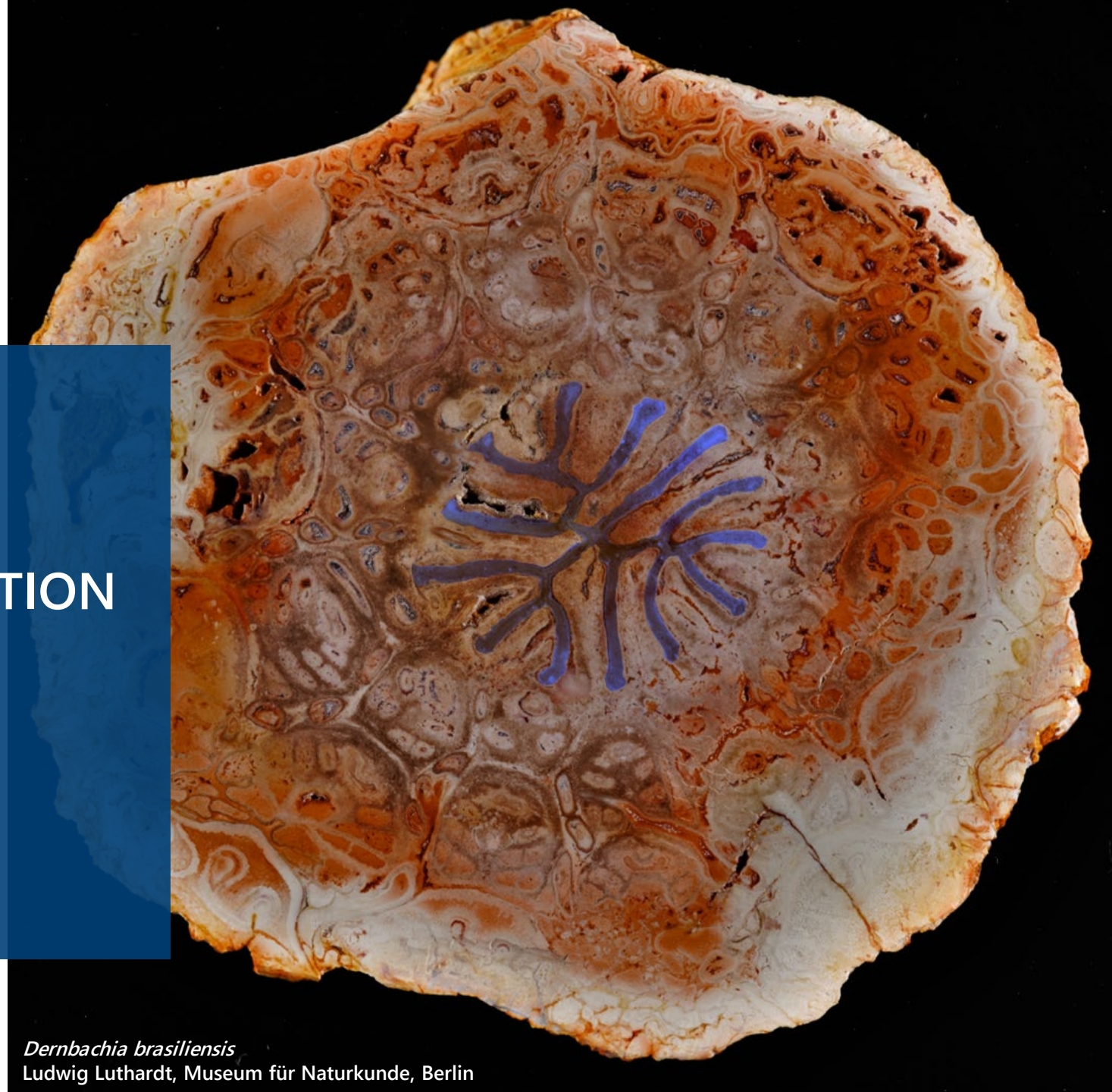
UNIVERSITY OF HOHENHEIM

Simulating Plant Vascular Form, Function, and Evolution

Computational Science Hub: 20.11.2025
Martin Bouda; Plant Ecophysiology (190j)



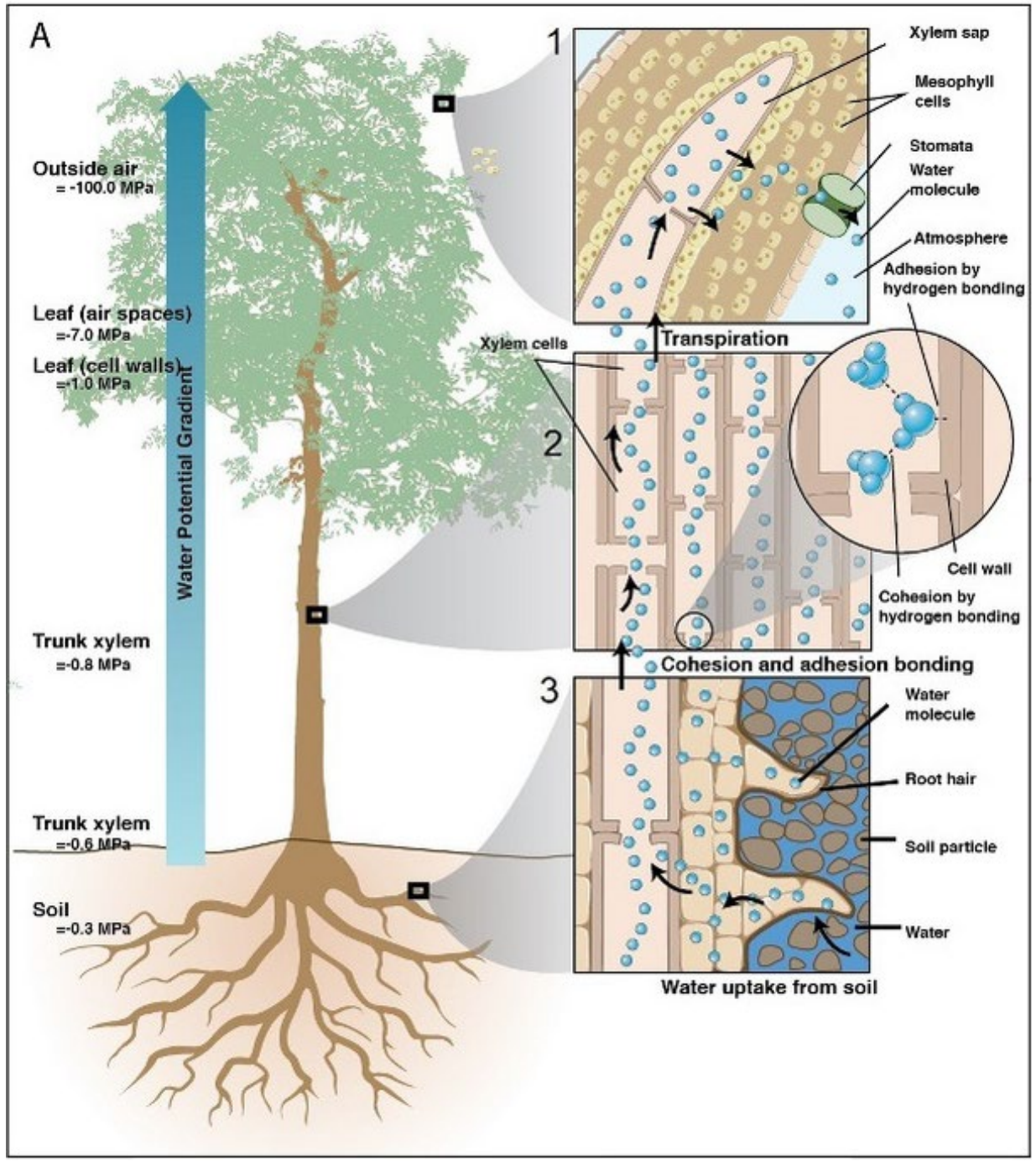
Dernbachia brasiliensis
Ludwig Luthardt, Museum für Naturkunde, Berlin

How does:

- Vegetation Affect Ecosystem Function under Drought?
- Drought Affect Plant Structure & Function?

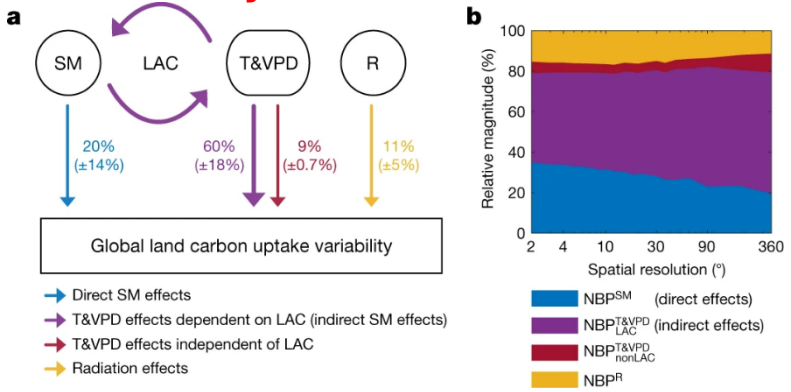
Vegetation Controls on Ecosystem Fluxes under Drought

Plant Water Use



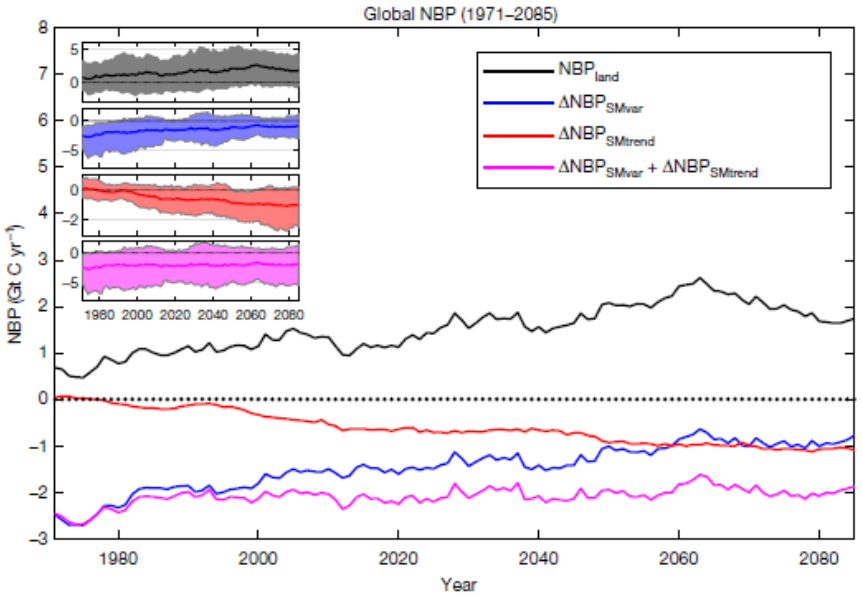
Predicting Transpiration & Soil Moisture is Important (…but We're not Very Good at it)

80% of interannual land carbon sink variability



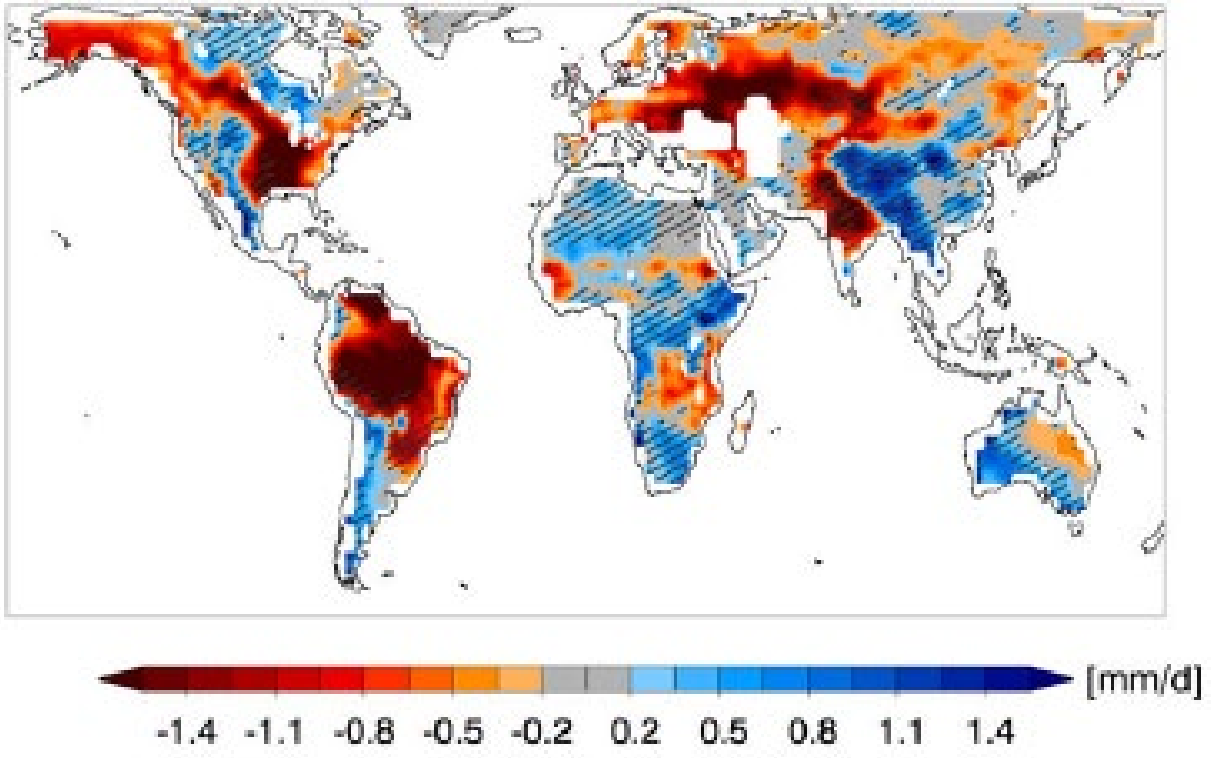
Humphrey et al. (2021) *Nature* 592:65-69.

90% of land carbon sink uncertainty



Green et al. (2019) *Nature* 565:476-479.

Prediction bias in CMIP5 model evapotranspiration (JJA)

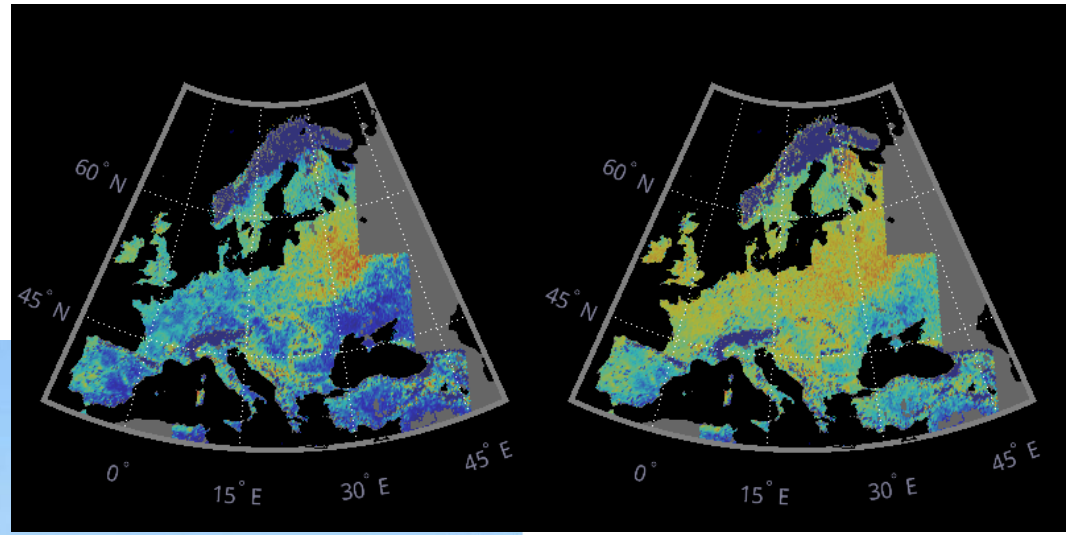


Mueller & Seneviratne (2014) *Geophys Res Lett* 41:128-134.

