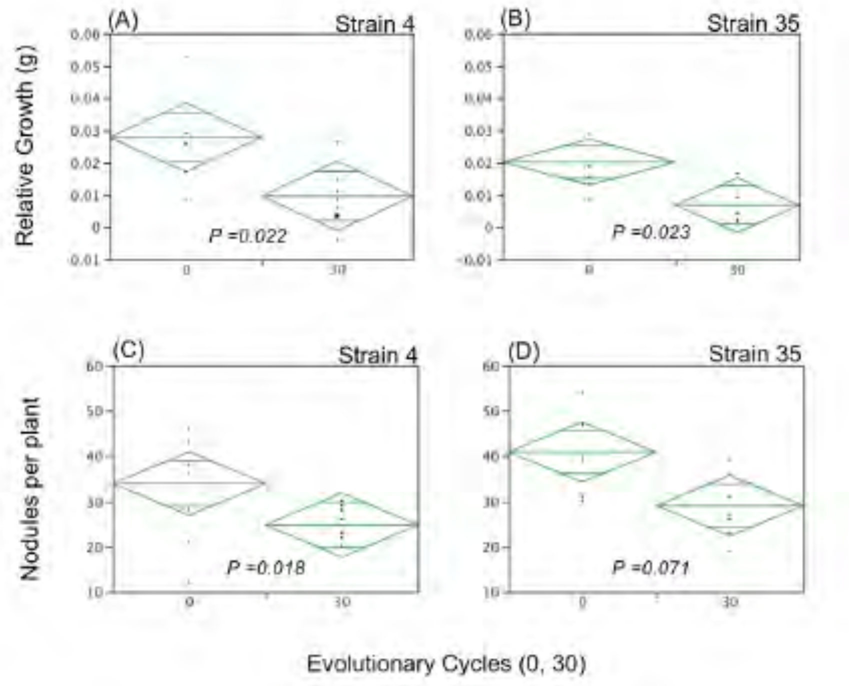
Chaoyuan Zheng[1,2,3], Baoming Ji[4], Junling Zhang[1,2], Fusuo Zhang[1,2] and James D. Bever[3]

3. Preferential allocations/rewards for cooperators

Evolutionary Instability of Symbiotic Function in *Bradyrhizobium japonicum*

Joel L. Sachs[1,2*], James E. Russell[1¤], Amanda C. Hollowell[1,2]

1 Department of Biology, University of California Riverside, Riverside, California, United States of America, 2 Institute for Integrative Genomic Sciences, University of California Riverside, Riverside, California, United States of America



Cheating /defection easily evolves (experimentally) in other root symbionts.

Paradox of stasis?

Cinnamon fern

Particularly for (sym)biotic interactions?

Long-term morphological stasis maintained by a plant–pollinator mutualism

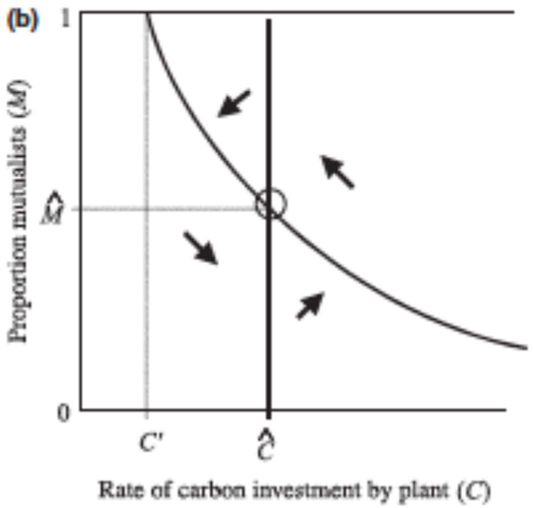
Charles C. Davis[a,1], Hanno Schaefer[a,b], Zhenxiang Xi[a], David A. Baum[c], Michael J. Donoghue[d,1], and Luke J. Ha

The role of biotic forces in driving macroevolution: beyond the Red Queen

Kjetil L. Voje, Øistein H. Holen, Lee Hsiang Liow and Nils Chr. Stenseth

Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066 Blindern, Oslo 0316, Norway

Oscillations in preferential allocations (rewarding) and % mycorrhizal cheaters

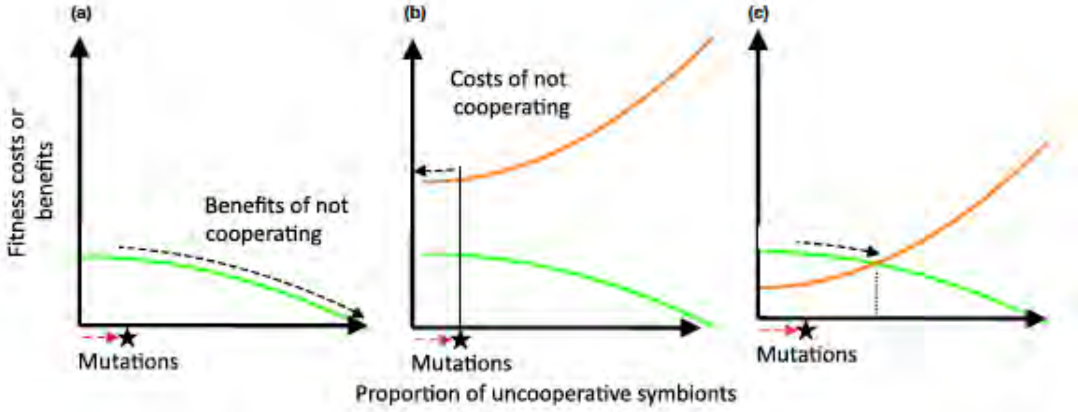


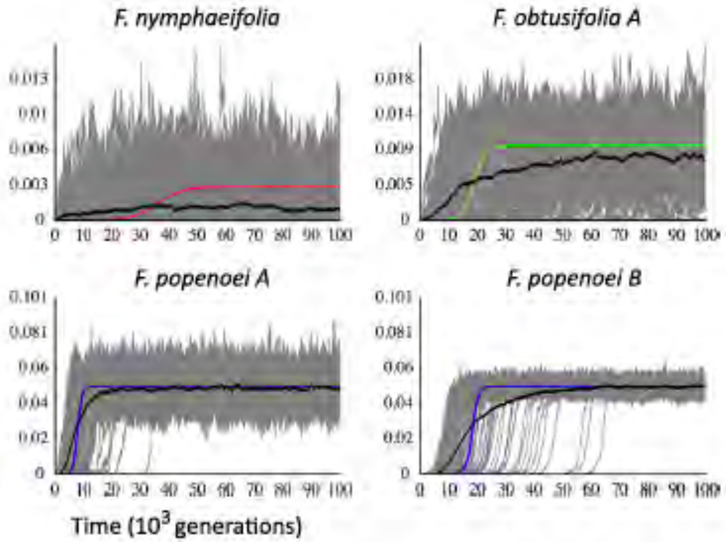
Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts

James D. Bever

Department of Biology, Indiana University, Bloomington, IN 47405, USA

Mutation-selection balance & equilibrium rewarding strength - cheating benefit

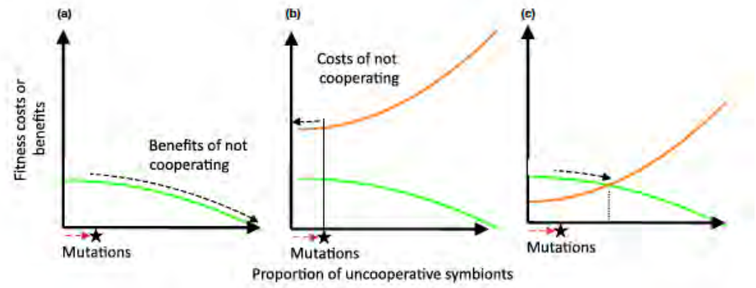




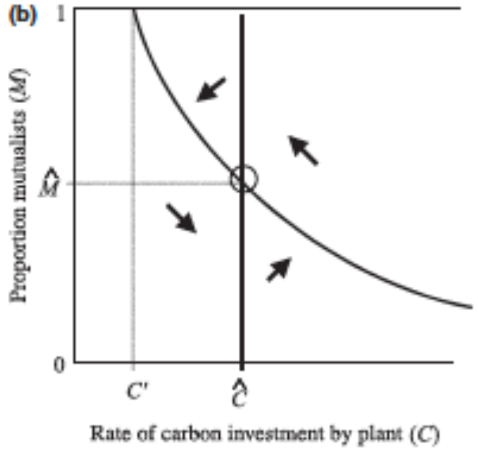
ECOLOGY LETTERS
Ecology Letters, (2017) 20: 922–932
doi: 10.1111/ele.12792

LETTER

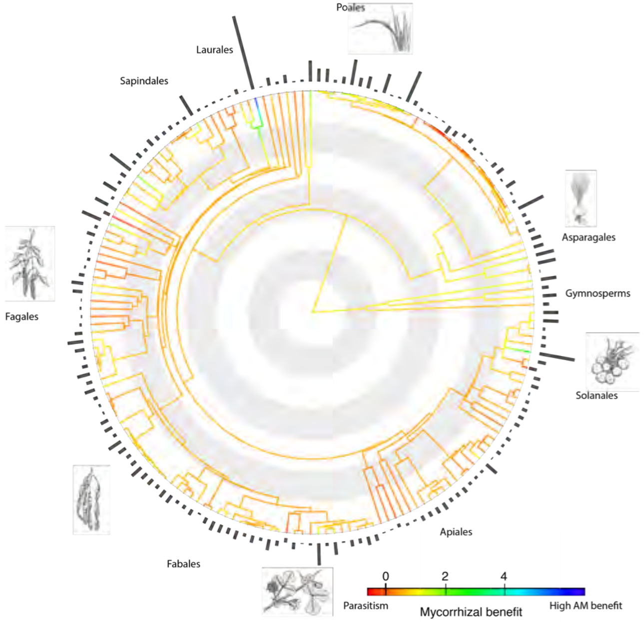
Why mutualist partners vary in quality: mutation–selection balance and incentives to cheat in the fig tree–fig wasp mutualism


(a)
(b)
(c)
Fitness costs or benefits
Benefits of not cooperating
Costs of not cooperating
Mutations
Mutations
Mutations
Proportion of uncooperative symbionts

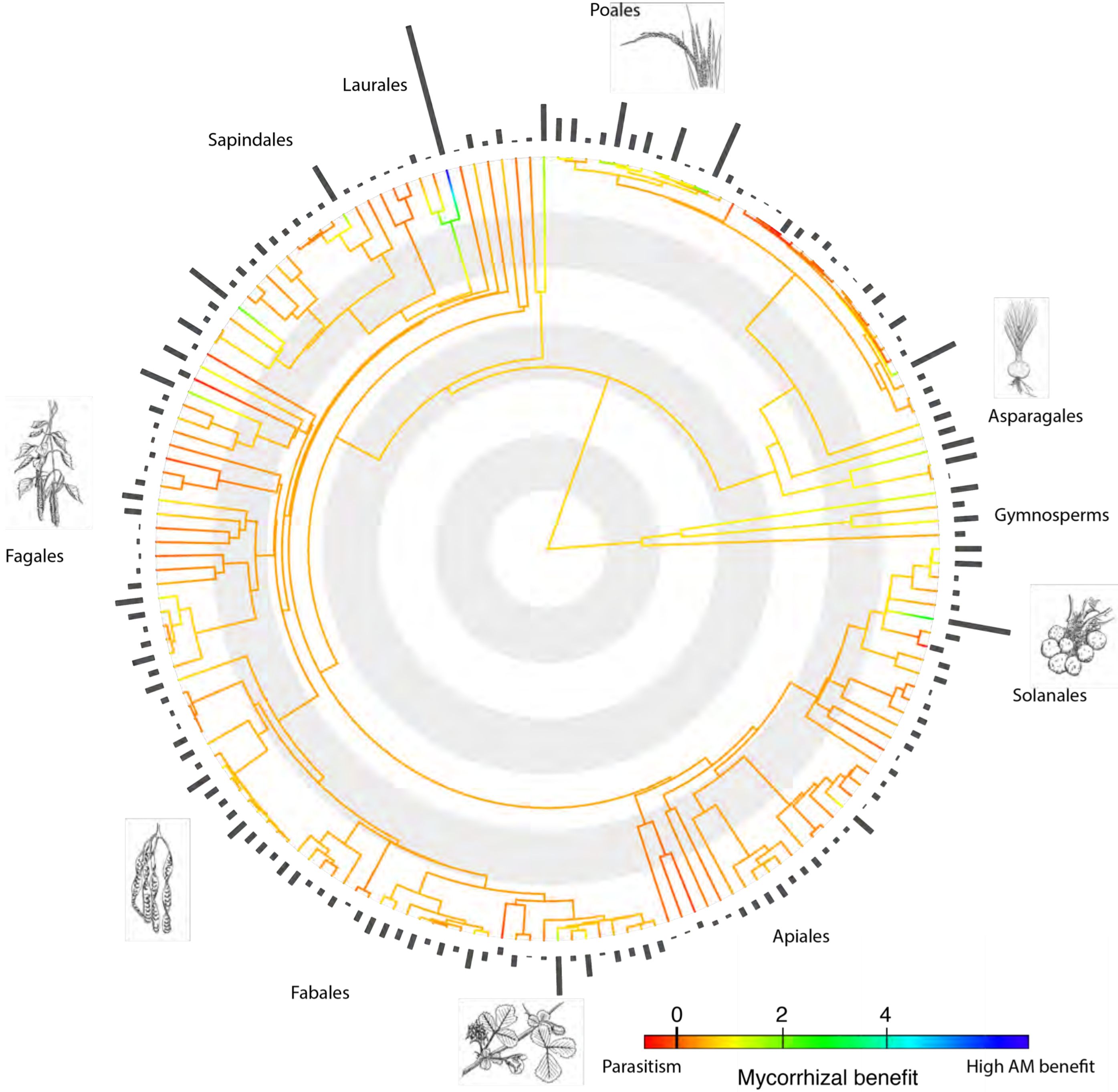
+


(b)
1
0
Proportion mutualists (M)
$\hat{M}$
C'
$\hat{C}$
Rate of carbon investment by plant (C)