Mismatched Scales of Cause and Effect

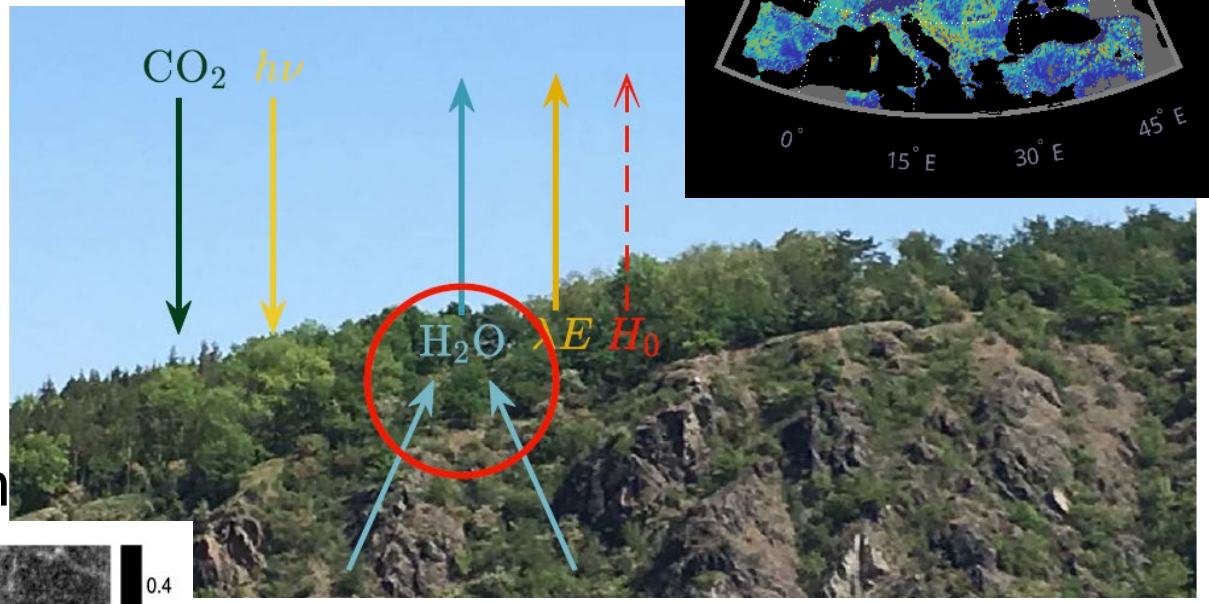
Earth system processes (e.g. carbon cycle)

100+ km



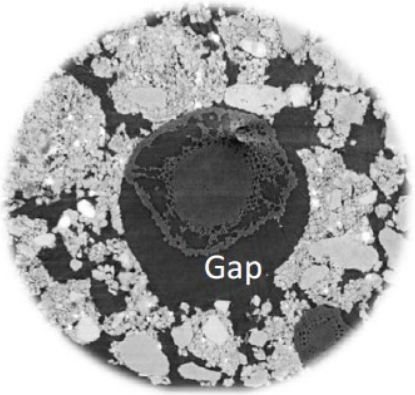
Land-atmosphere feedback:

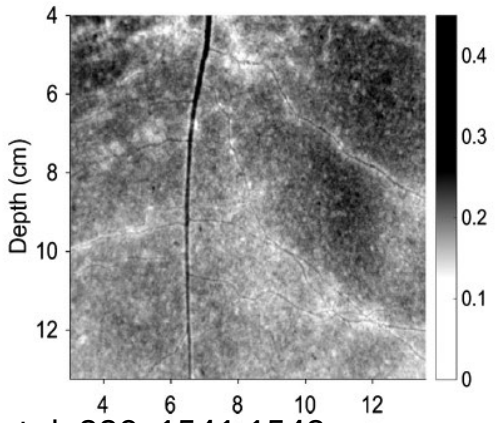
10m-10km



Integrates to

Root Water Uptake: mm-m





Limits

Carminati et al. (2020) New Phytol. 226: 1541-1543.

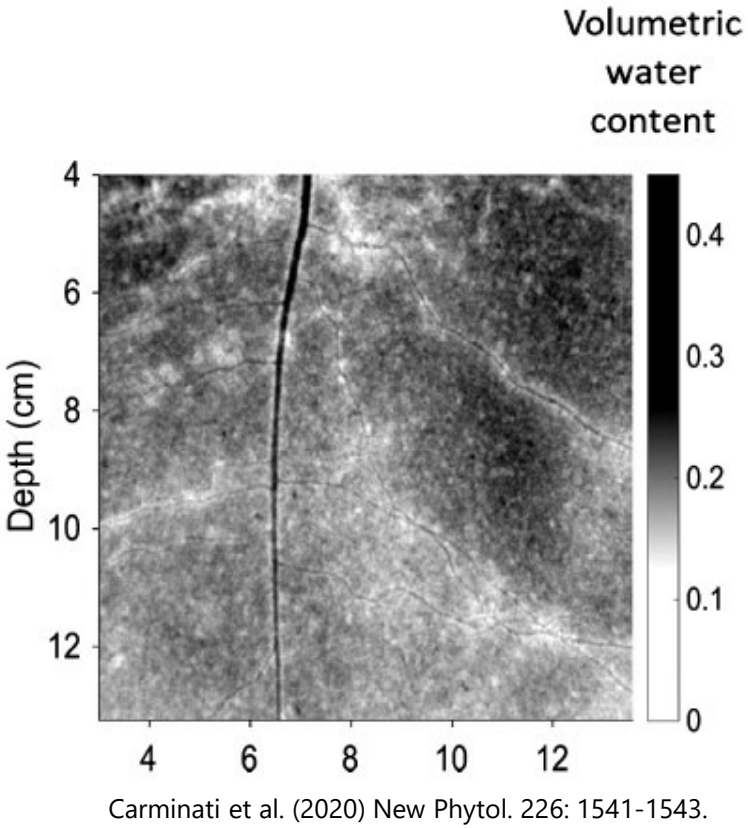
Soil Moisture Heterogeneity

Heterogeneity increases as soil dries due to nonlinearities in flow equation:

$$C(\psi)\frac{\partial \psi}{\partial t} = \nabla(K(\psi)\nabla\psi)$$

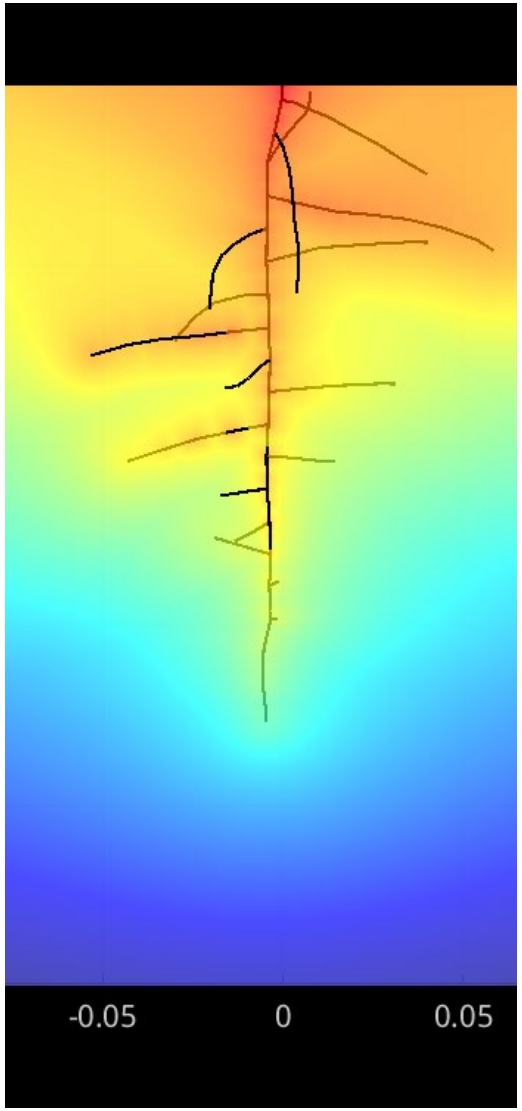
This presents a major computational problem at larger scales:

- Flowrate controlled by small-scale variation, not large-scale "mean" values



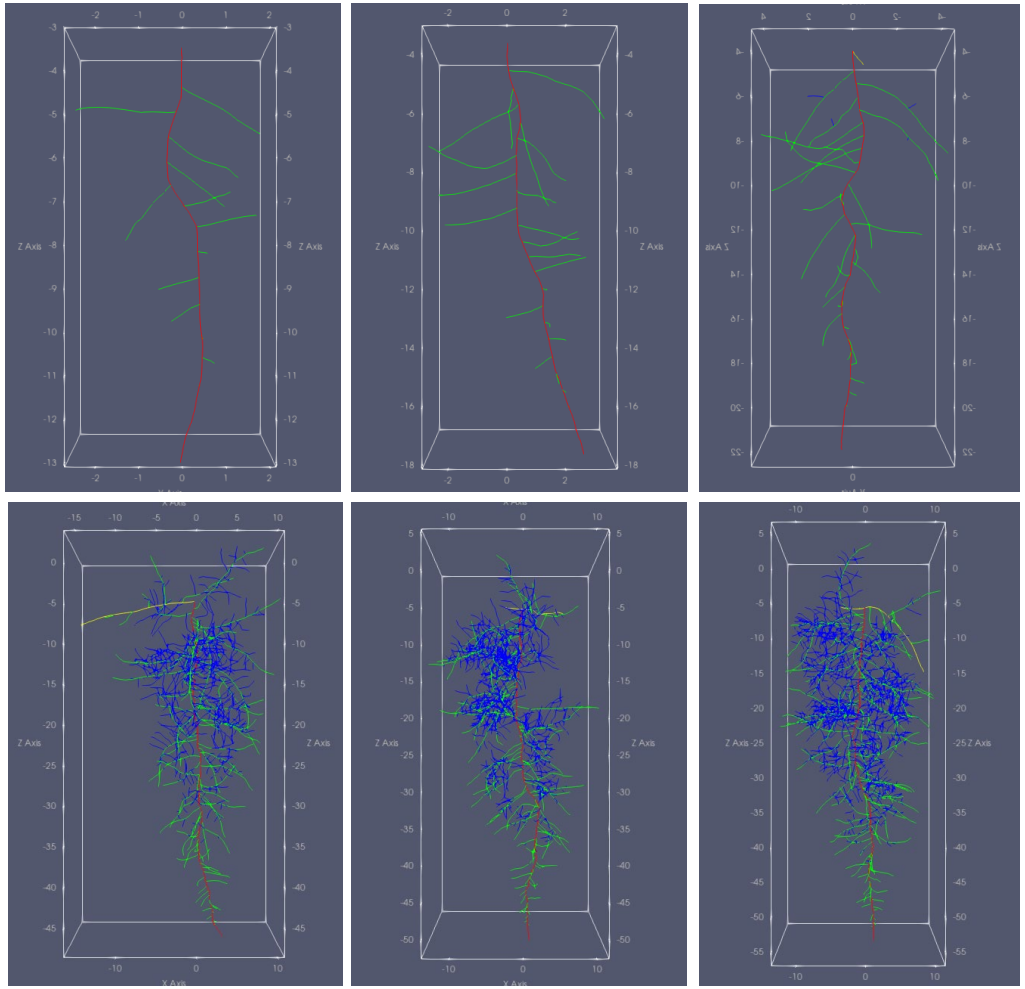
Carminati et al. (2020) New Phytol. 226: 1541-1543.

Neutron Tomography



Flow Model

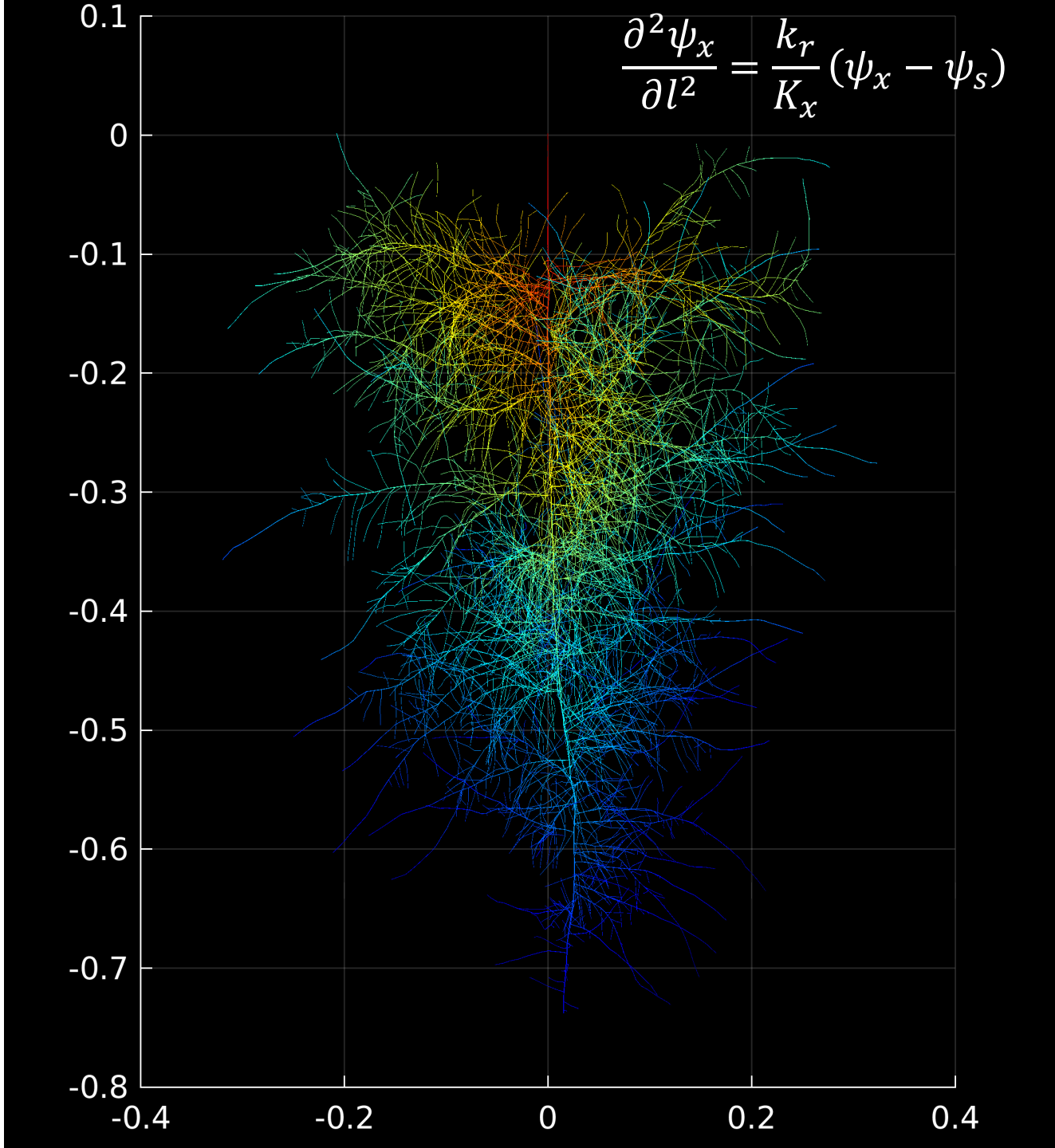
Simulate Growth and Uptake



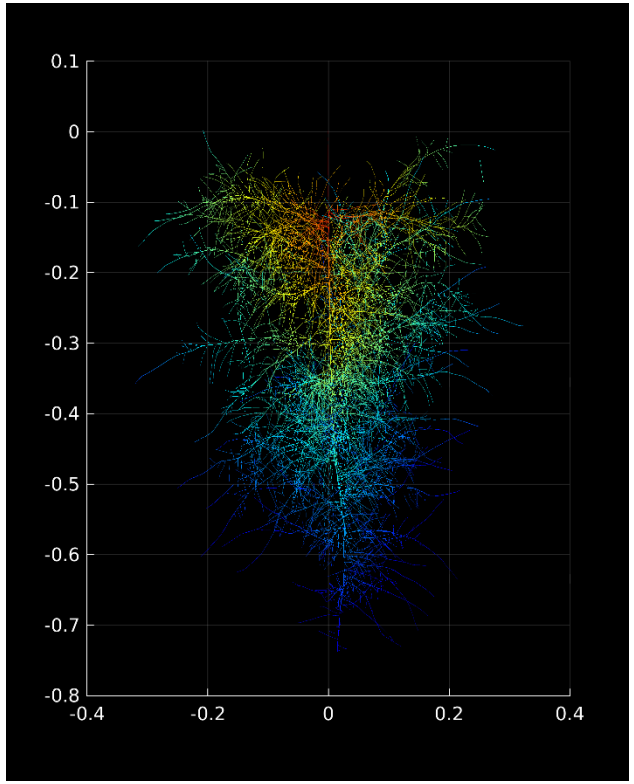
CPlantBox; Zhou et al. (2020) *In Silico Plants.* 2(1):diaa001