=

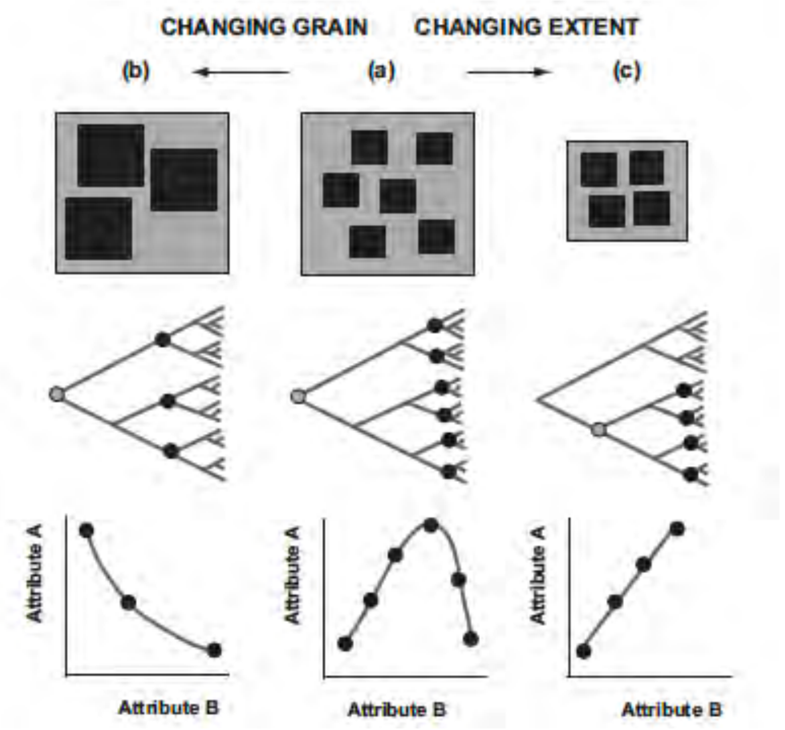

Poales
Laurales
Sapindales
Asparagales
Gymnosperms
Fagales
Solanales
Apiales
Fabales
0
2
4
Parasitism
Mycorrhizal benefit
High AM benefit

?

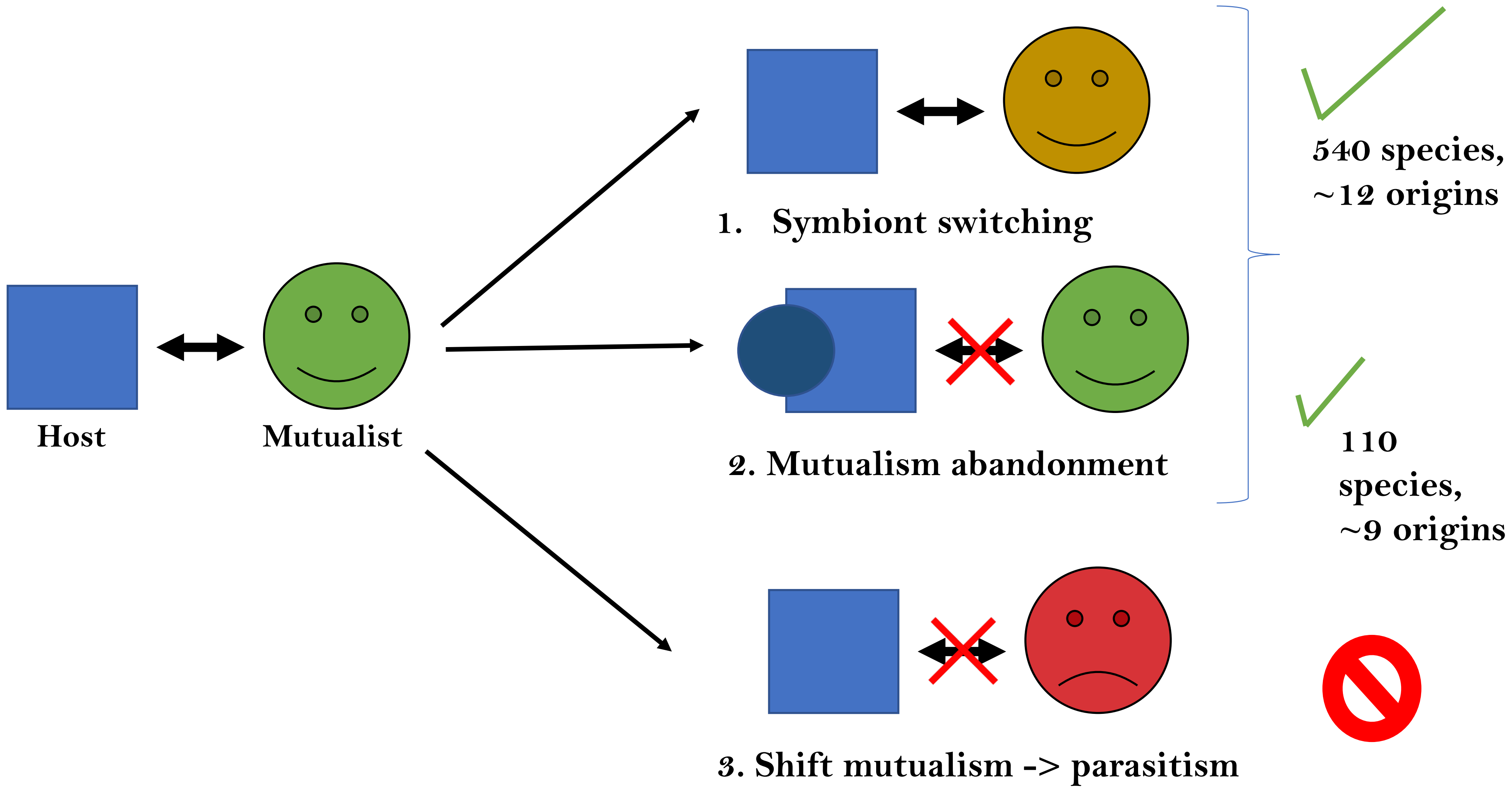


And/or, wrong (phylogenetic) scale?

Ideas?



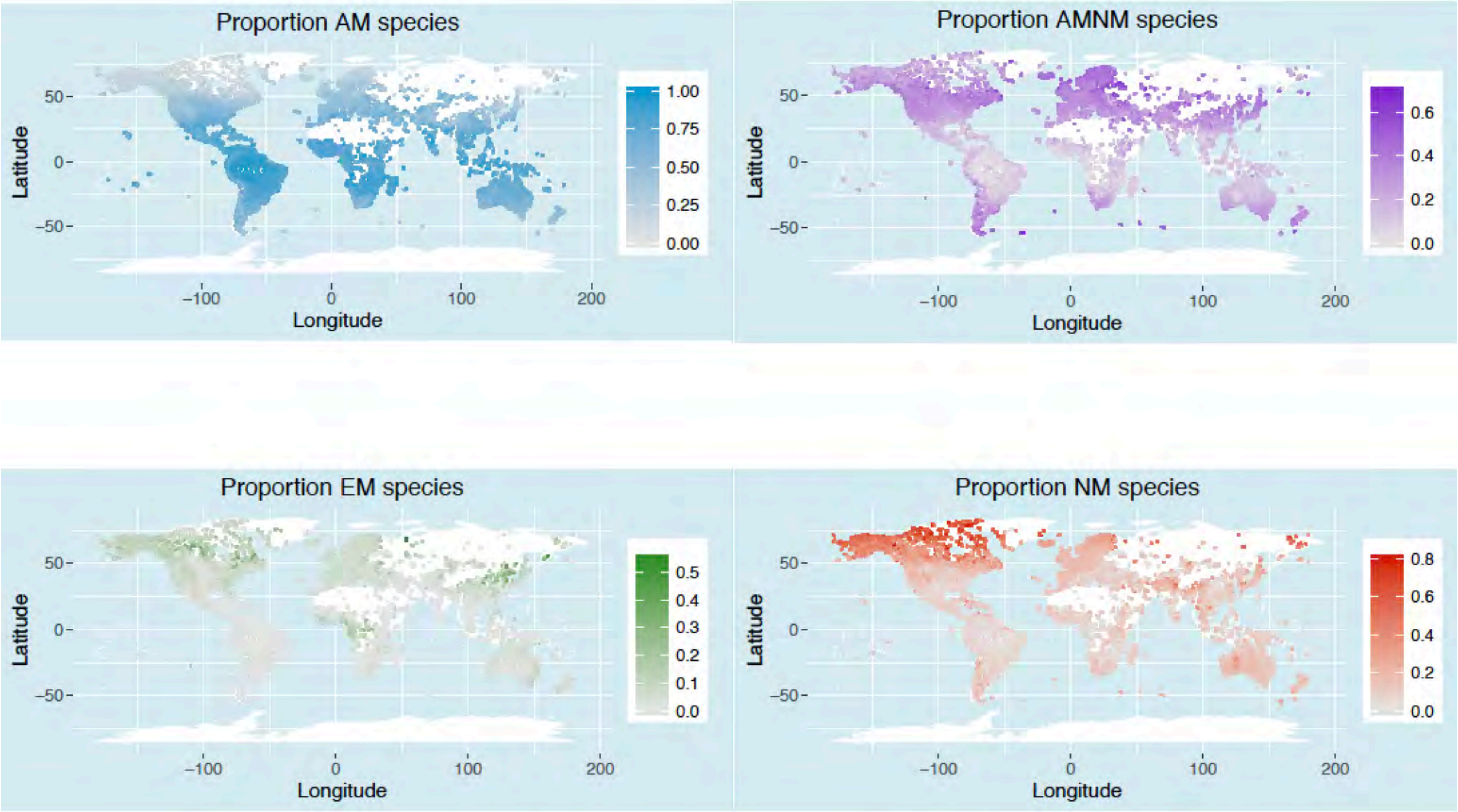
What ecological factors drive losses?