Effects on water uptake under drought of
- root system architecture,
- root anatomy,

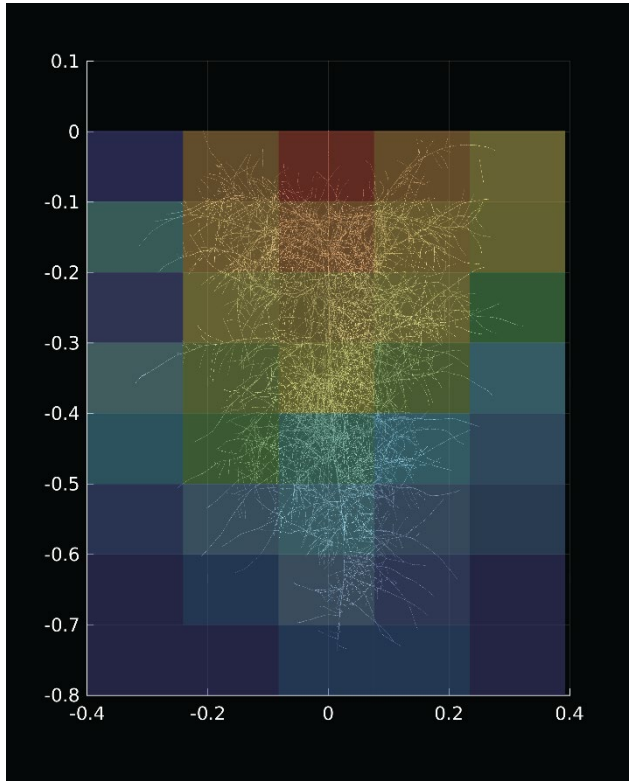
…at the small scale.



Scaling Up via Analytical Integrals of Flow Equation



The full 3D problem in continuous form can be formulated as **a linear system** in terms of $\bar{\psi}_x$.



So an **exact upscaling** can be achieved by partial Gaussian elimination, yielding $\hat{\psi}_x$ for each soil block of uniform ψ_s.

1) On any root segment, use continuous solutions $\psi_x = f(s)$ to define **mean segment potential**:

$$\bar{\psi}_x = \frac{\int_0^L \psi_x(s)\, ds}{L}$$

2) A **weighted average** for any soil block $\hat{\psi}_x$ can be found:

$$\hat{\psi}_x = \frac{\sum_1^n k_r L\, \bar{\psi}_x}{\sum_1^n k_r L}$$

(for *n* root segments in each soil block)

which **yield exact solutions** for total uptake in soil bloc Q_R in simple Darcian:

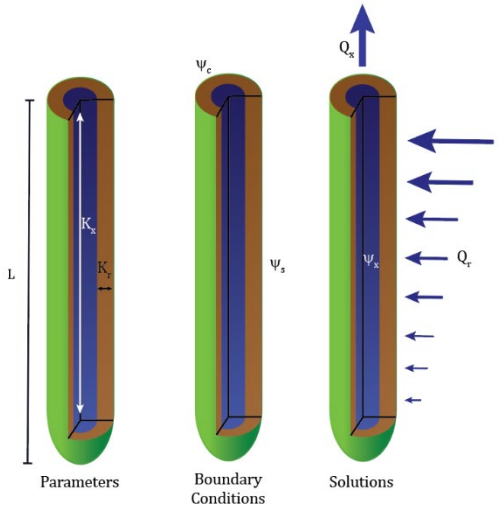
$$Q_R = -\sum_1^n k_r L\, \left(\hat{\psi}_x - \psi_s\right)$$

when soil water potential ψ_s is uniform in each block.

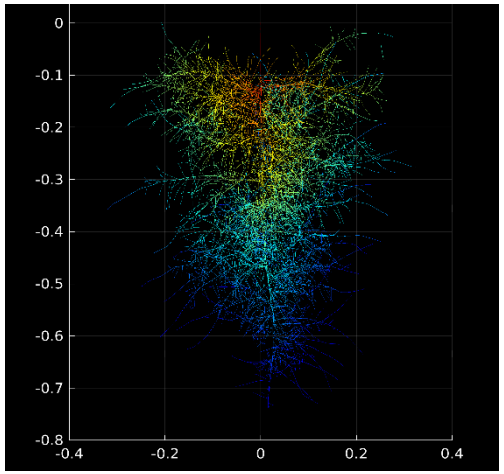
Bouda & Saiers (2017) *Advances in Water Resources* **110**: 319–334

Upscaling Root System Hydrodynamics

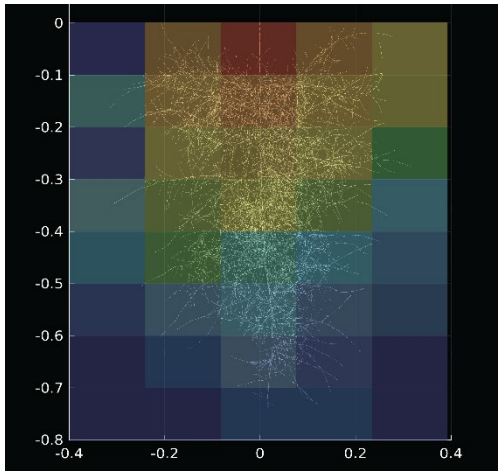
Single-root flow model



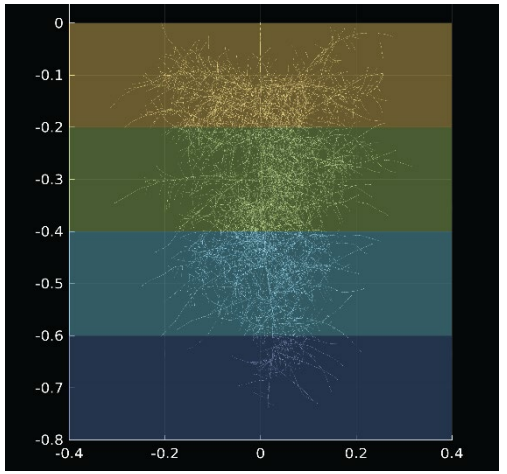
Full 3D solution



Arbitrary soil blocks



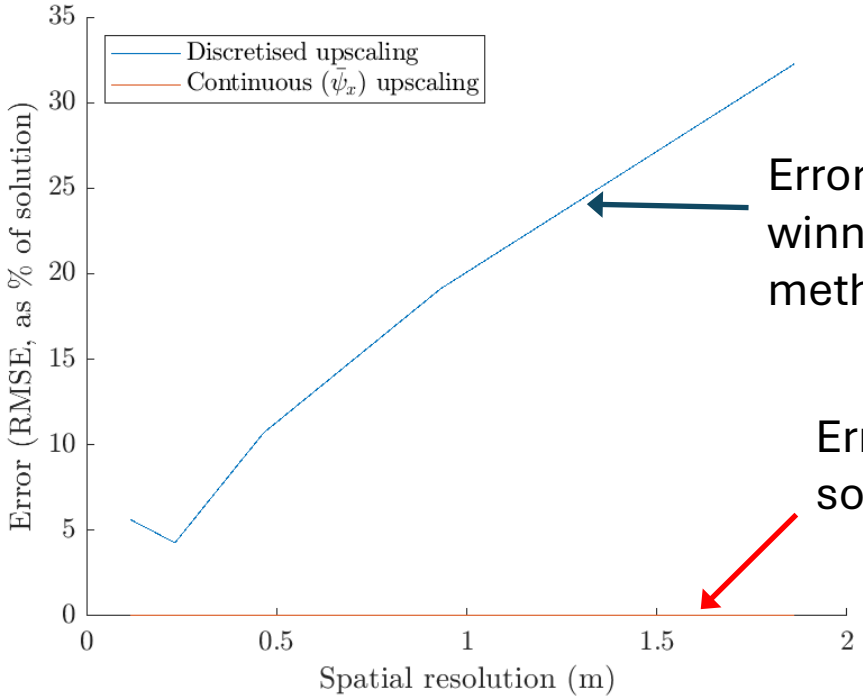
Layers for Earth System Model



Code for upscaling at https://github.com/mbouda/genUpscAlg (in beta-testing)

Result: exact solutions to root water uptake equations at any scale

Right: For large shrubby root system at meter resolution, **discretisation error** can be significant.



Error in award-winning upscaling method

Error with exact solutions

Bouda and Saiers, 2017, *Advances in Water Resources* 110:319–334.
Bouda (2019) *J. Advances in Modeling Earth Systems* 11:4597–4613.

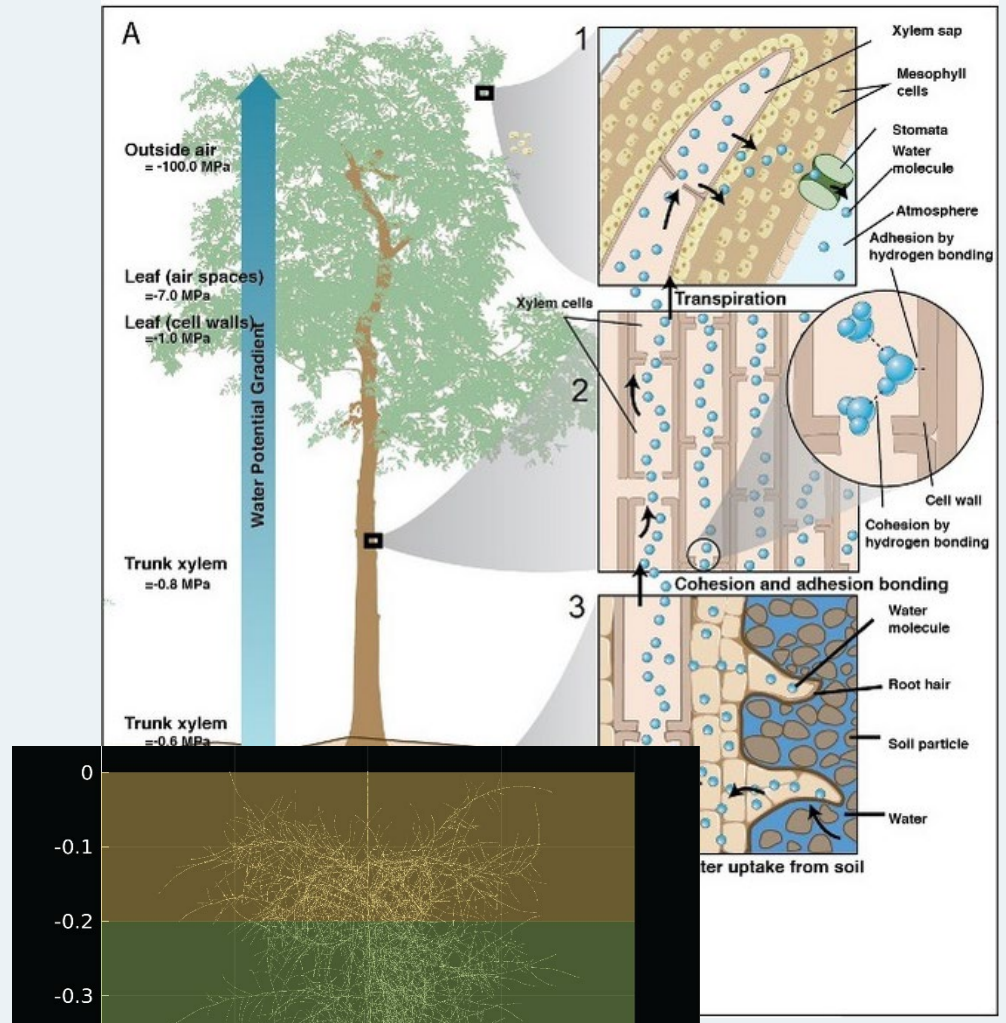
IMPROVE ECOSYSTEM FLUX PREDICTIONS?

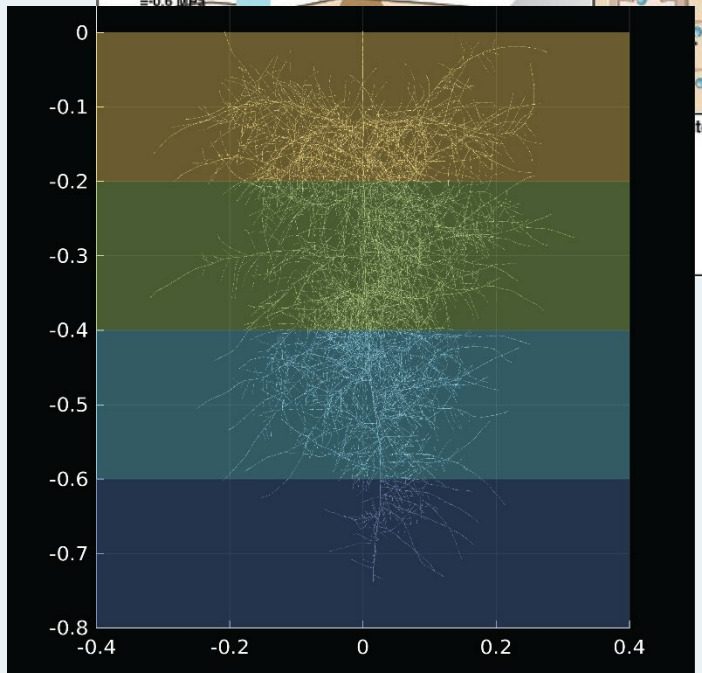
Parameterise this model directly at larger scales

Use it to characterise soil-plant hydrodynamics of the ecosystem

Ask what controls ecosystem hydrodynamics

Predict fluxes under drought





HydroScale Project:

Mechanistic scaling
of soil-plant hydrodynamics
in the Earth System

(2024-2026)

FUNDED BY
GAČR
CZECH SCIENCE FOUNDATION

Focus: Soil-plant hydrodynamics

- Root water uptake
- Soil moisture heterogeneity
- Scaling mechanisms

Aim: Invert the model

- Quantify large-scale effects of small-scale processes
- Implement in predictive framework for water flow under water limitation

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Institute of Hydrodynamics of the CAS

Measurement Sites in the HydroScale Project

Institute of Hydrodynamics of the CAS

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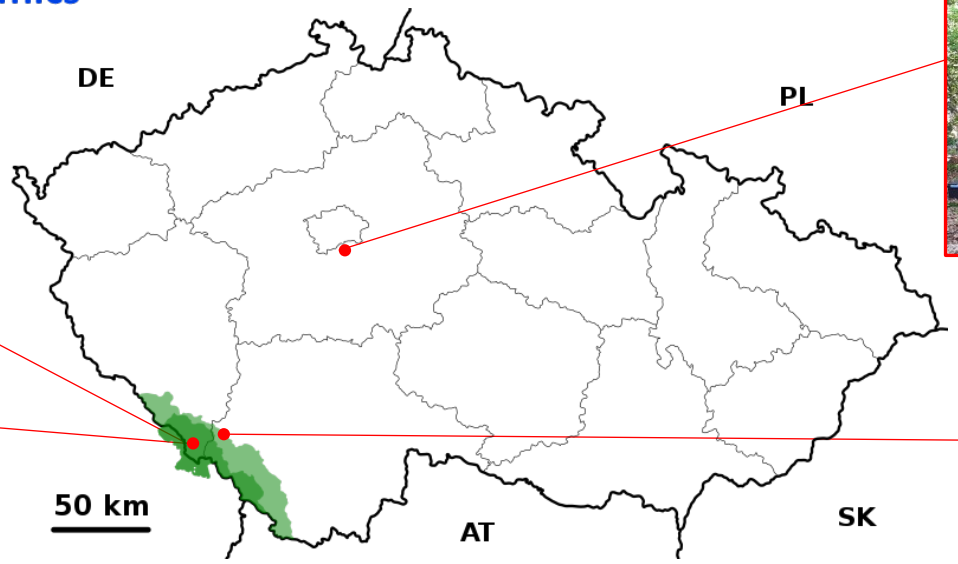


Map: David Paloch (CC2.5)

Location	Catchment character	Forest stands	Site elevation (m a.s.l.)	Mean Temp. (deg. C)	Precipitation (mm/yr)	PET (mm/yr)	P-PET (mm/yr)
Pruhonice	Lowland	[1] Beech	325	10	595	700	-100
Liz	Montane headwater	[2] Beech [3] Spruce	855-890	7	847	550	300
Rokytka	Peatbog, forest	[4] Beech [5] Spruce	1107-1145	5	1611	600	1000

INSTRUMENTATION

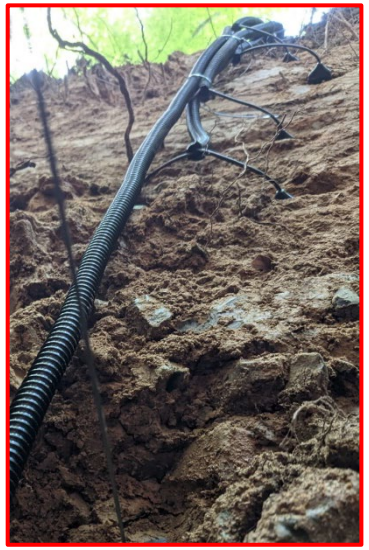
Growth increment and Sapflow on 7-8 trees

Stem water potential on up to 4 trees

Soil water potential & content

Root lengths over depth and time

4 profiles at 8 depths to 2m

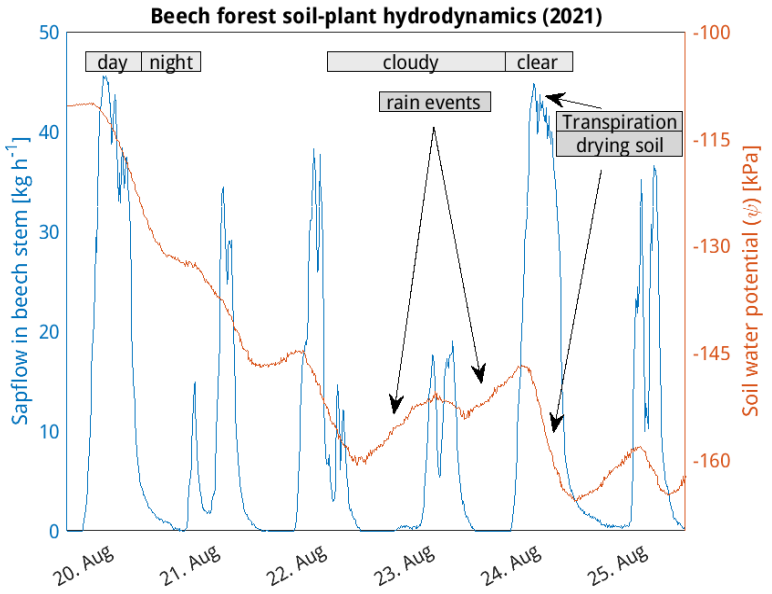


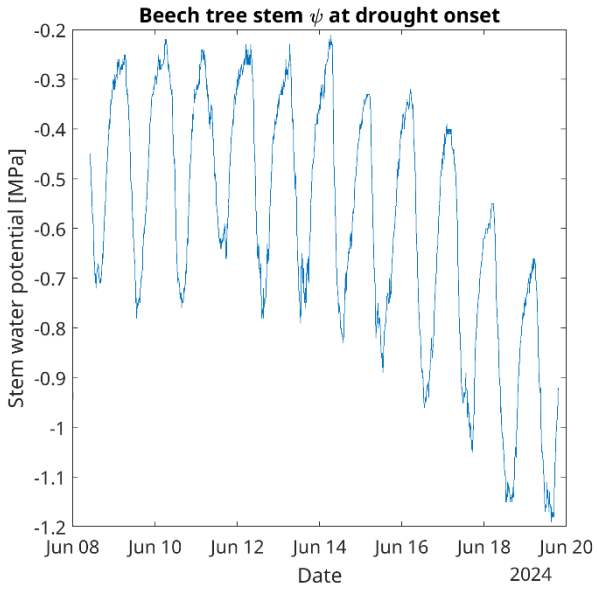
8 minirhizotrons

+ Reference measurements:
- Catchment meteorology & runoff
- Canopy hemispherical photographs
- Scholander chamber water potentials

Adapted from Sperry et al. (2016) New Phytol. 212:577-589.

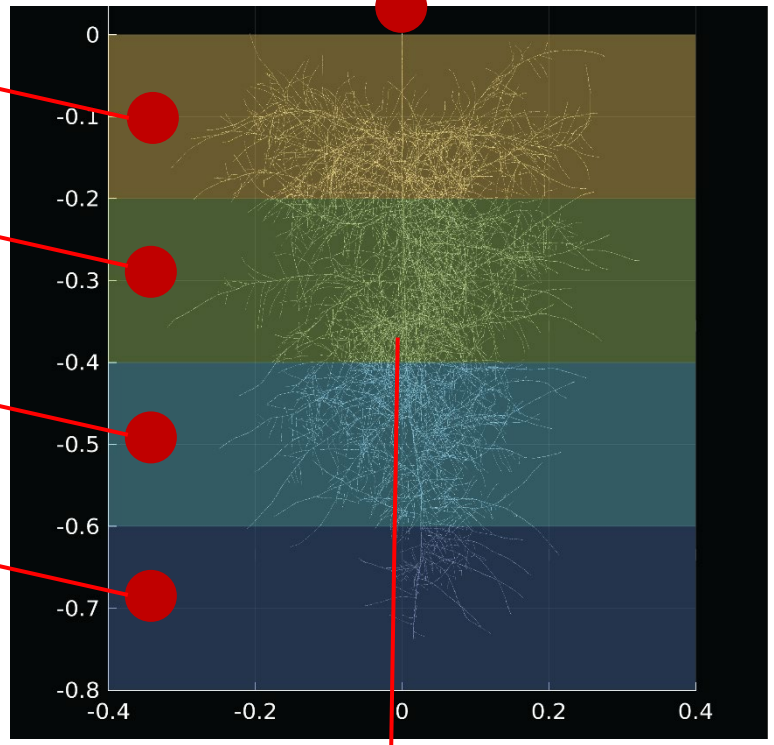
Invert Upscaled Hydrodynamic Model to Data





Observed tension and water content in soil

Observed tension and water flows in stems

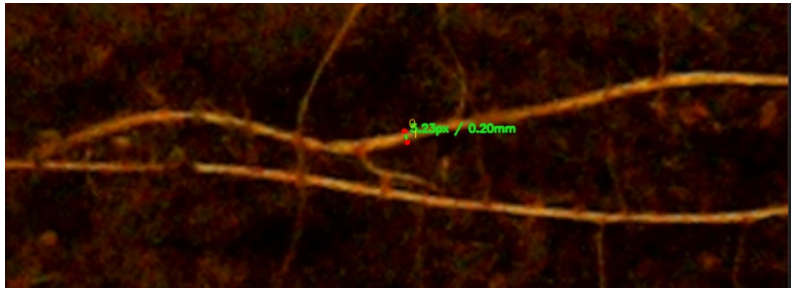


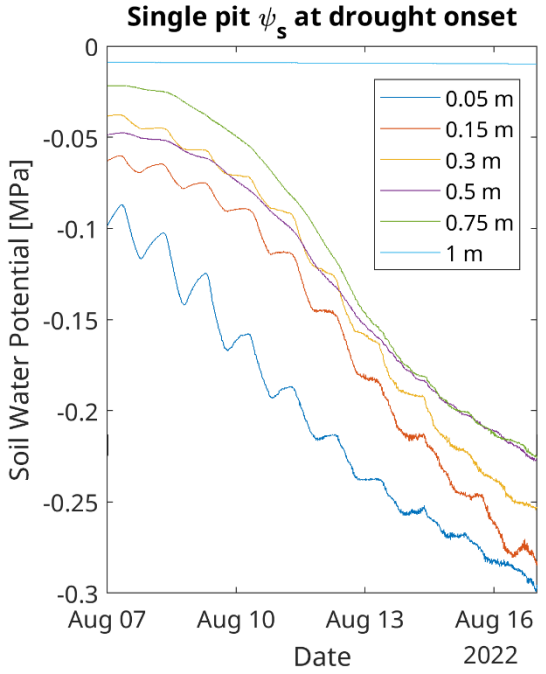
What processes control large-scale hydraulic parameters?

Time-series analysis:

At what time-scale do they change?

E.g. daily, or with root lengths?





Calculate per-layer resistances in stand-scale model of soil-root flow

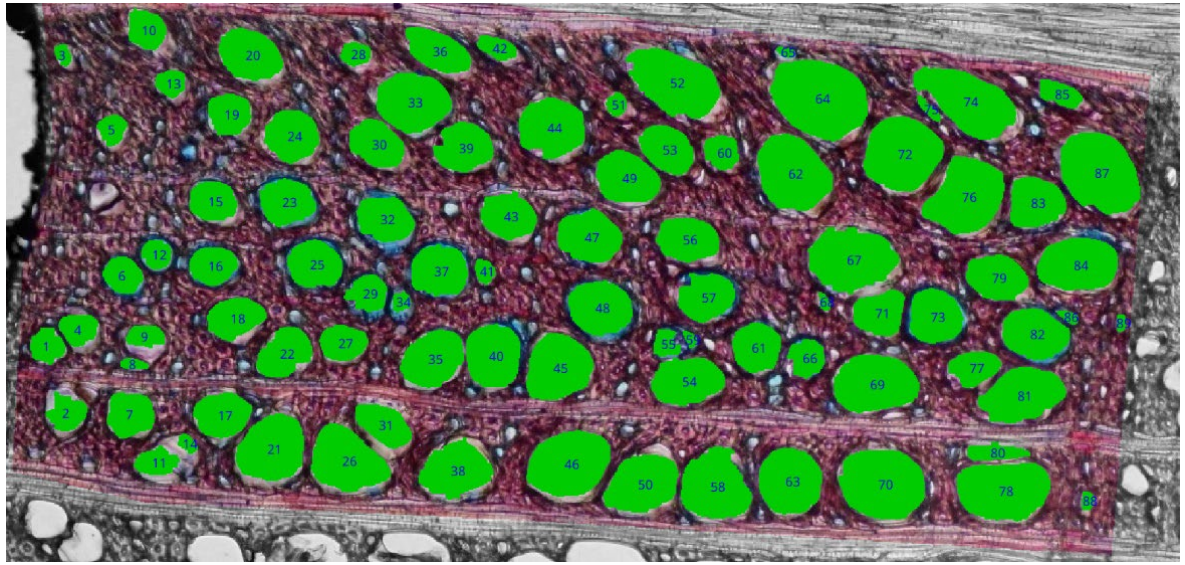
Image Analysis

Feature segmentation:

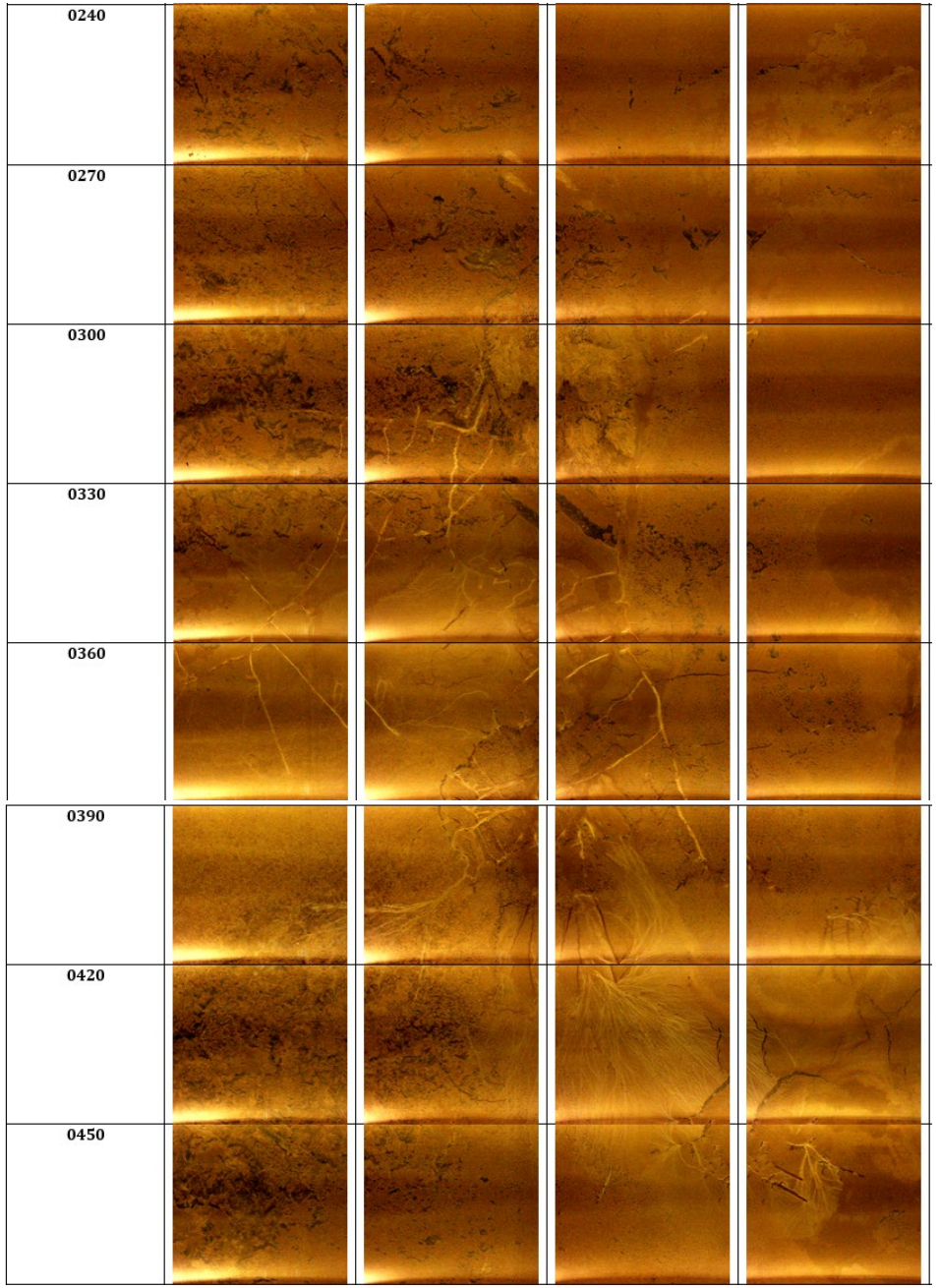
- Semi-automated (Matlab)
- Convolutional Neural Net

Extract:

- Root length vs depth (change over time)
- Wood vessel dimensions



Wood anatomy (light micrograph)