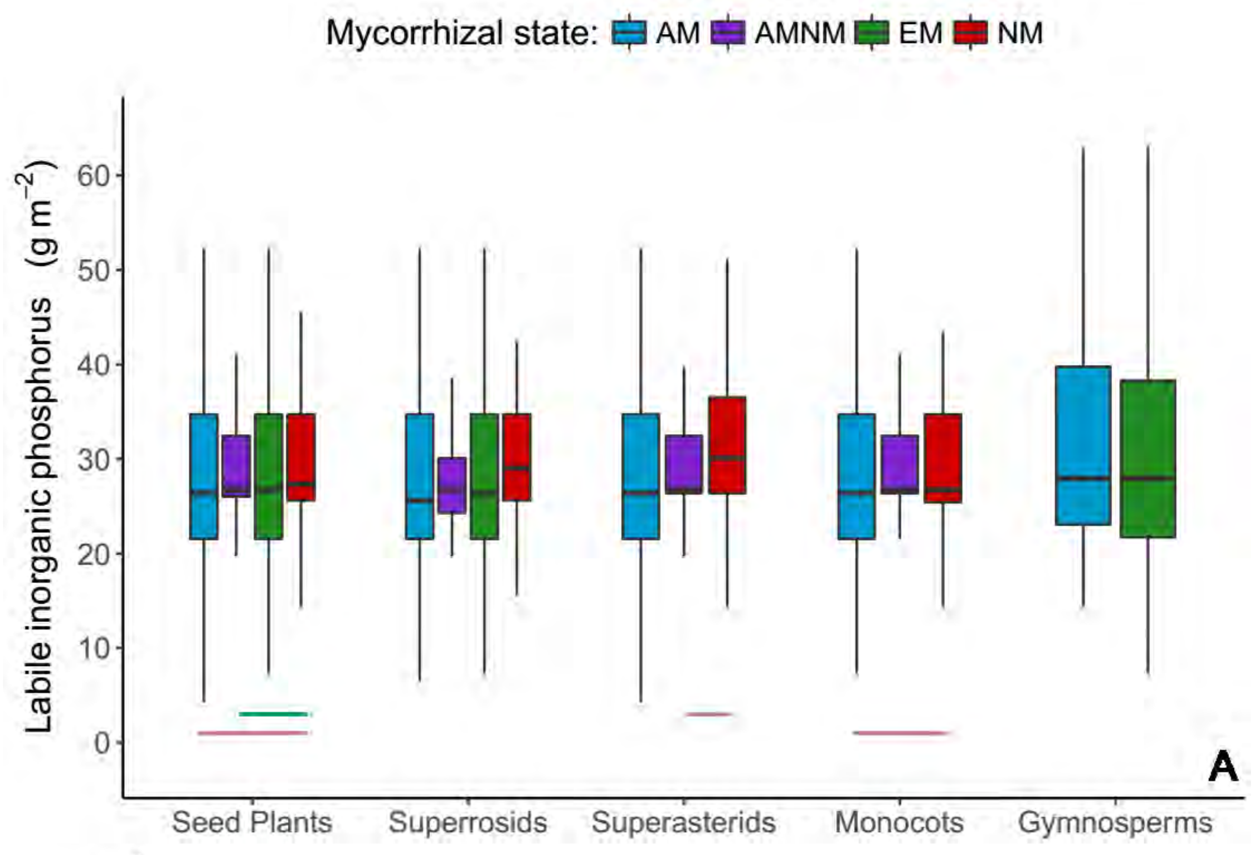


Prof. Hafiz Maherali, Guelph

Commonly thought: soil nutrients, particularly phosphorus

What ecological factors drive losses?



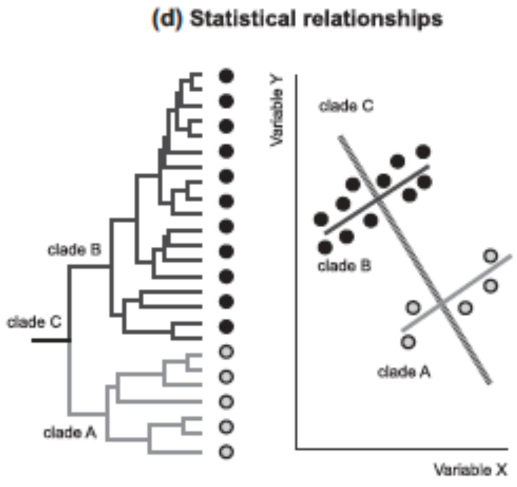


No clear effect of P on mycorrhizal status.

- Again, scaling issues?

Conclusions

- Large-scale comparative work can discover important drivers in (social) evolution
- Think about the scale of your trait
- Move back-and-forth between levels.
- Negative results – when can you be sure?



Thanks to..

Prof. Toby Kiers, VU Amsterdam

Prof. Stuart West, University of Oxford

UNIVERSITY OF OXFORD

SURF SARA

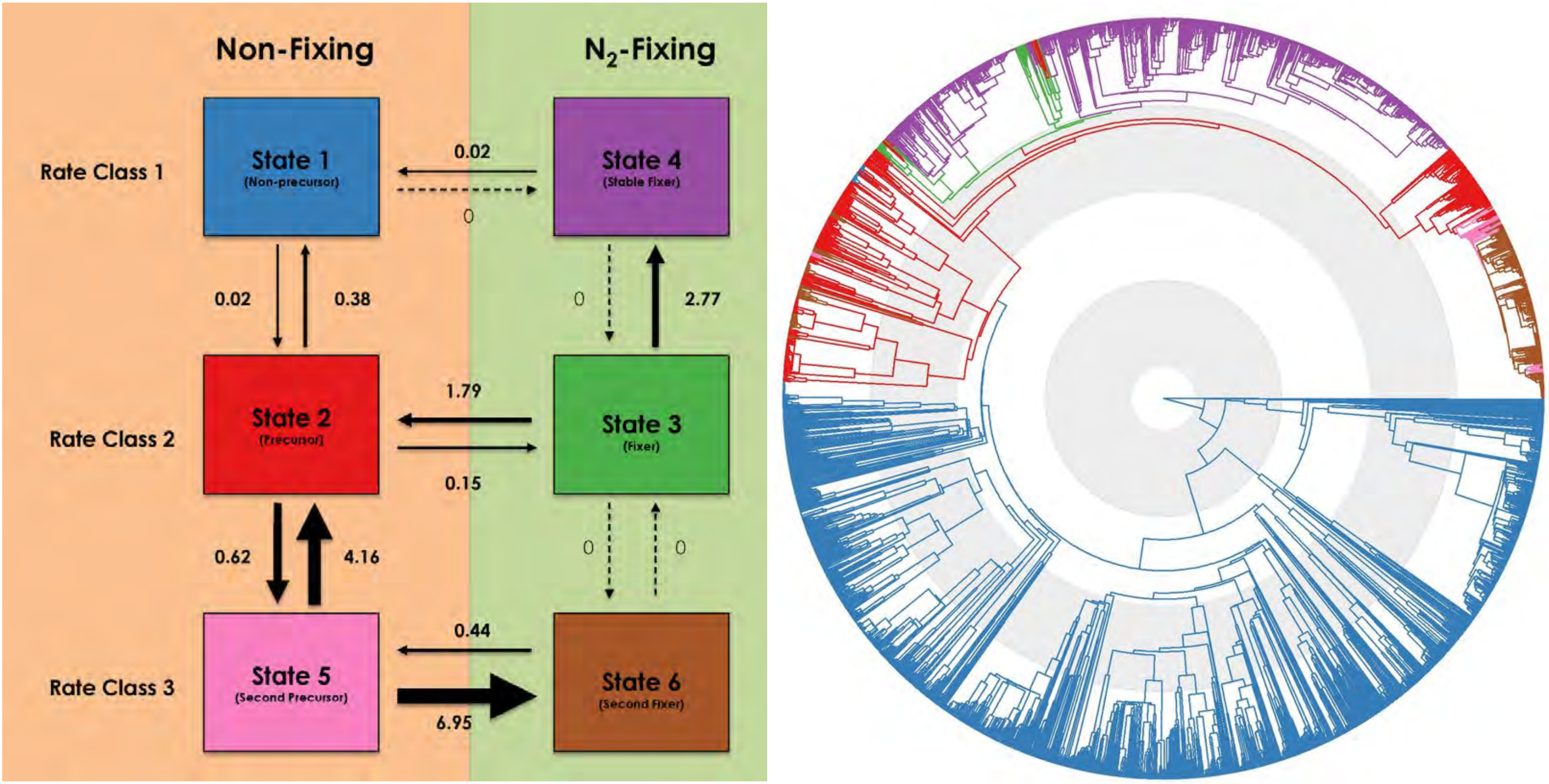
newton international fellowships

THE ROYAL SOCIETY

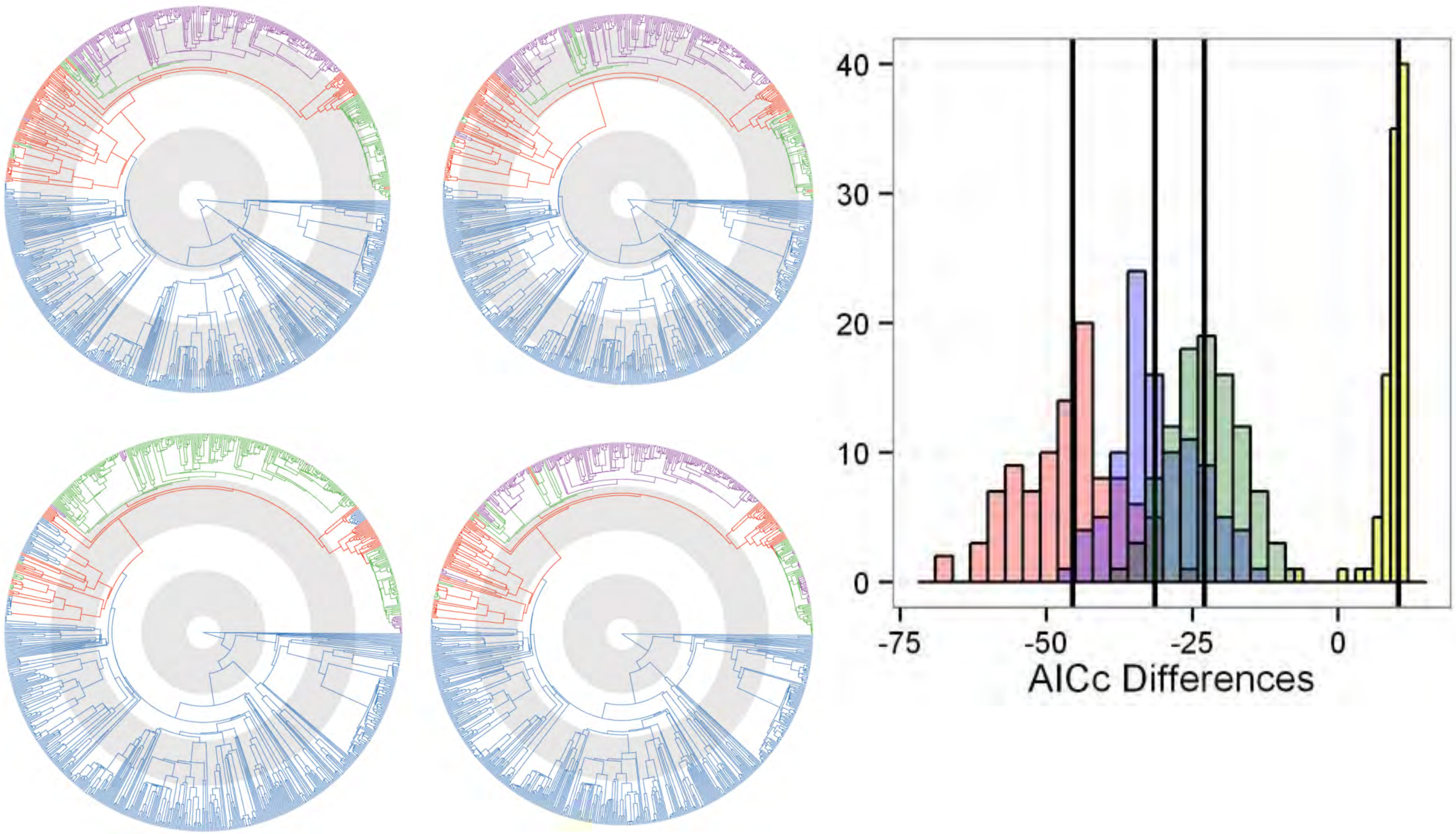
BALLIOL COLLEGE UNIVERSITY OF OXFORD

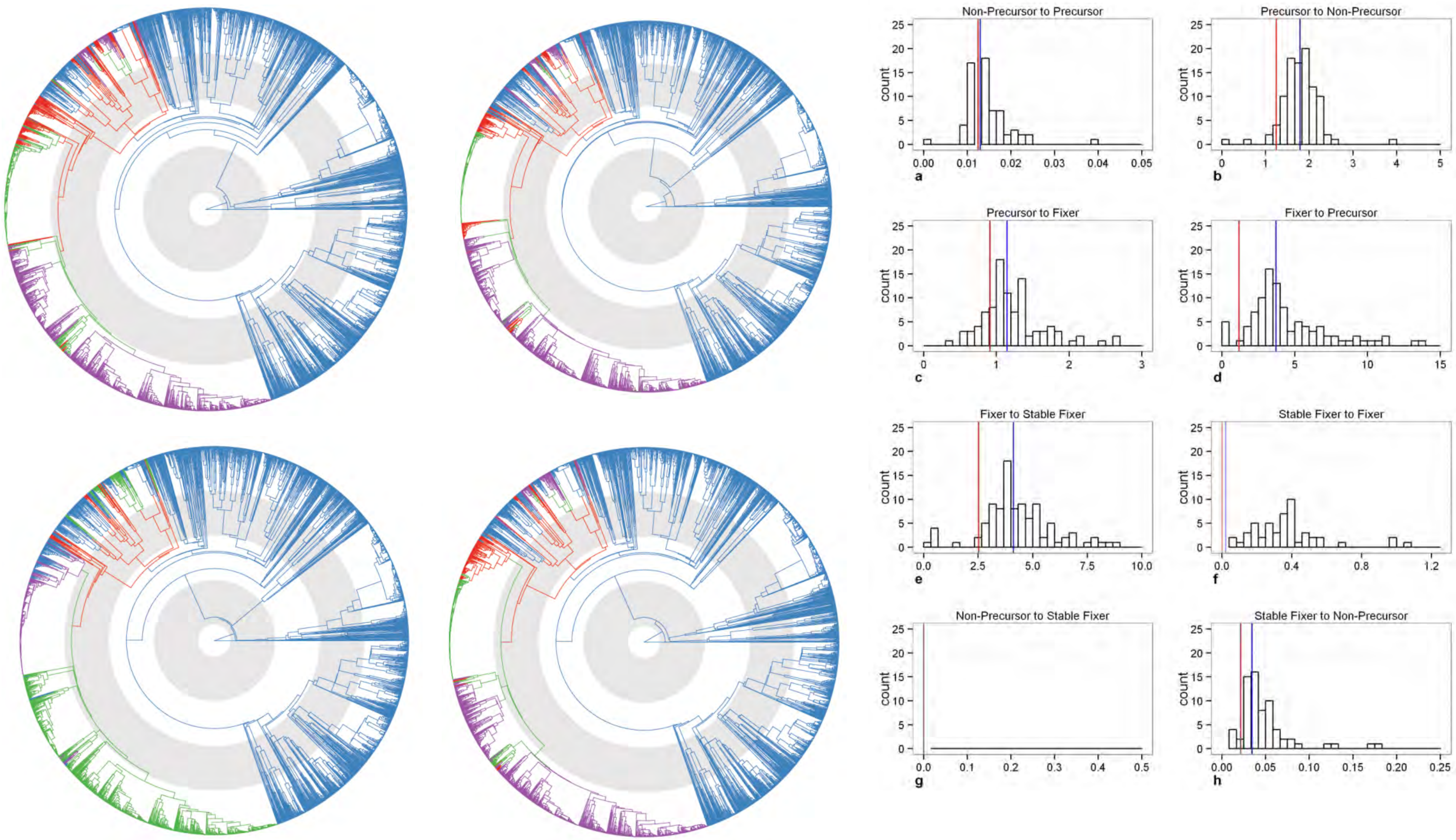
www.gijsbertwerner.com / @Gijsbertwerner

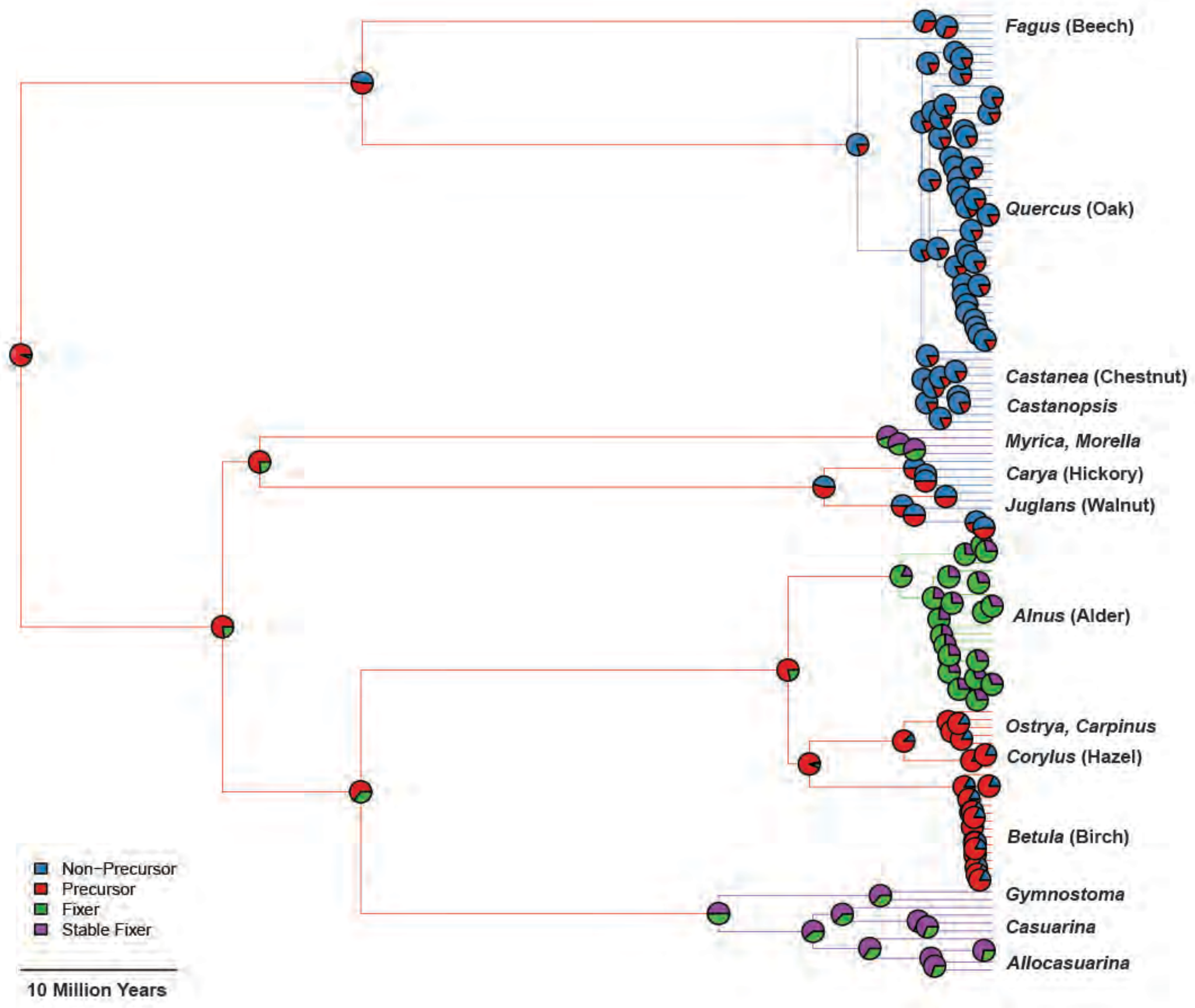
Model	Number of rate classes	Number of parameters	AICc weights
Homogenous	1	2	<<0.01 %
Single precursor	2	8	55.5 %
Limited single precursor*	2	4	0.27 %
Two precursors	3	14	42.9 %
Three precursors	4	20	1.38 %
Four precursors	5	26	<<0.01%



Non-Fixing
N_2-Fixing
Rate Class 1
Rate Class 2
Rate Class 3
State 1
(Non-precursor)
State 2
(Precursor)
State 3
(Fixer)
State 4
(Stable Fixer)
State 5
(Second Precursor)
State 6
(Second Fixer)
0.02
0
0.02
0.38
0
2.77
1.79
0.15
0.62
4.16
0
0
0.44
6.95

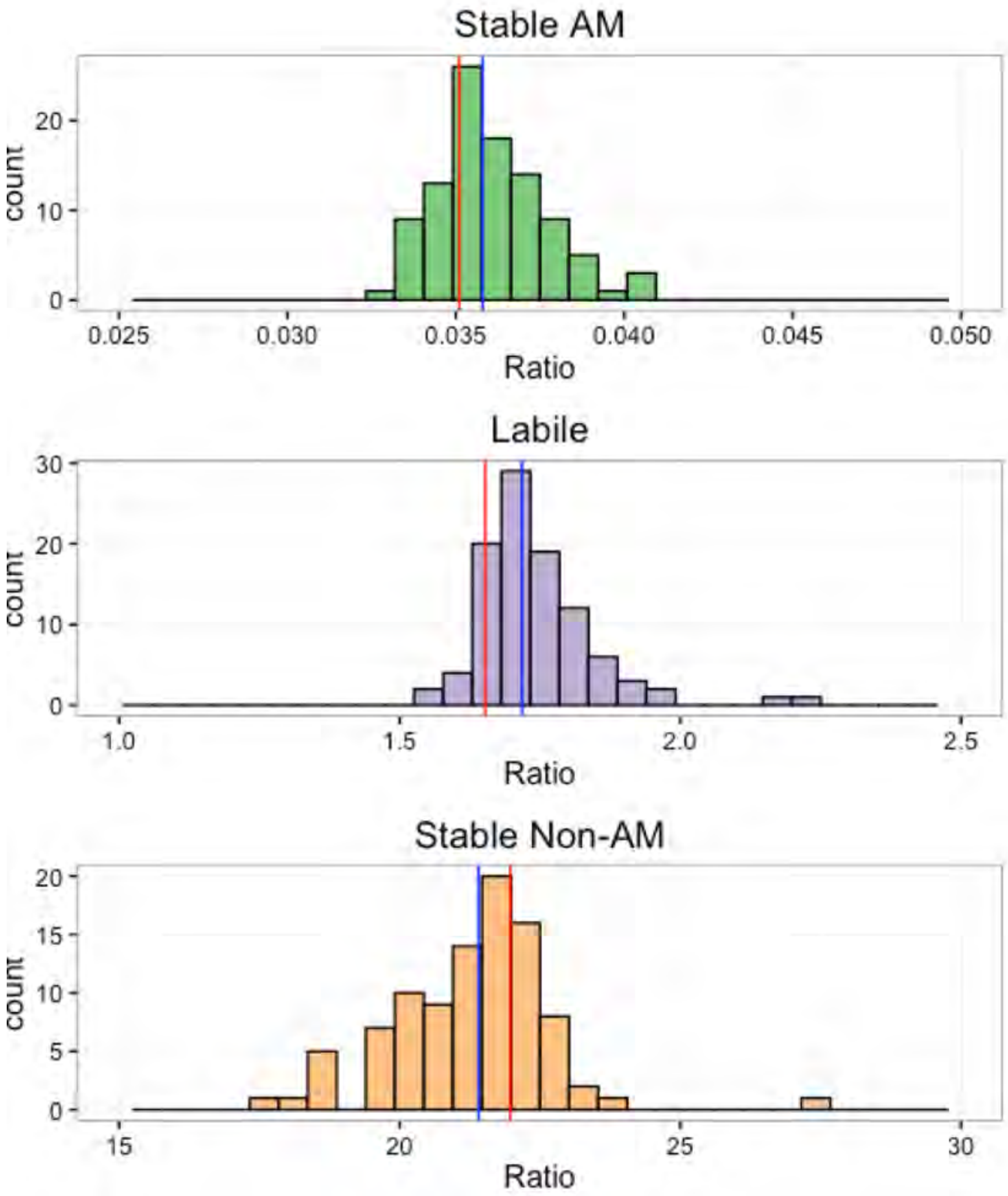

40
30
20
10
0
-75
-50
-25
0
AICc Differences


Non-Precursor to Precursor
Precursor to Non-Precursor
Precursor to Fixer
Fixer to Precursor
Fixer to Stable Fixer
Stable Fixer to Fixer
Non-Precursor to Stable Fixer
Stable Fixer to Non-Precursor
count
a
b
c
d
e
f
g
h