Roots imaged belowground

Post-drought Recovery of Tree Hydraulic Conductance

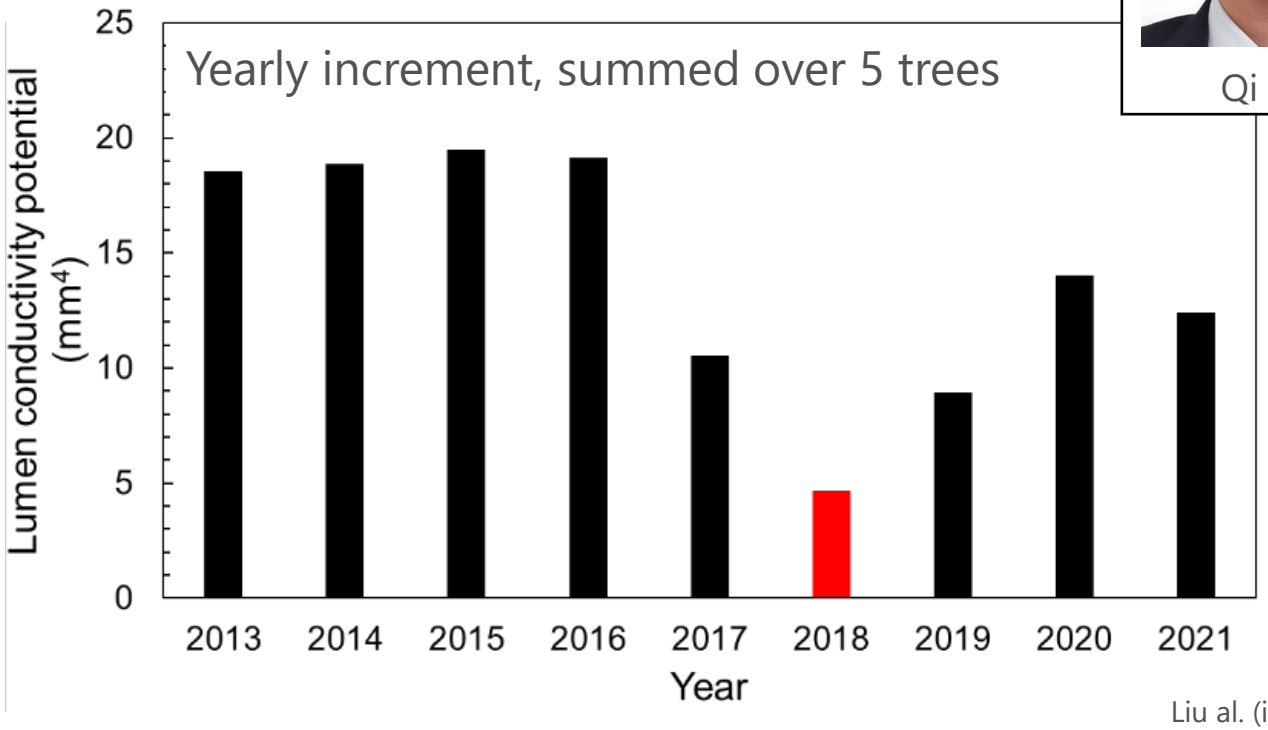
Qi Liu

After 2018 drought:

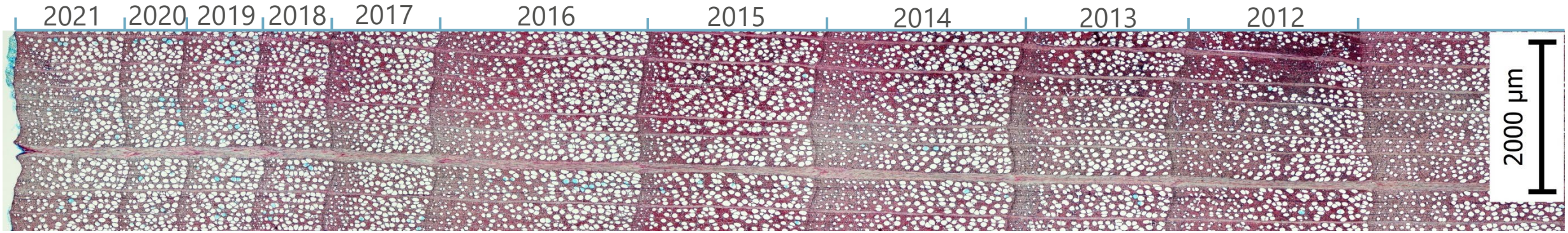
Wood cores show trees had not fully recovered hydraulic conductance by 2021

Sap flow data shows forest transpiration was affected

Full recovery may take long given Beech wood anatomy



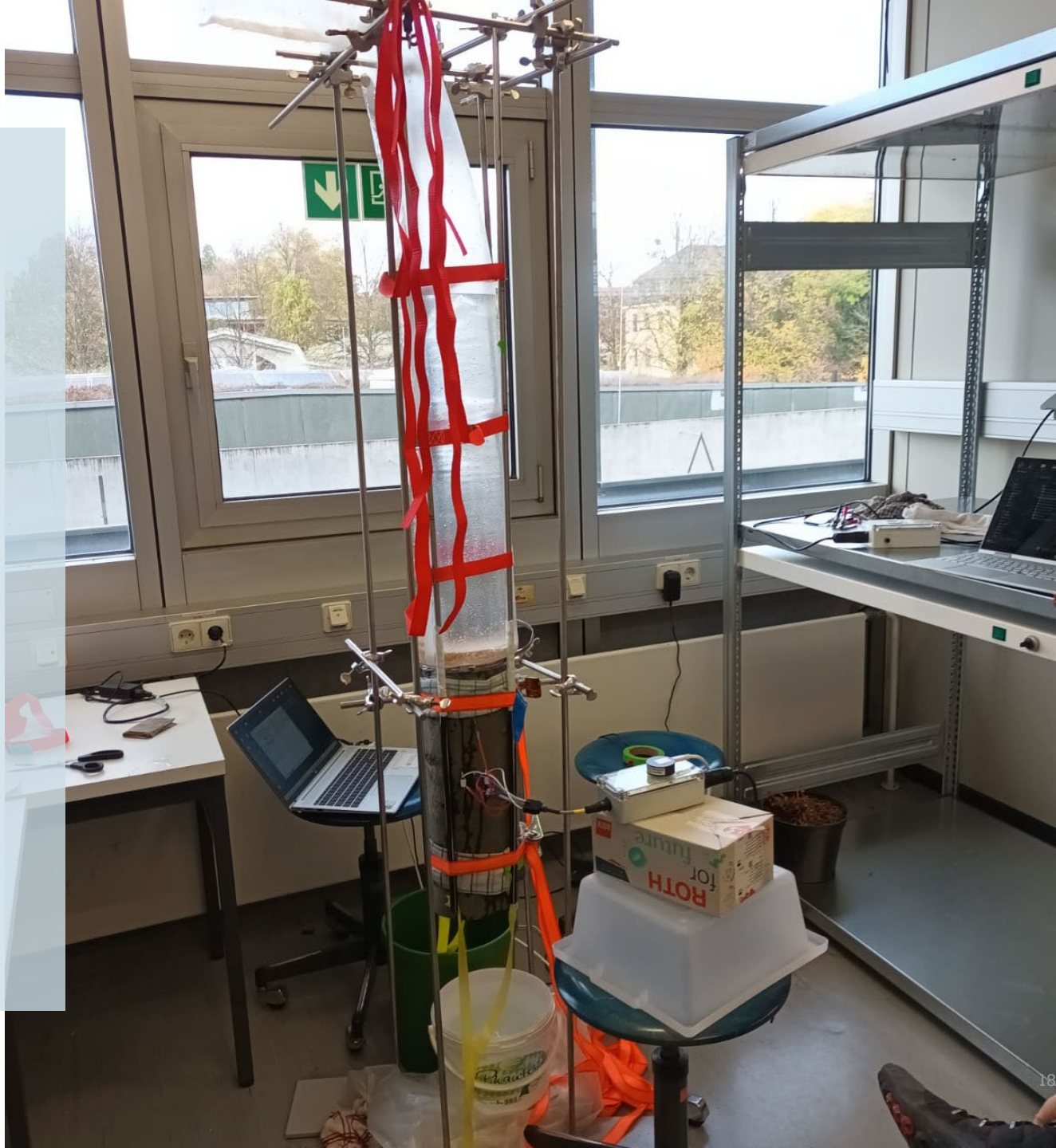
Liu al. (in prep)



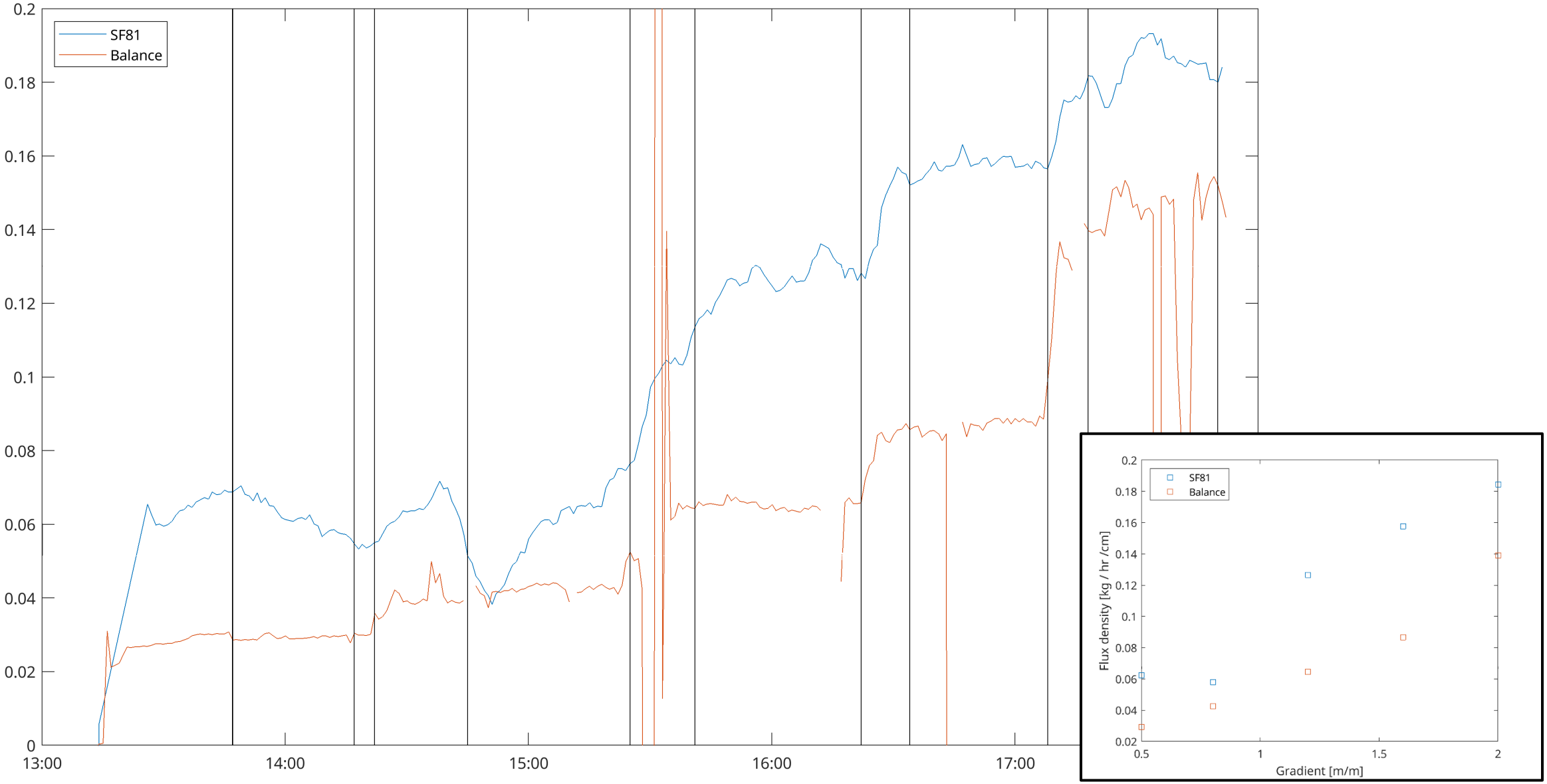
Experiment

Estimate uncertainty in Sap Flow measurement

Masters Thesis: Jan Saltekin

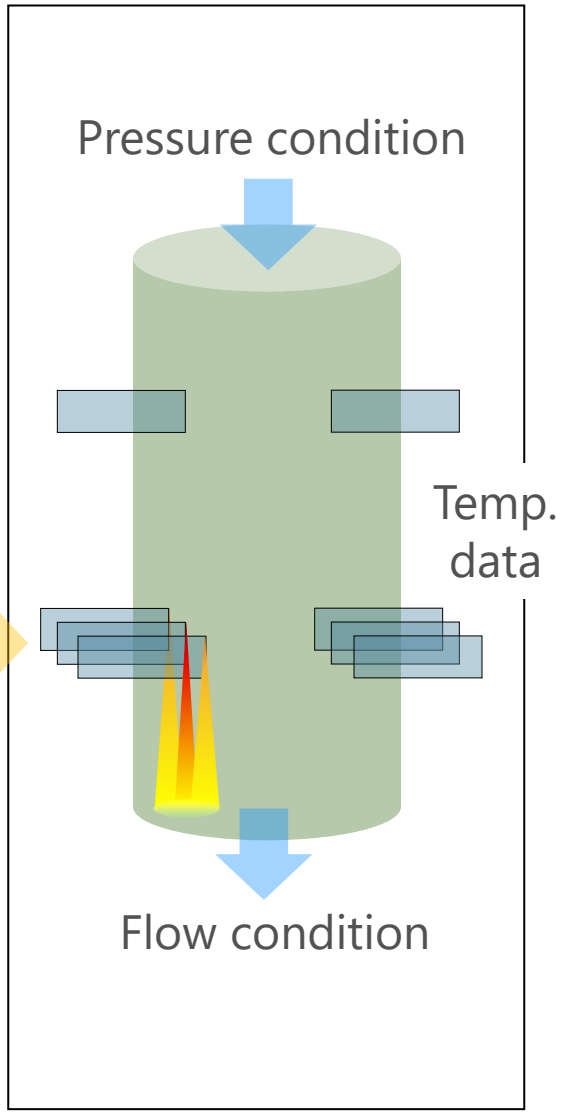


Flow over time: SF-81 probe versus balance



Multiphysics Simulation

- Model heat and water flow (steady flow equations)
- Finite Element Method (COMSOL)
- Fit model to observations to understand heat loss – flow rate relationship & provide probe calibration
- Sensitivity analysis:
  apply to larger trunks?



FEM

Experimental Setup

Research Questions

What controls forest transpiration when water is limited?

How long can plants get water and fix carbon during drought?

Do our sensors work?