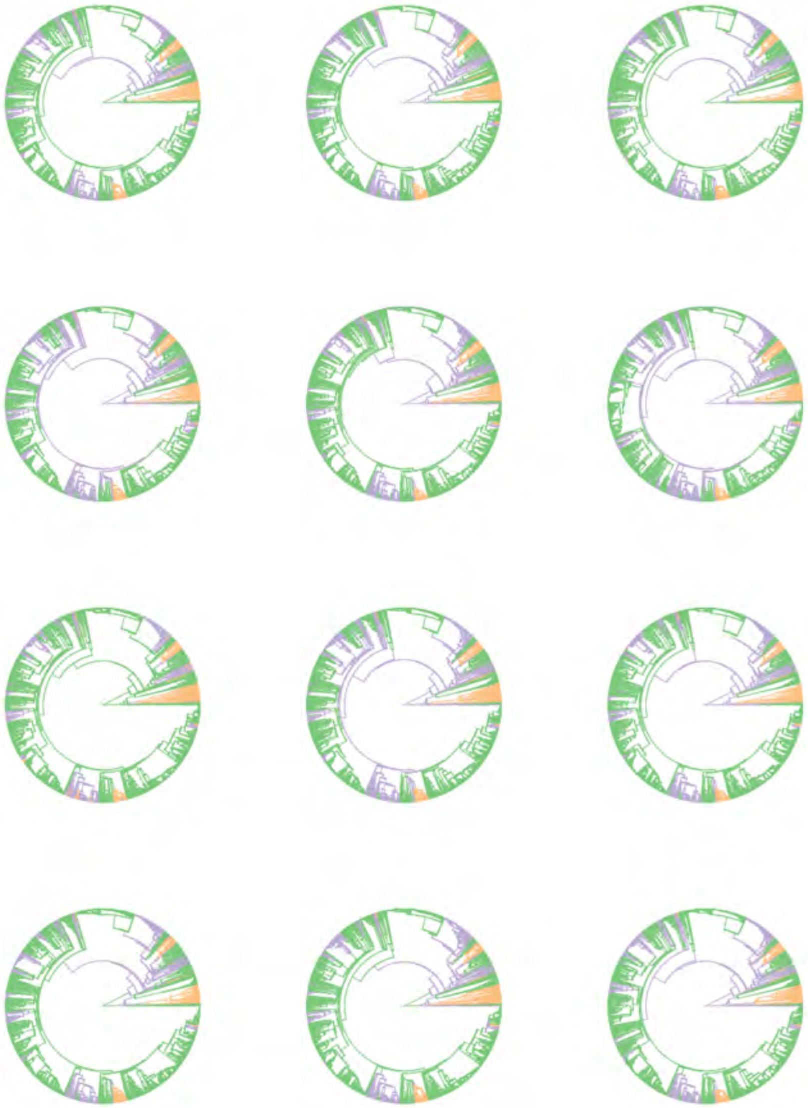


Fagus (Beech)
Quercus (Oak)
Castanea (Chestnut)
Castanopsis
Myrica, Morella
Carya (Hickory)
Juglans (Walnut)
Alnus (Alder)
Ostrya, Carpinus
Corylus (Hazel)
Betula (Birch)
Gymnostoma
Casuarina
Allocasuarina
Non-Precursor
Precursor
Fixer
Stable Fixer
10 Million Years

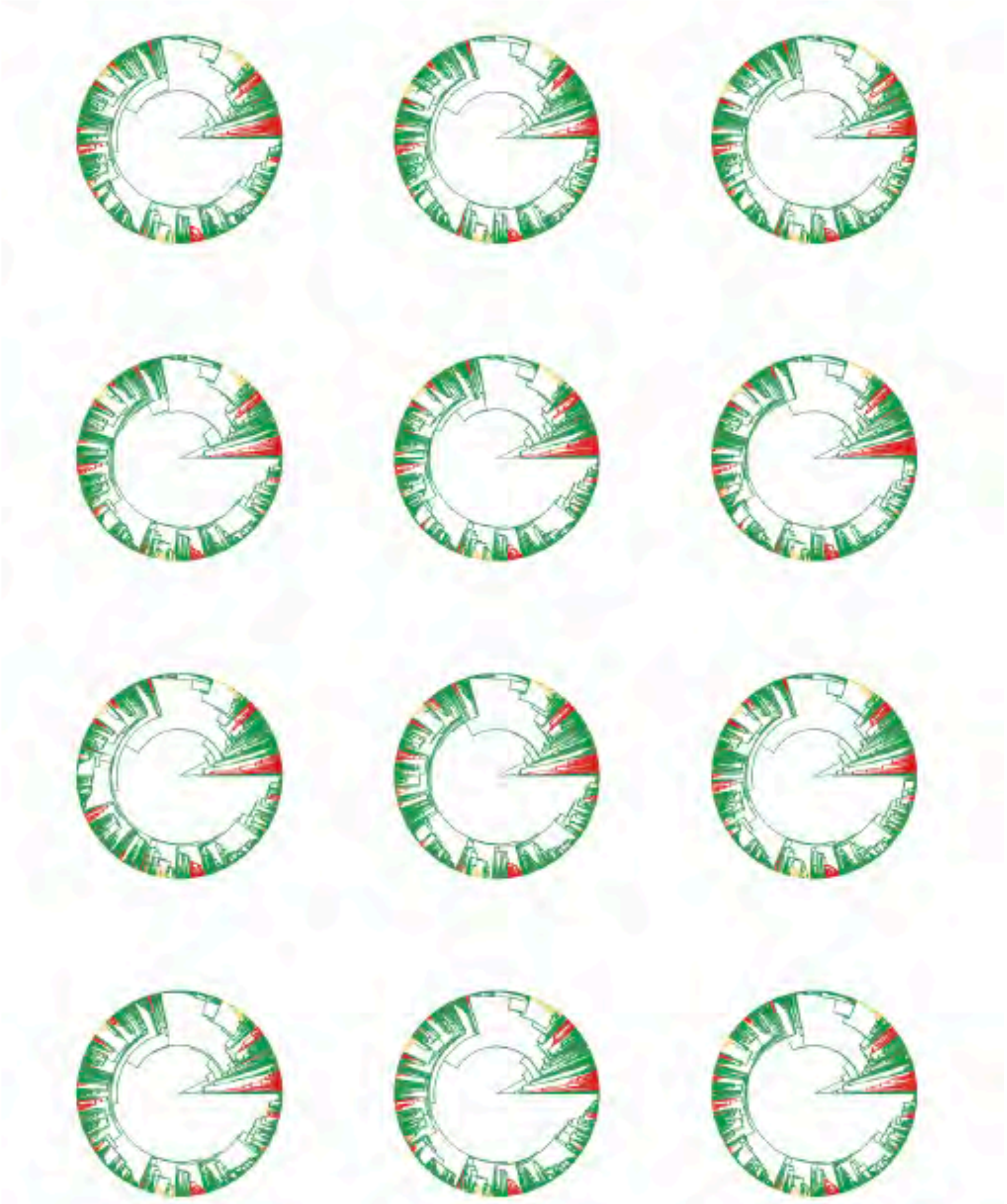
Three stability classes are robust to phylogenetic uncertainty..



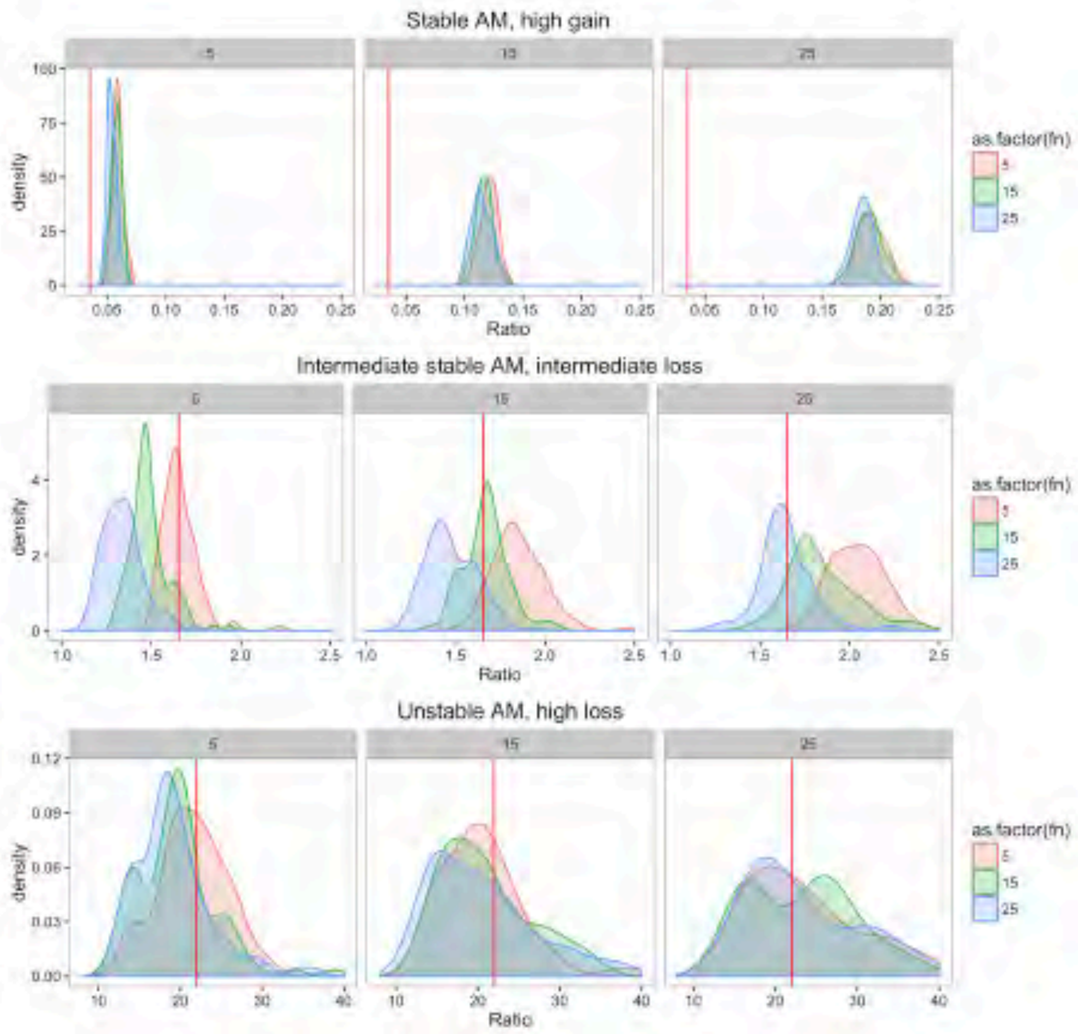
Three stability classes are robust to phylogenetic uncertainty..



And correlated revolution is also robust..



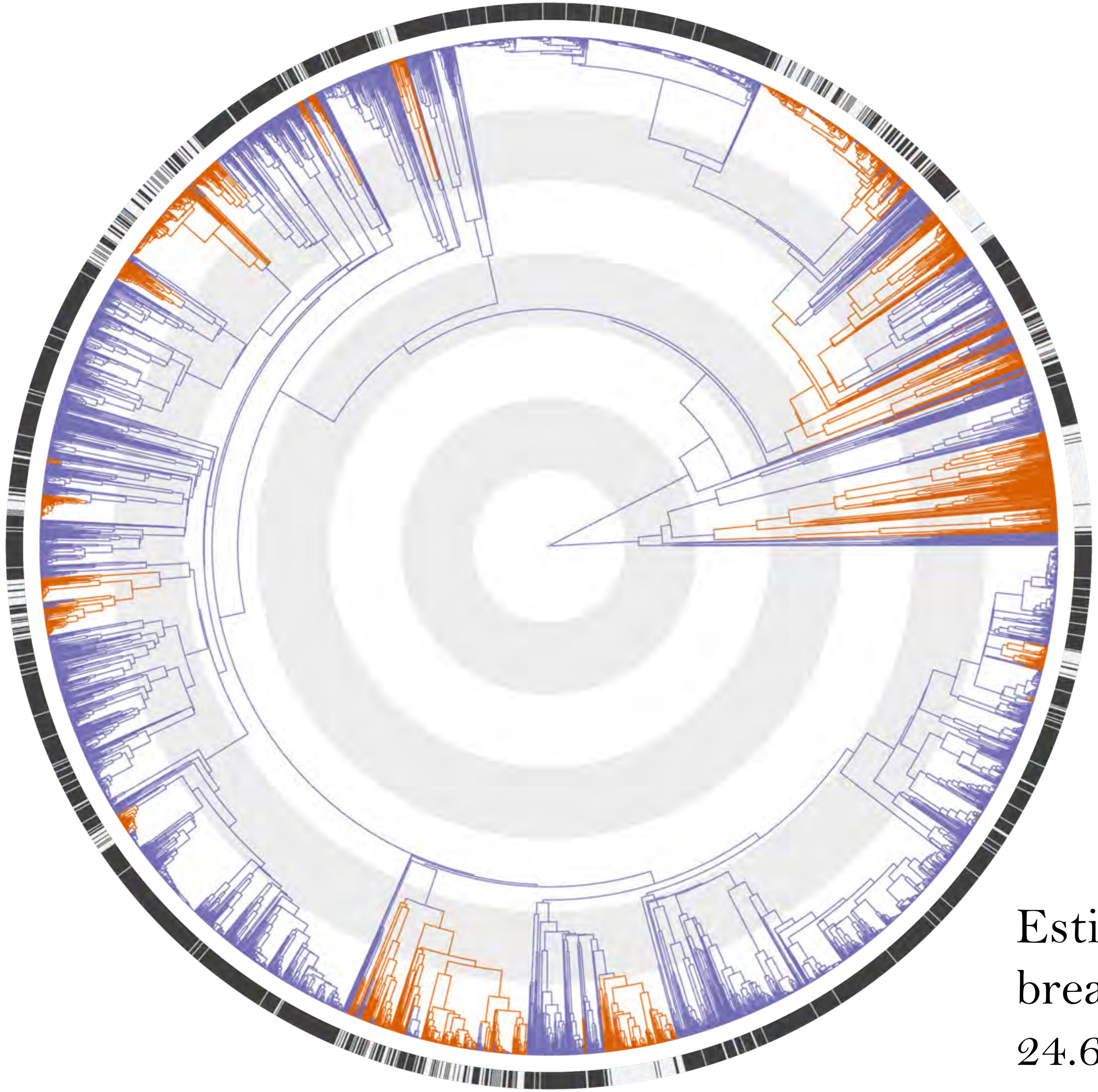
...and to data uncertainty & bias



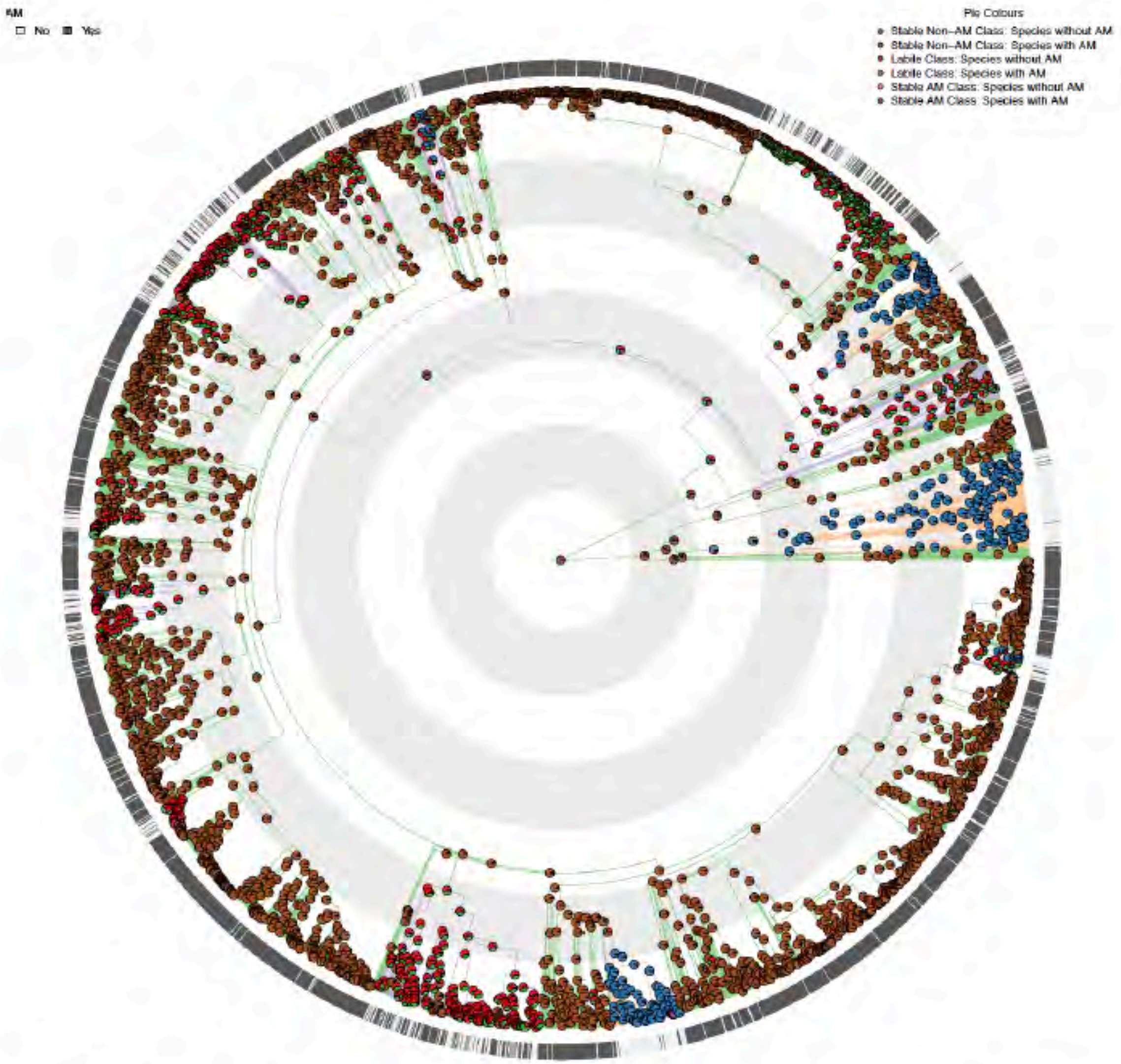
Even up to 25% false positive and 25% false negative!

SI Table 2: Mean Δ-AICc across 100 replicates of different resimulated false positive and false negative rates.

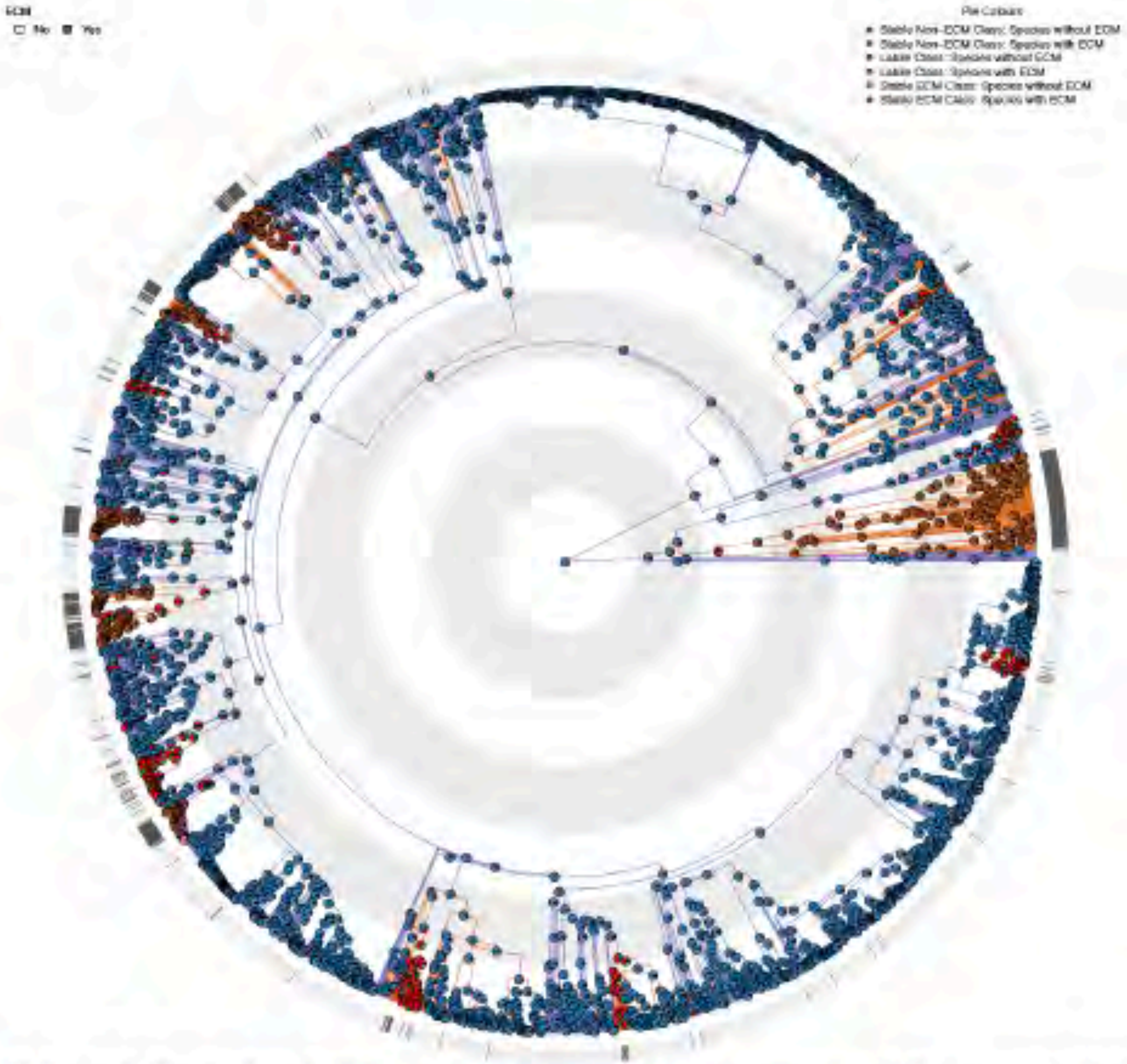
False positive rate	False negative rate	Mean Δ-AICc
5%	5%	470.6
5%	15%	494.7
5%	25%	520.9
15%	5%	472.8
15%	15%	495.9
15%	25%	518.2
25%	5%	467.5
25%	15%	489.3
25%	25%	518.0



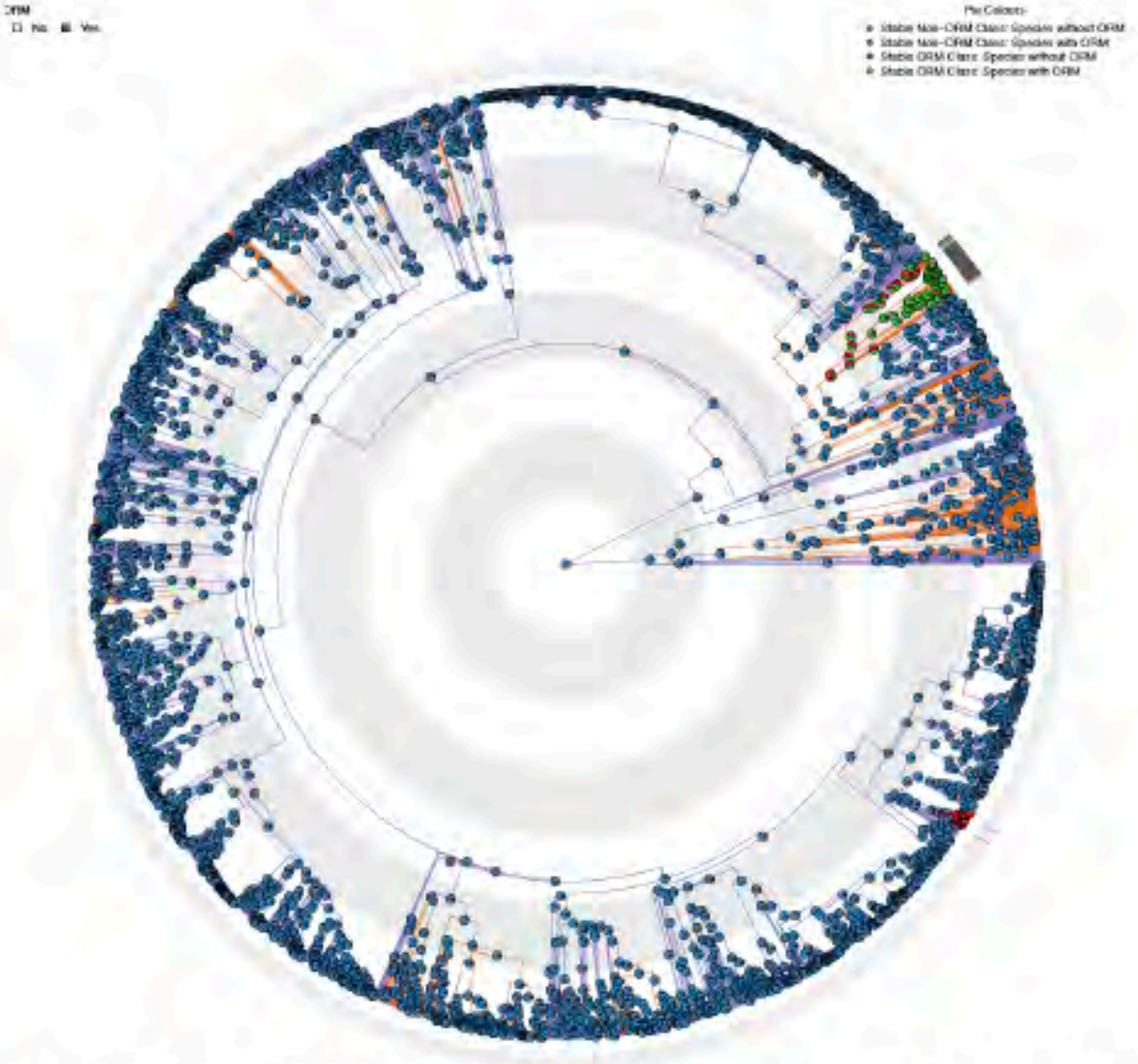
Estimated # breakdowns:
24.6 (25.4, SD 7.7)