Computational Techniques

Flow simulations (PDE Models)

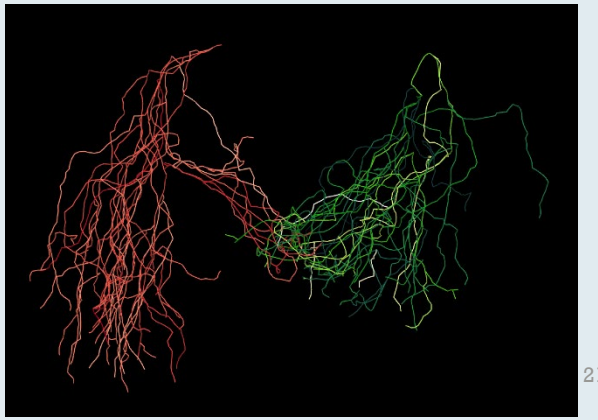
- On complex geometries (root networks)
- Finite Element Method (multiphysics)

Image analysis

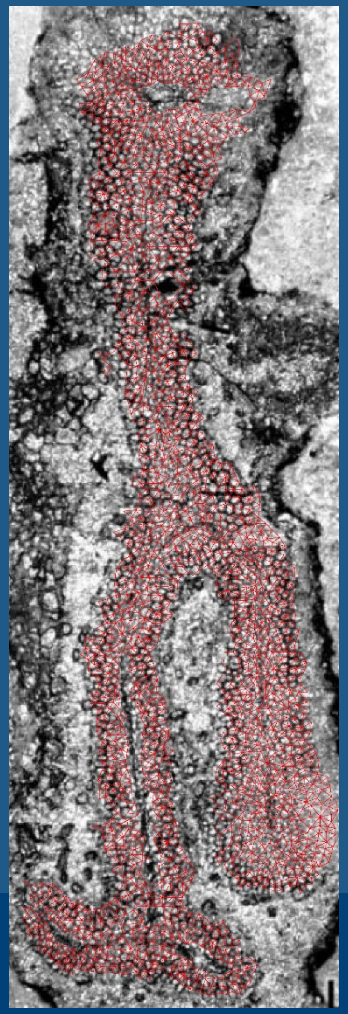
Time-series data analysis

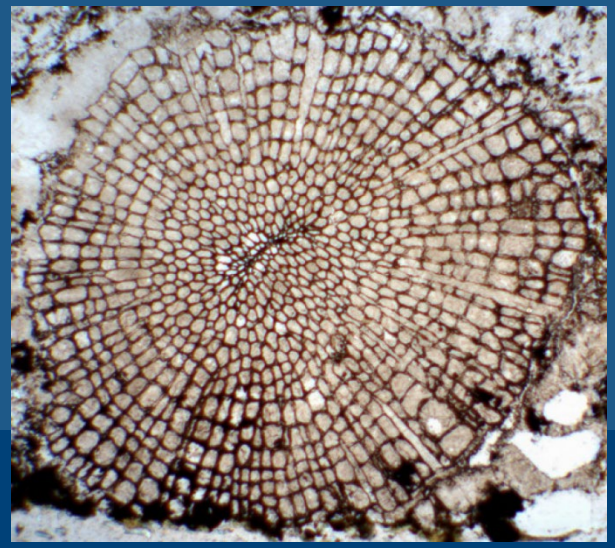
Growth simulation (root systems)

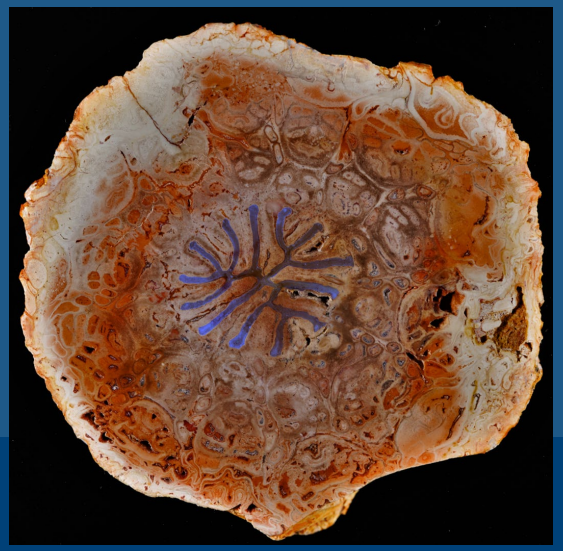
[Competing AI agents under resource heterogeneity]

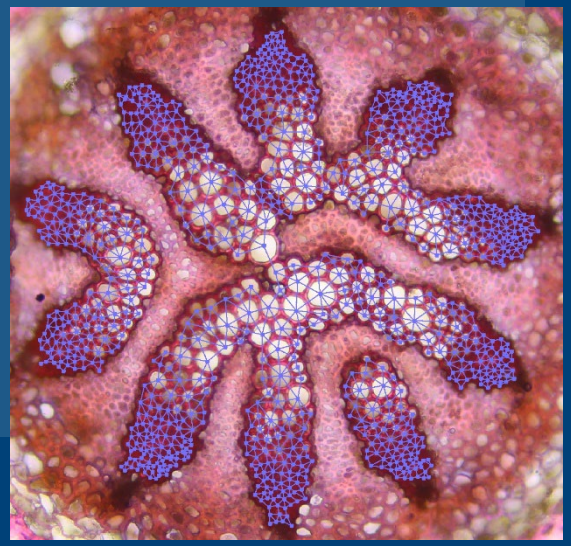


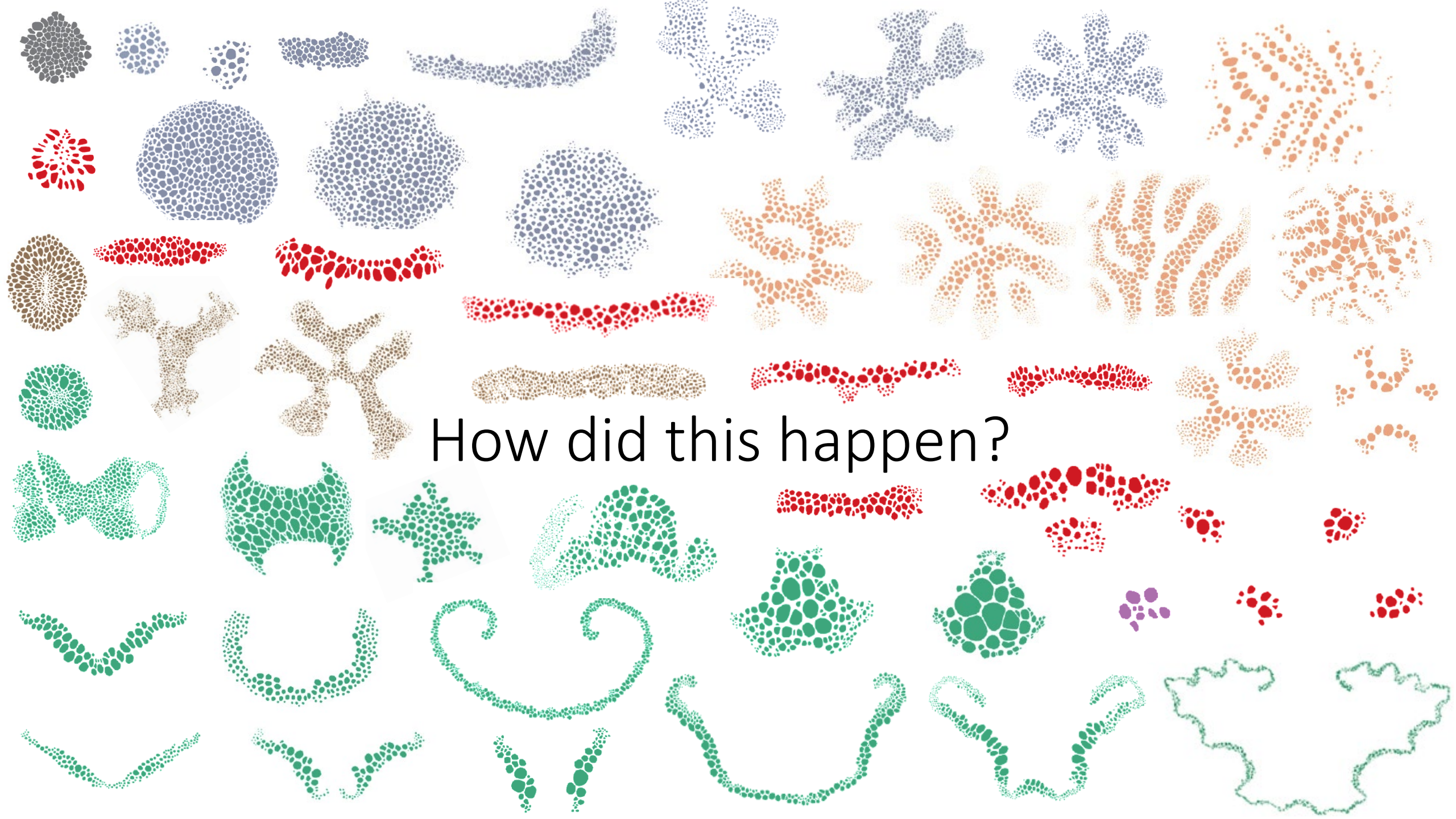
Selection by Drought in Plant Vascular Evolution



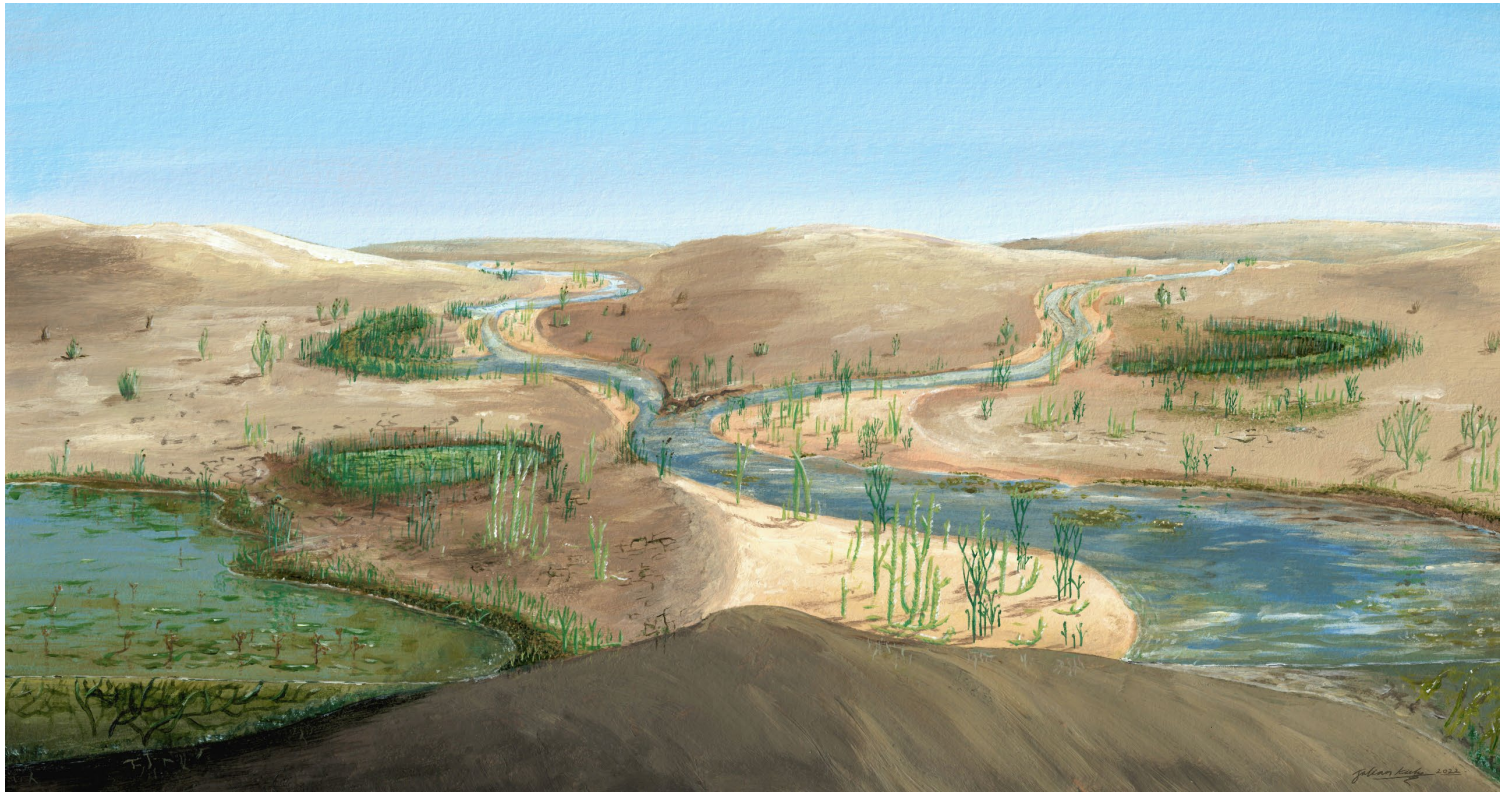




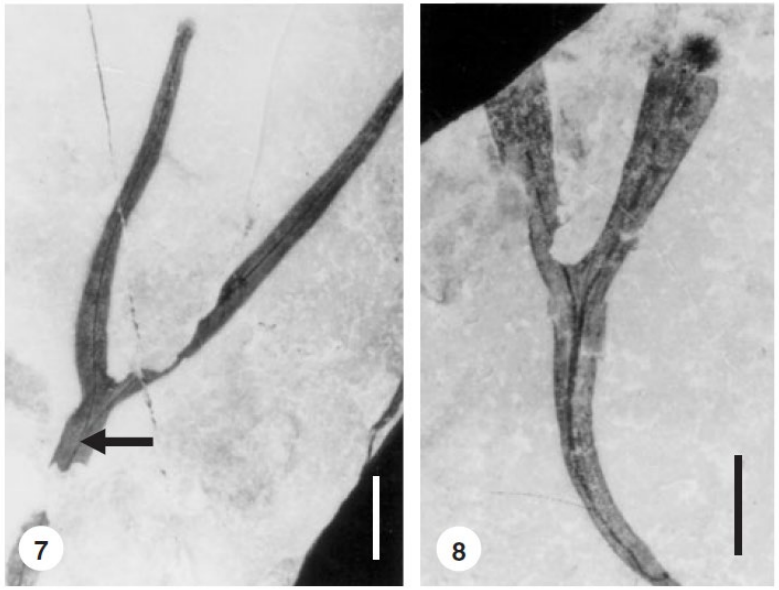



How did this happen?

Earliest vascular plants (Silurian): tiny hydrophytes.



Central vascular strand: cylinder, few cells across.

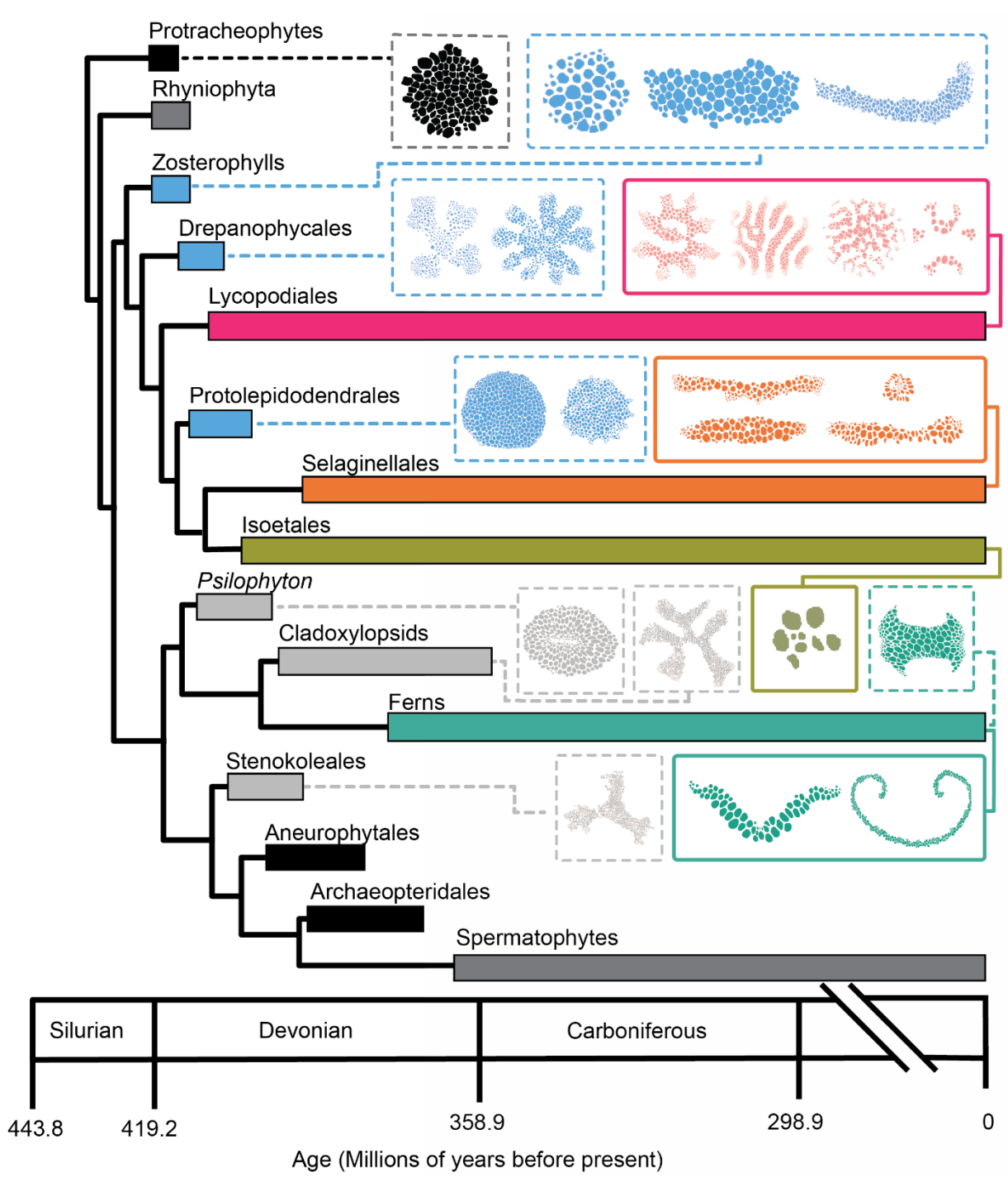


Early Devonian Landscape (Top)
© Julian Kiely, 2022.
Cooksonia, 420 MYA (Right)
Edwards et al., *Bot. J. Linn. Soc.*, 2004, **146**, 399–413.
(Far Right)
Bertie Formation, Upper Silurian, Royal Ontario Museum IP49684

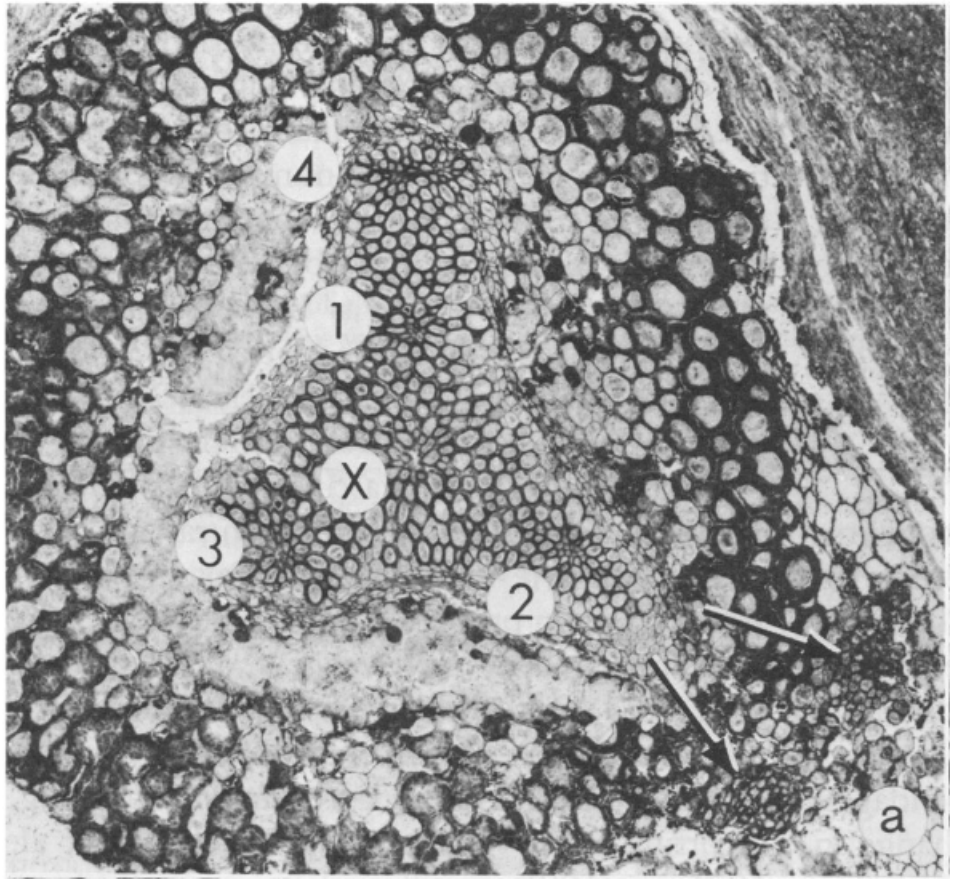
Devonian radiation

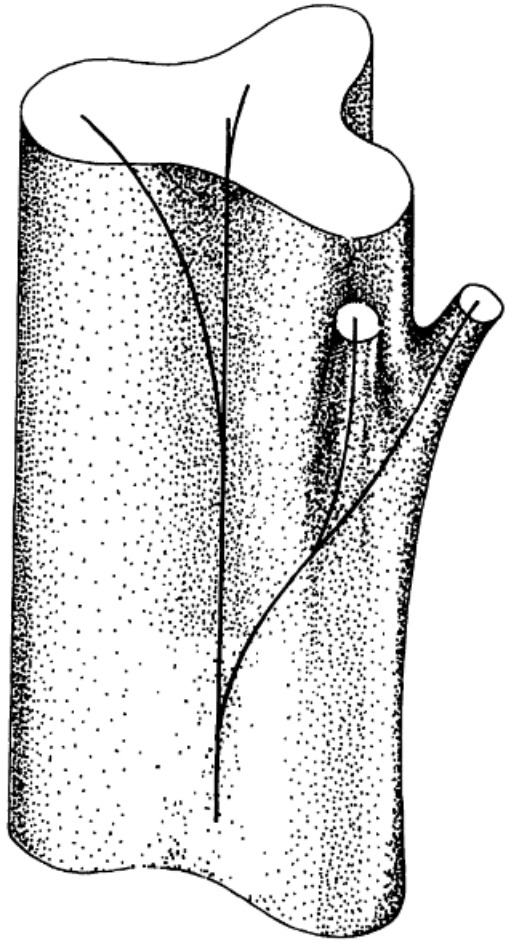
(Illustration: Late Devonian landscape © Julian Kiely, 2022)

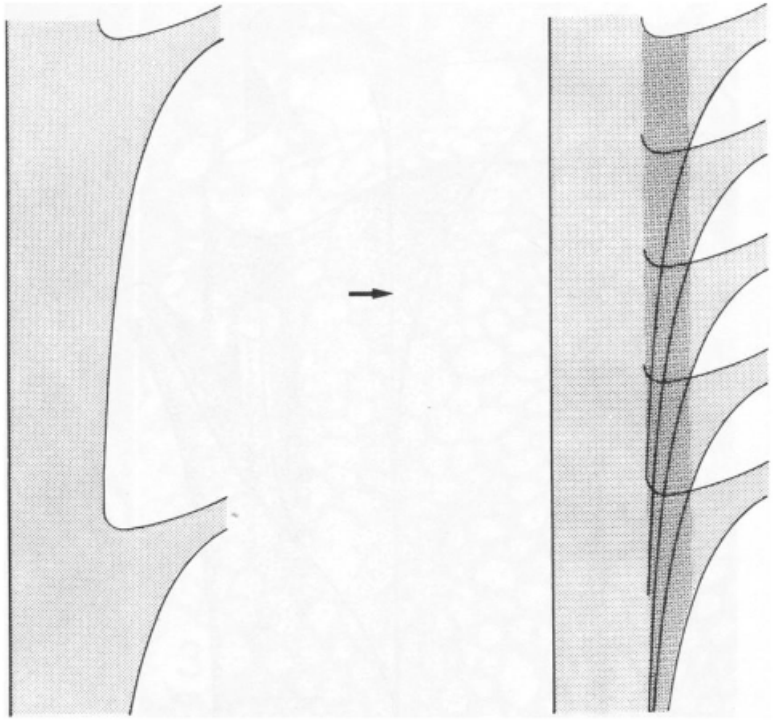
- Xylem strand diversity and complexity increases as plants:
  - radiate into drier habitats
  - increase in stature
- No known selective pressure
- Thought to be developmental artefact



Stelar evolution as a developmental artefact

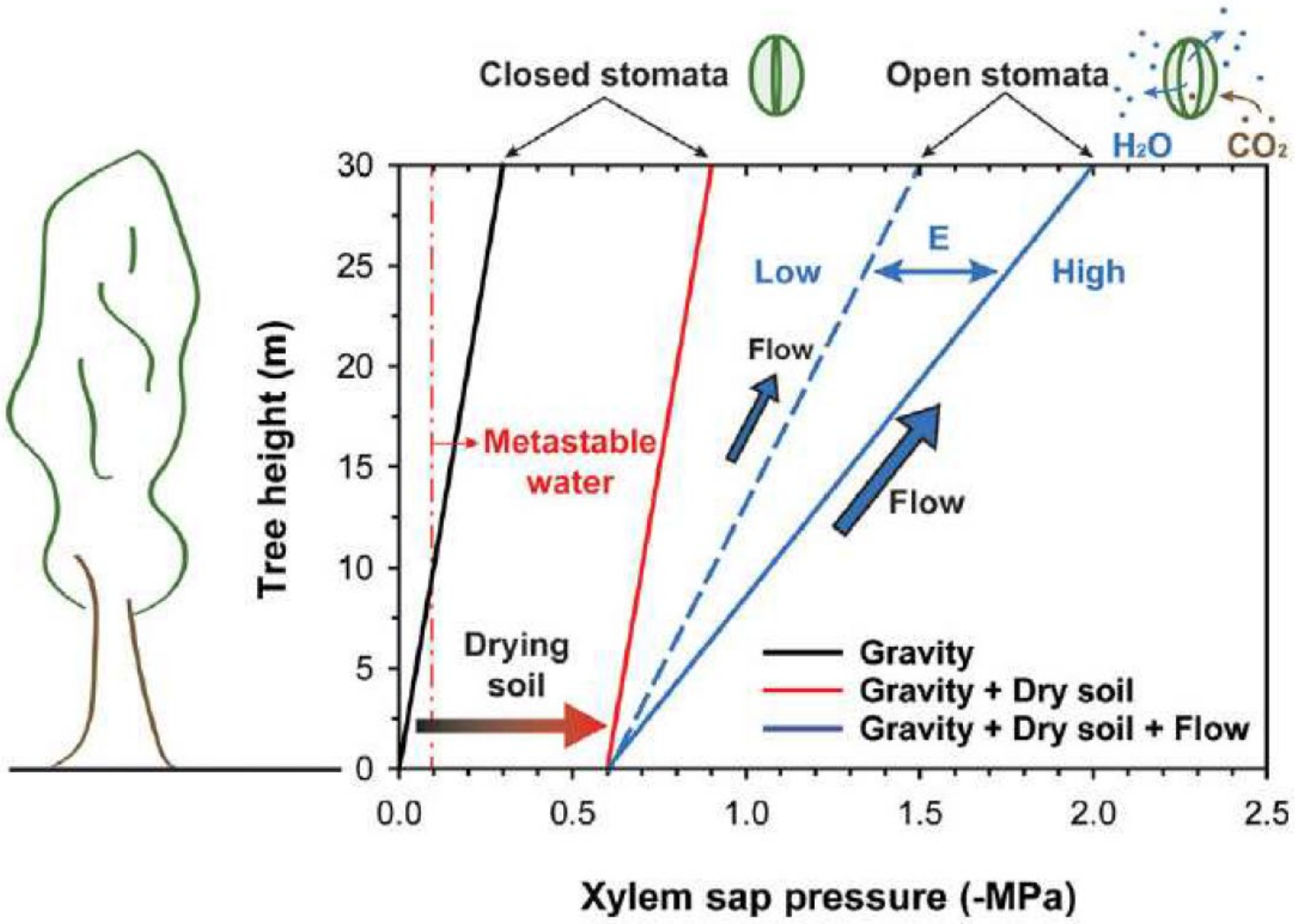






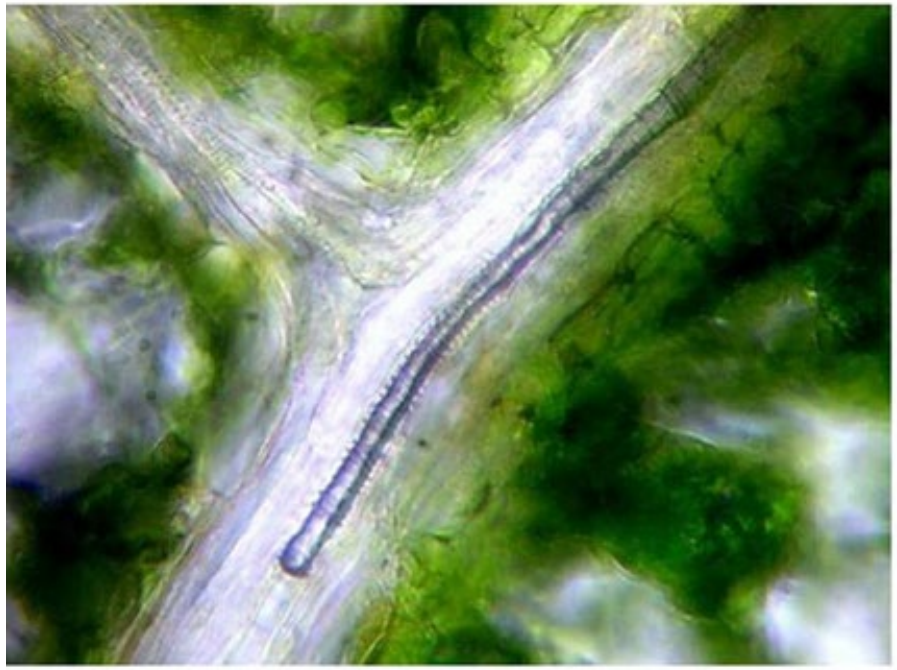
Wight (1987) *Paleobiology* 13(2):208-214.

Xylem water is a metastable liquid under tension



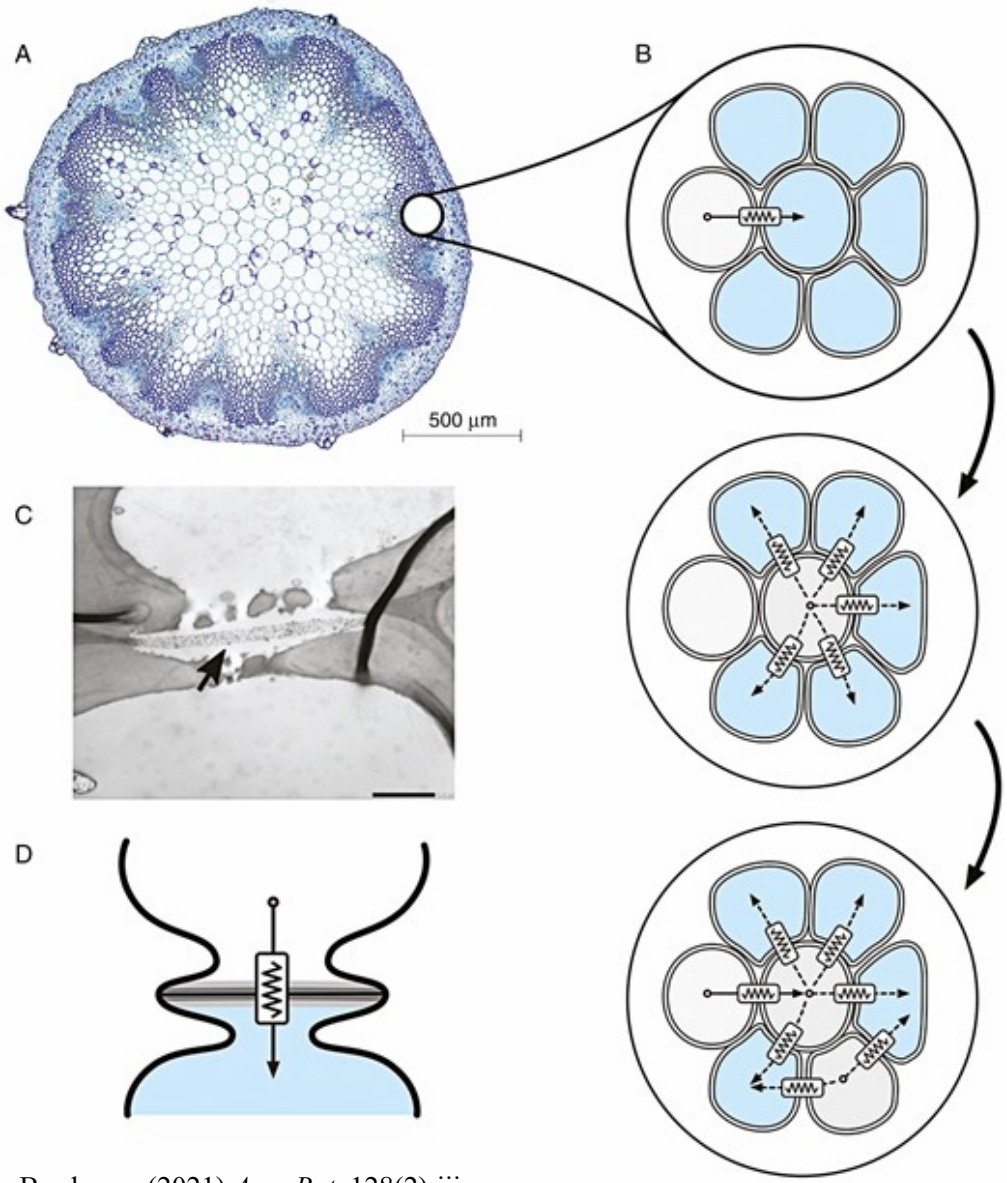
Ventruas et al. (2017) *J. Integr. Plant Biol.* 59(6):356-389.