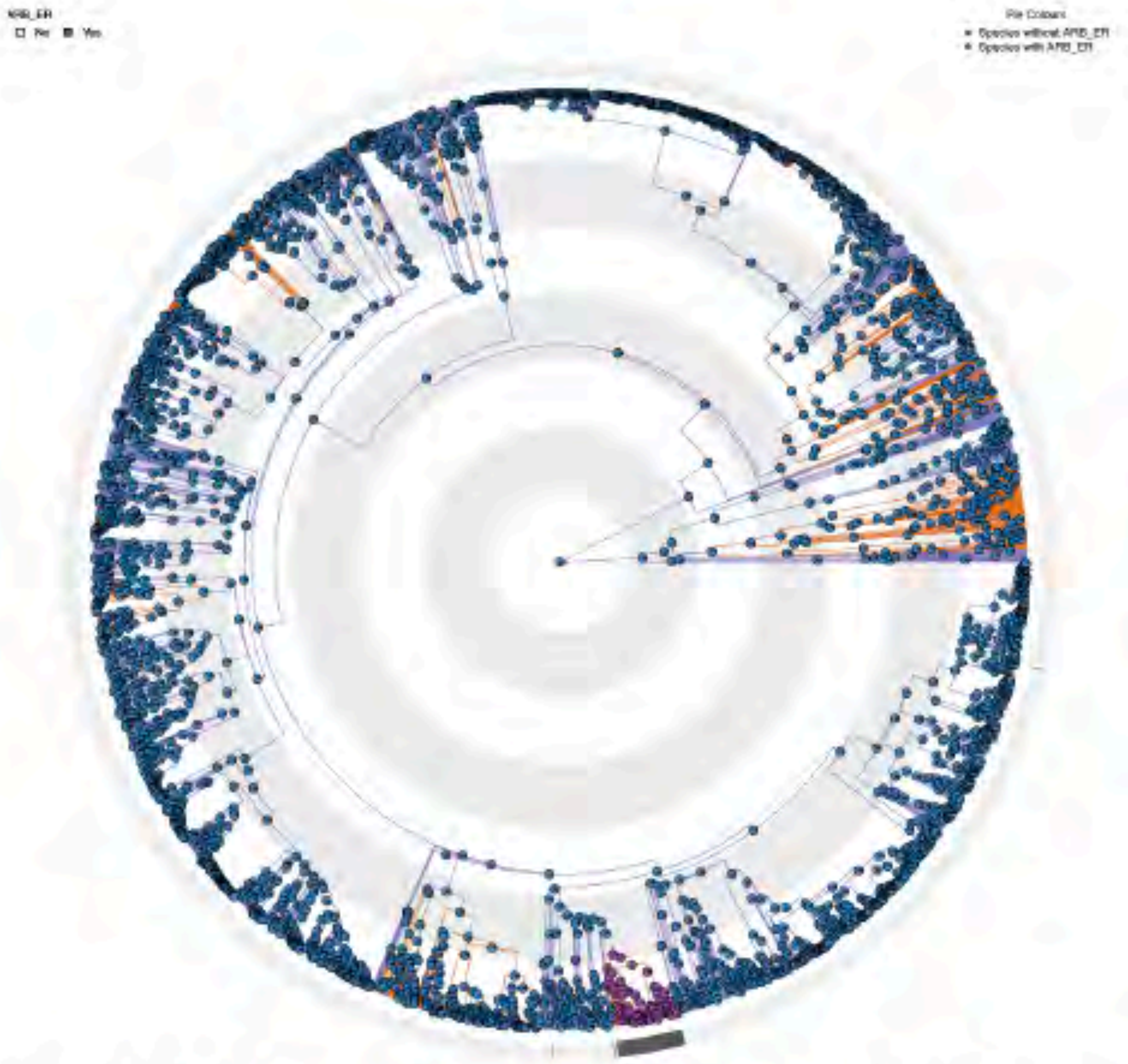
SI Figure 2: Three stability classes of the plant-AM fungal mutualism (See SI Figure 1) are found throughout the seed plants. Branches are coloured according to stability classes from SI Figure 1 (green, purple and orange pastel colours), while pie charts indicate the character state for each node also matching the colours from SI Figure 1. The coloured band around the phylogeny indicates the reported presence (dark grey) or absence of AM interactions across 3,736 species. Grey and white concentric circles indicate periods of 50 million years. An expanded version of this figure, containing fully legible species names (when zooming in) is available online as a high-resolution pdf-file.



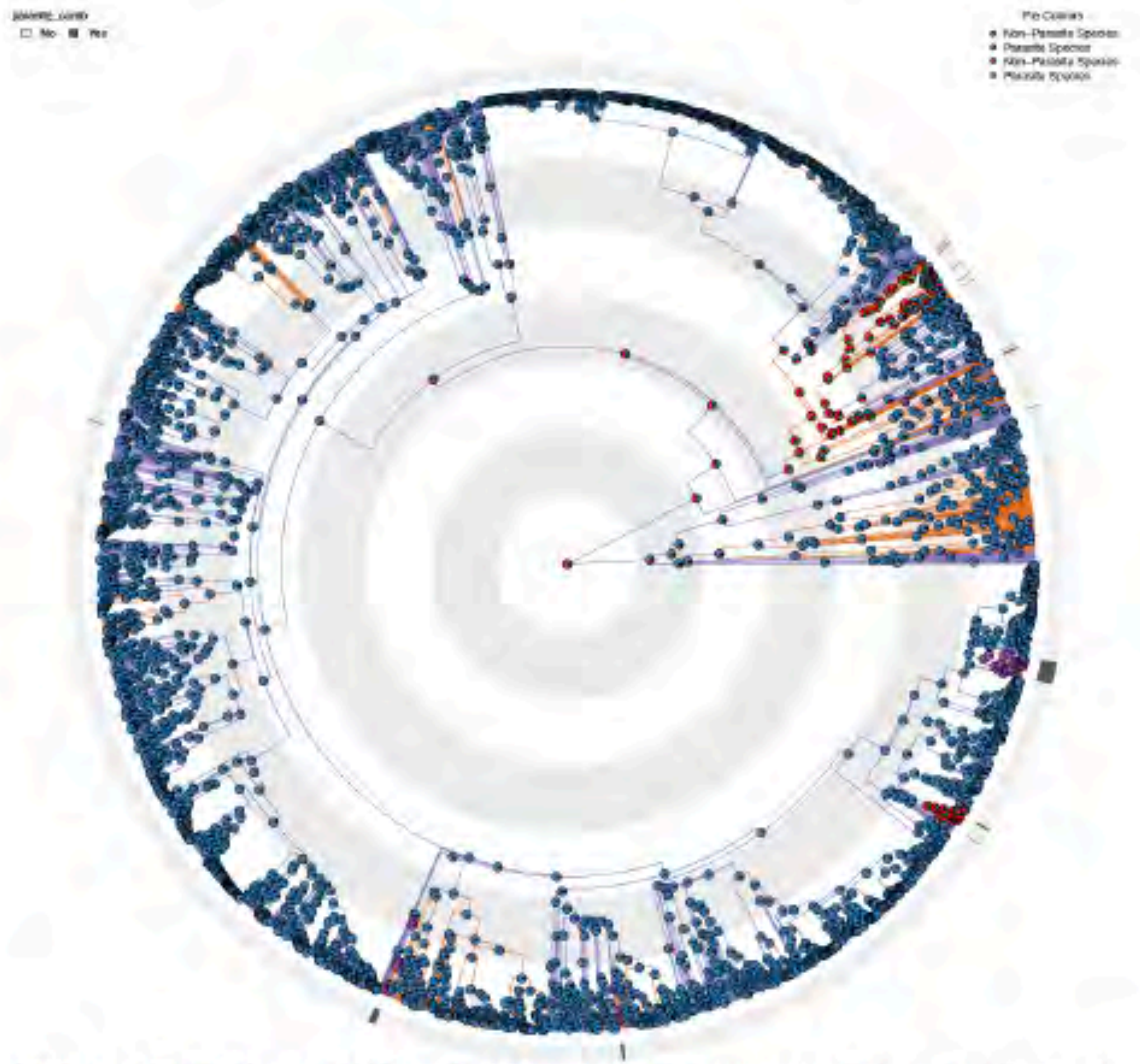
SI Figure 3: The pie charts in this figure depict the ancestral state reconstruction of plant-ectomycorrhizal fungi (EM) interactions under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of EM interactions across our 3,736 species. The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We visually observe that AM-loss in many cases co-occurs with an evolutionary shift to EM fungal interactions, most prominently in the Pines.



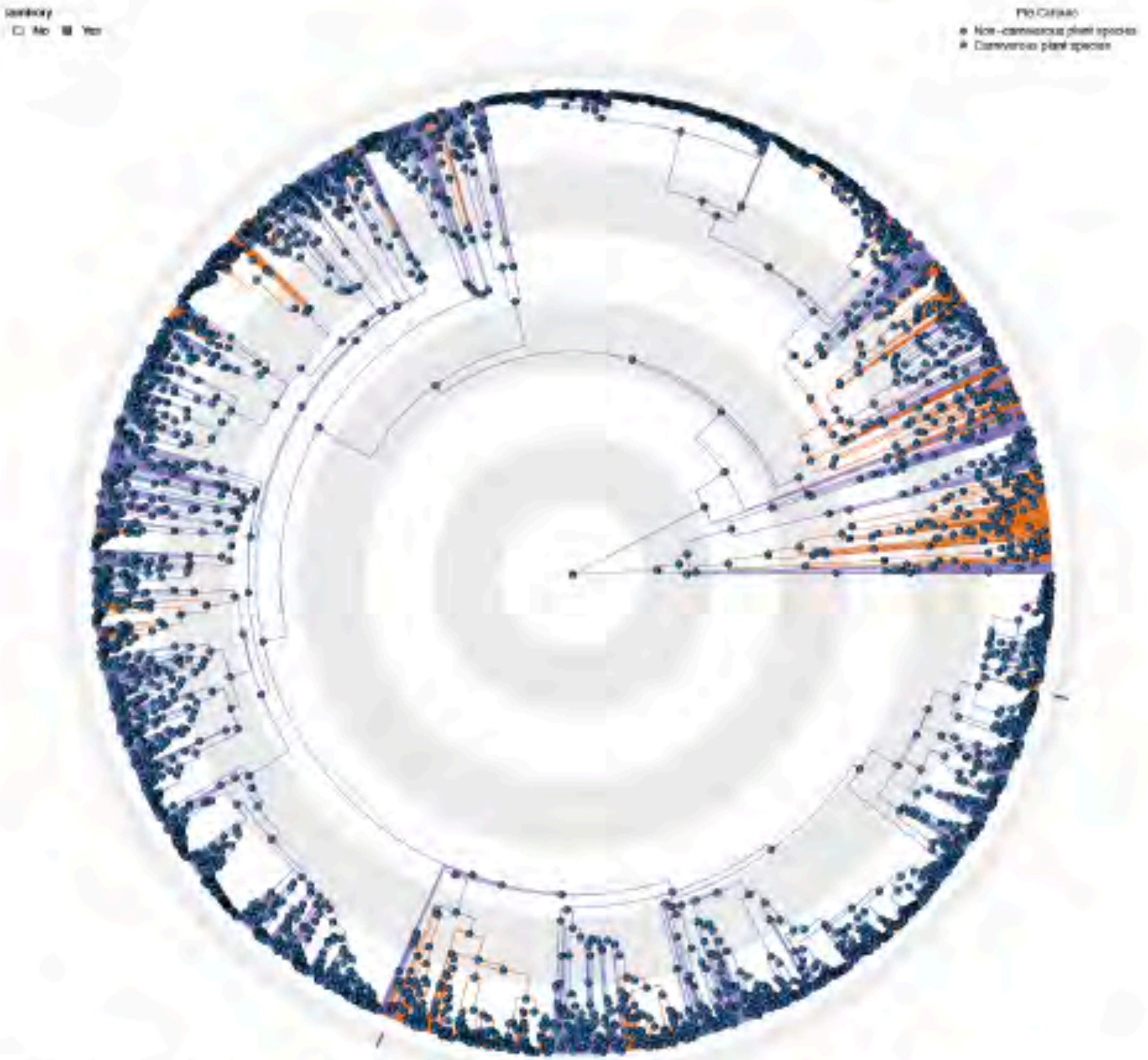
SI Figure 4: The pie charts in this figure depict the ancestral state reconstruction of plant-orchid fungi (ORM) interactions under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of ORM interactions across our 3,736 species. The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We visually observe that AM-loss co-occurs with a shift to ORM fungi in the Orchids.



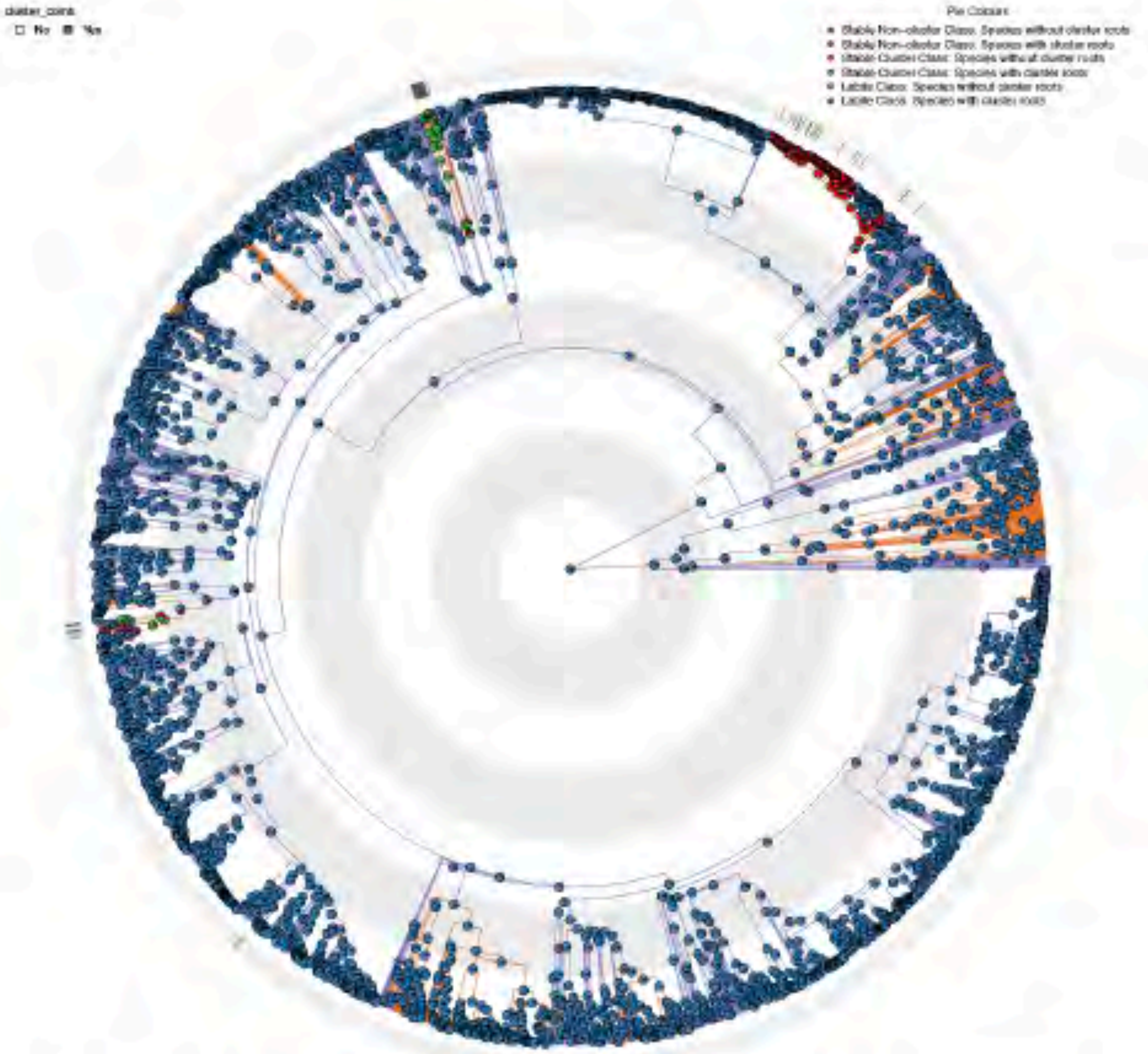
SI Figure 5: The pie charts in this figure depict the ancestral state reconstruction of plant interactions with Arbutoid (ARB) and Ericoid (ER) mycorrhizal fungi under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of ARB or ER interactions across our 3,736 species. The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We visually observe that the evolution of the ARB/ER interactions perfectly co-occurs with the loss of AM interactions in the Ericales.



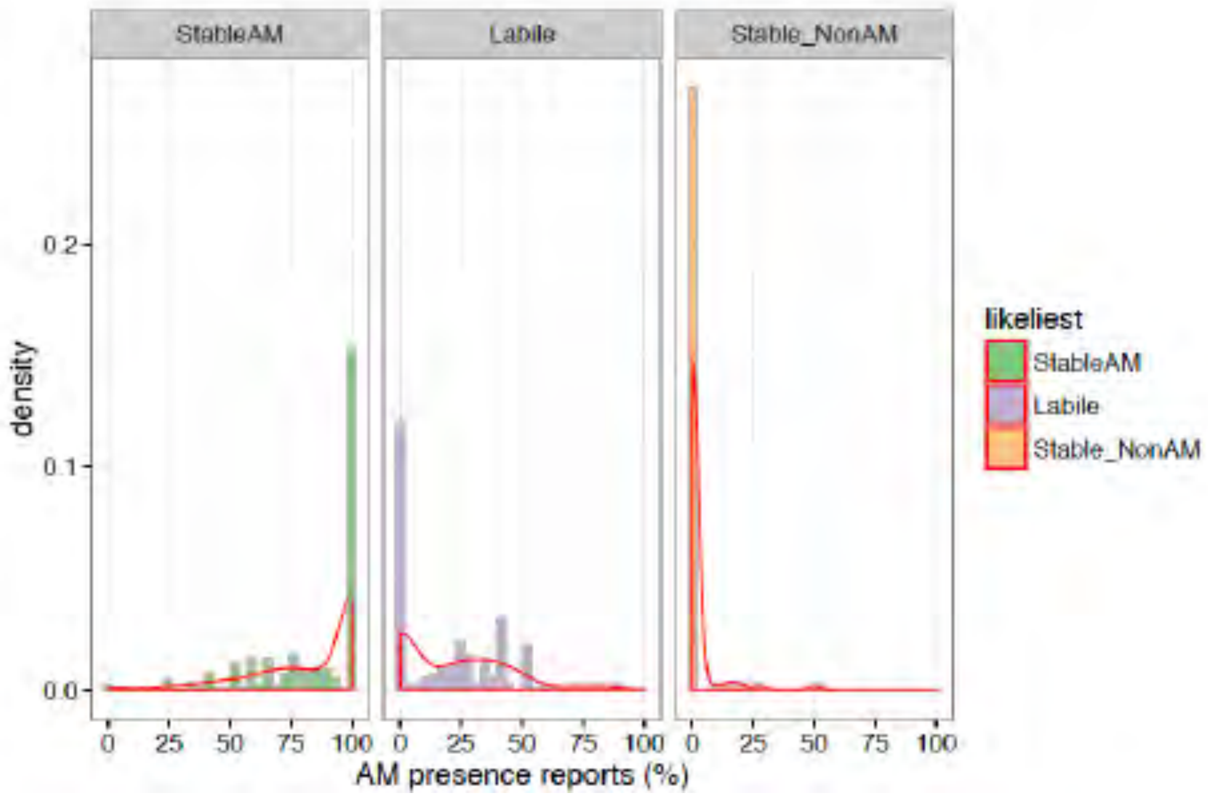
SI Figure 6: The pie charts in this figure depict the ancestral state reconstruction of plant parasitism under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of plant parasitism across our 3,736 species (i.e. the data that the reconstruction indicated by the pie charts is based on). The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We observe that, visually, AM-loss co-occurs with a shift to plant parasitism in four clades.



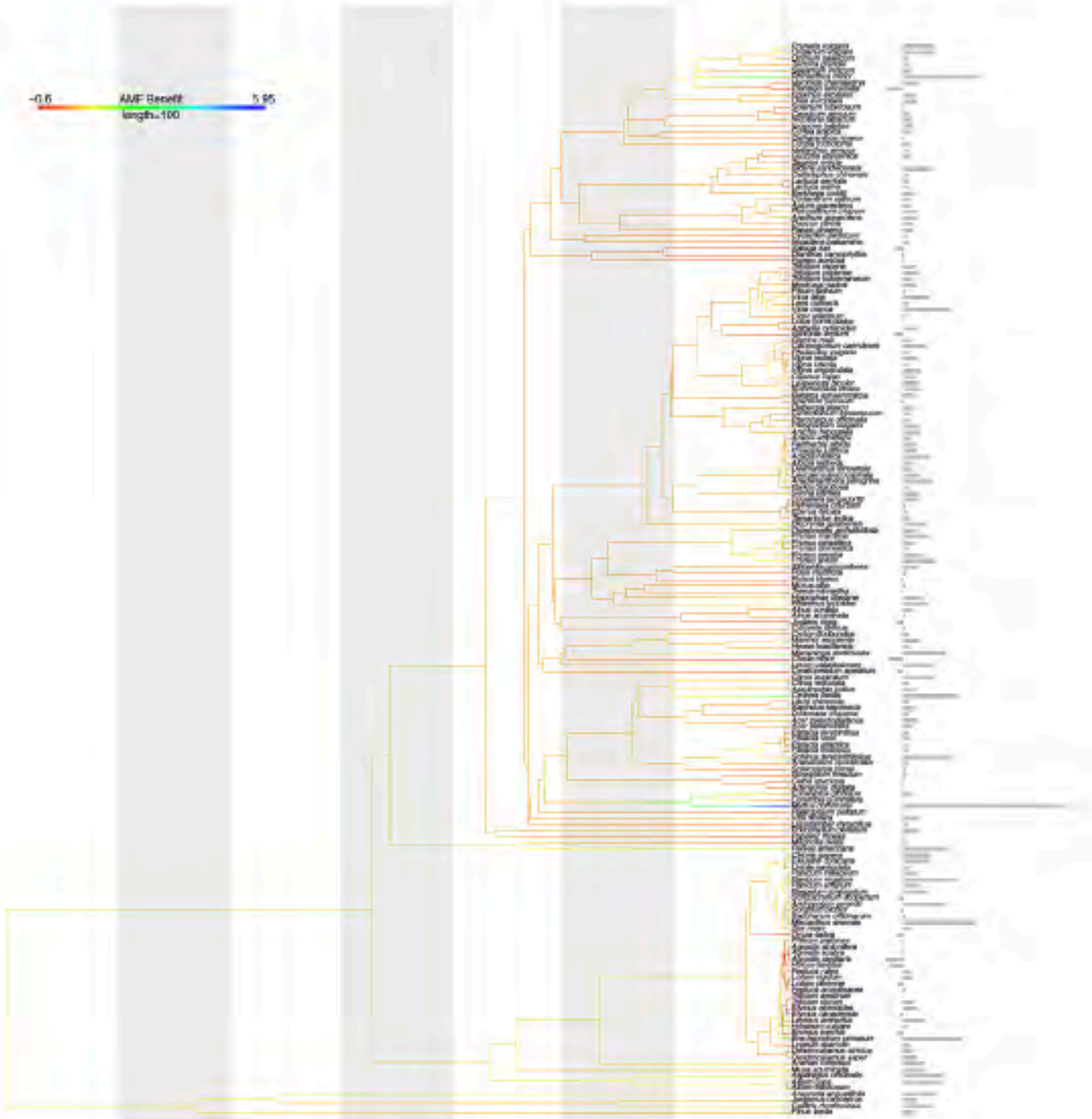
SI Figure 7: The pie charts in this figure depict the ancestral state reconstruction of plant carnivory under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of carnivory across our 3,736 species (i.e. the data that the reconstruction indicated by the pie charts is based on). The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We observe that, visually, AM-loss co-occurs with a shift to plant carnivory in two clades.



SI Figure 8: The pie charts in this figure depict the ancestral state reconstruction of cluster roots under the best HRM-model (SI Table 1). The coloured band across the phylogeny indicate the reported presence (dark grey) or absence of cluster roots across our 3,736 species (i.e. the data that the reconstruction indicated by the pie charts is based on). The branch colours indicate the reconstructed presence (purple) or absence (orange) of AM fungi under the best HRM-model for plant-AM interactions (Table 1, SI Figures 1 & 2). We observe that, visually, AM-loss co-occurs with a shift to cluster roots in three clades.



StableAM
Labile
Stable_NonAM
density
0.0
0.1
0.2
0
25
50
75
100
AM presence reports (%)
likeliest
StableAM
Labile
Stable_NonAM


-0.6
AMF Benefit
5.95
length=100