Vapour-phase embolism:



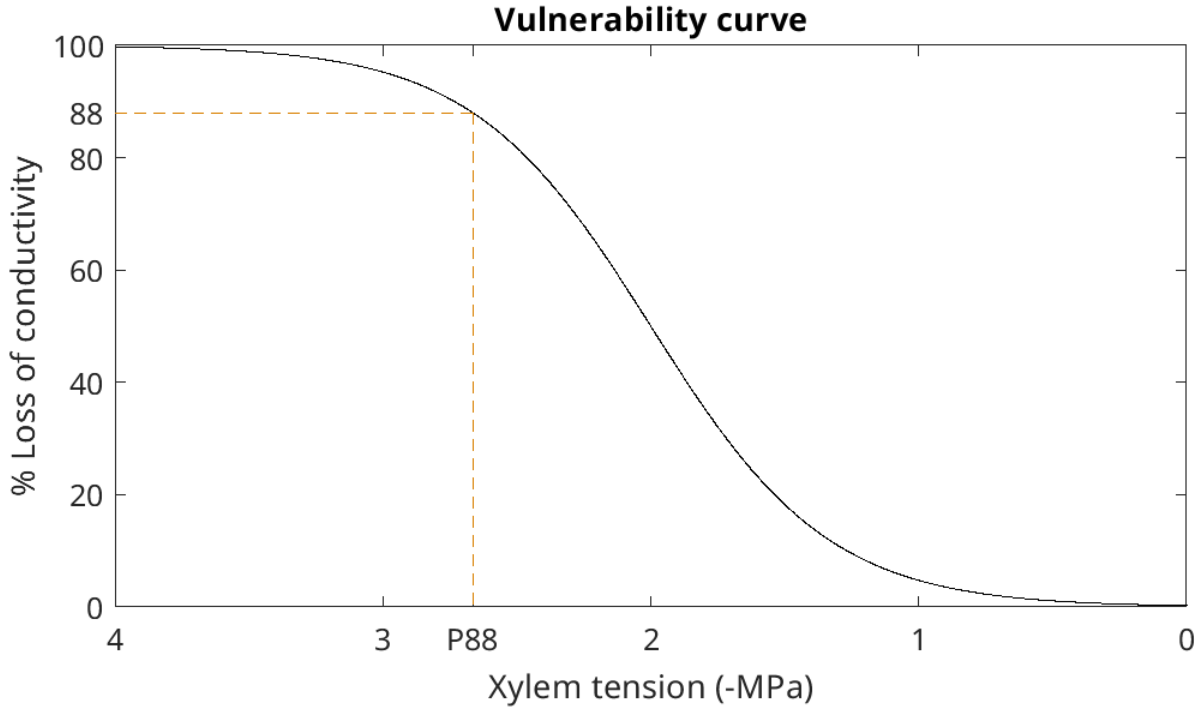
Cochard & Delzon (2013) *Ann. For. Sci.* 70:659–661

Hydraulic failure through embolism spread

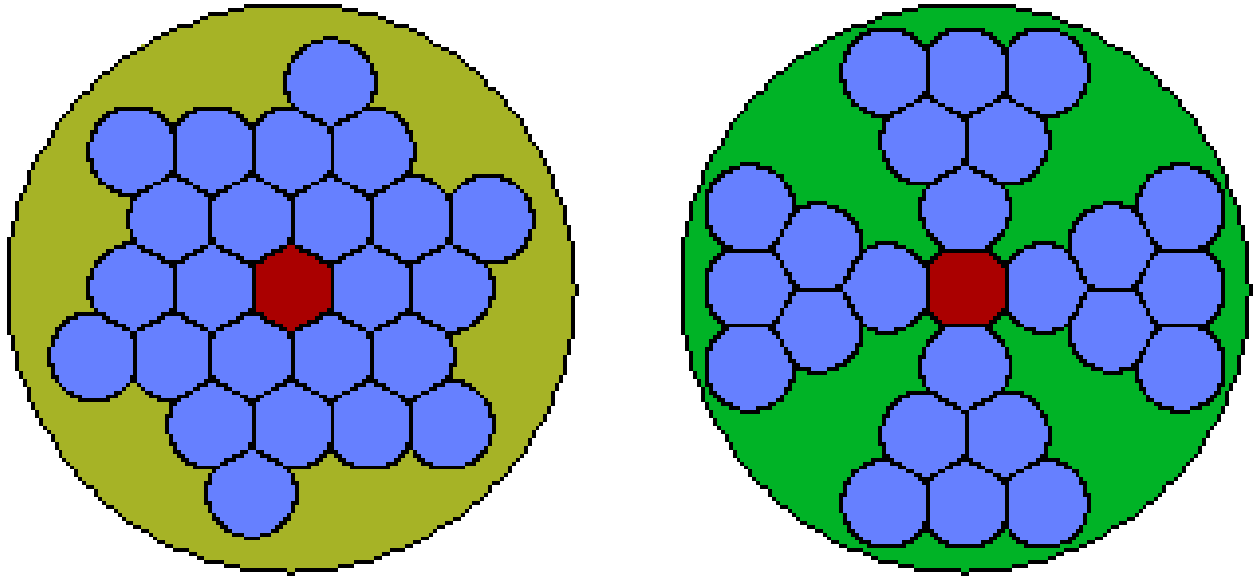


Brodersen (2021) *Ann. Bot.* 128(2):iii-v.

- As xylem tension exceeds ASP: embolism spreads
- Runaway embolism spread: catastrophic loss of conductivity
- % loss conductivity: P50, P88

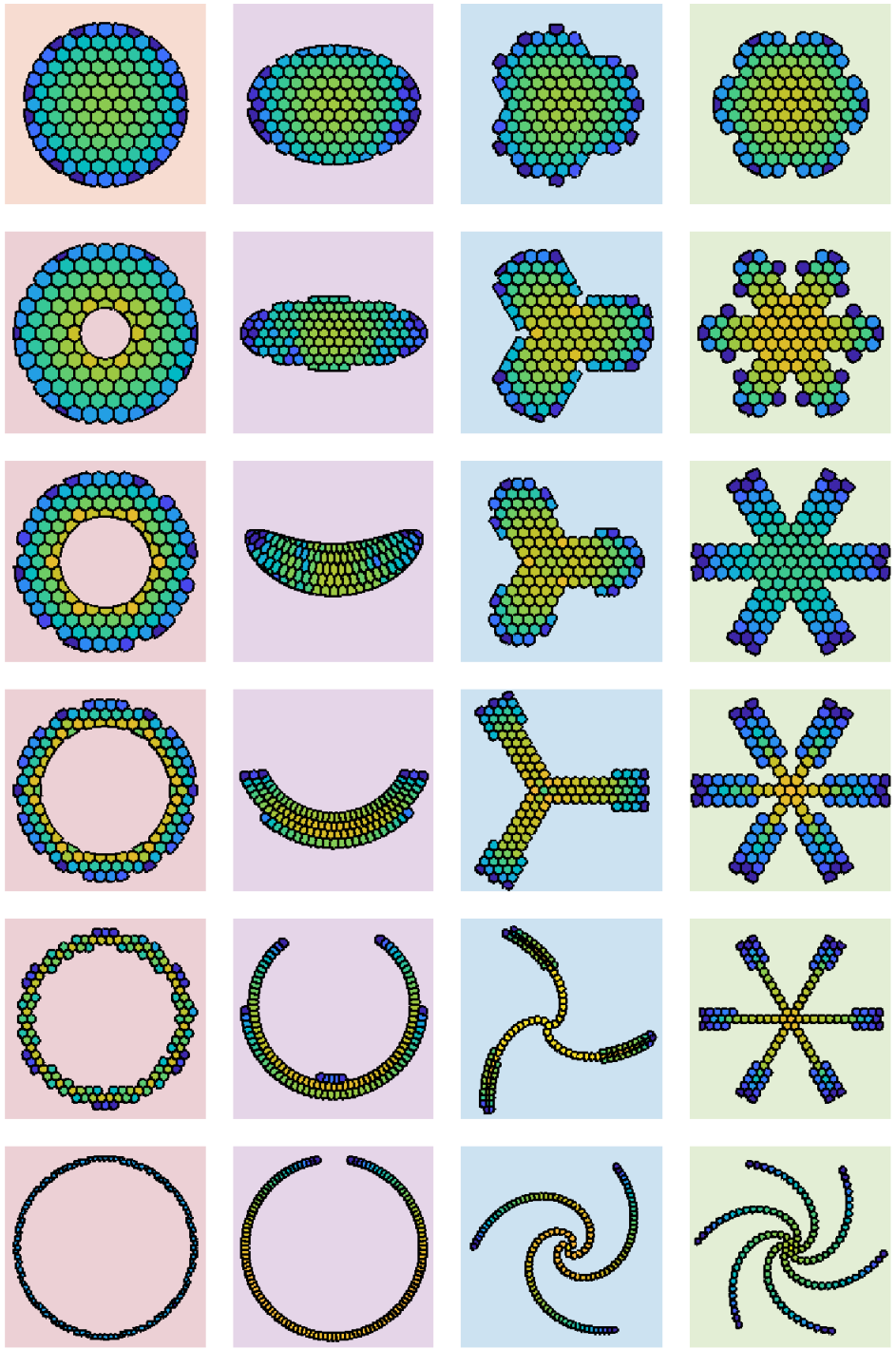


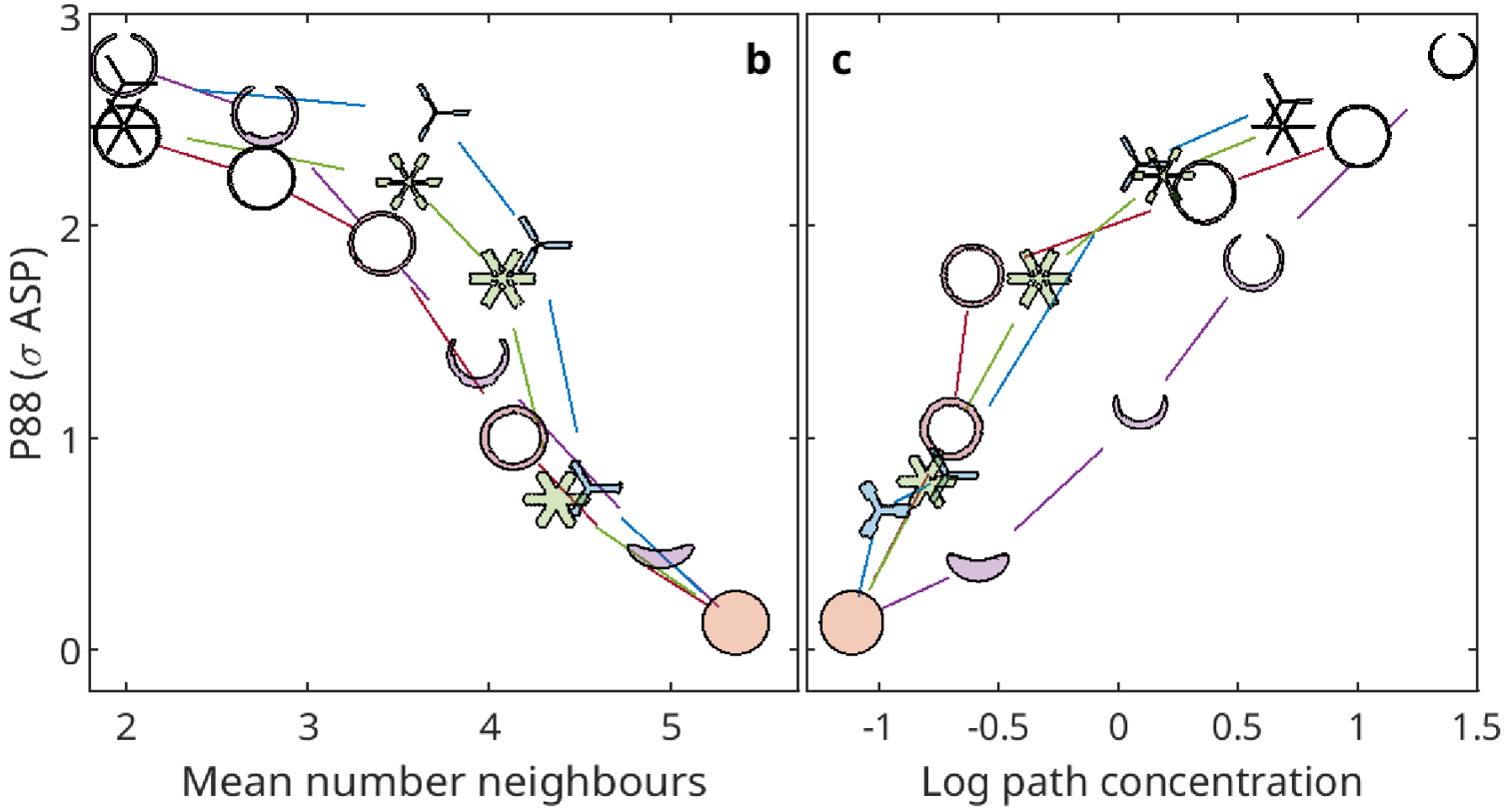
Embolism spread thought experiment



- 25 conduits in each stele
- Water tension at median value of pit membrane air-seeding resistance distribution
- Embolism will spread to 50% neighbouring conduits
- Xylem strand shape determines outcome

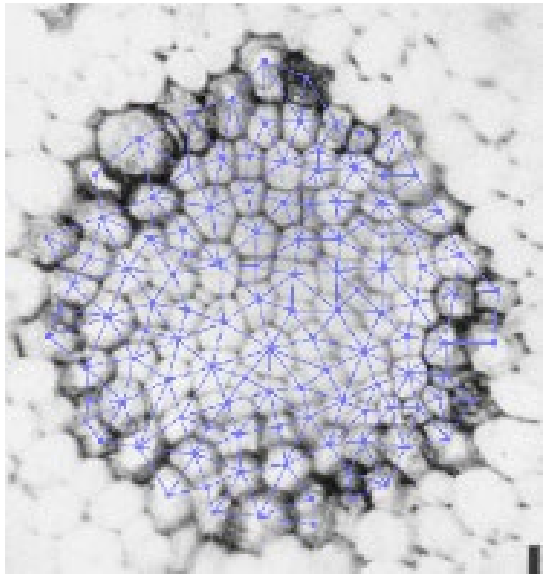
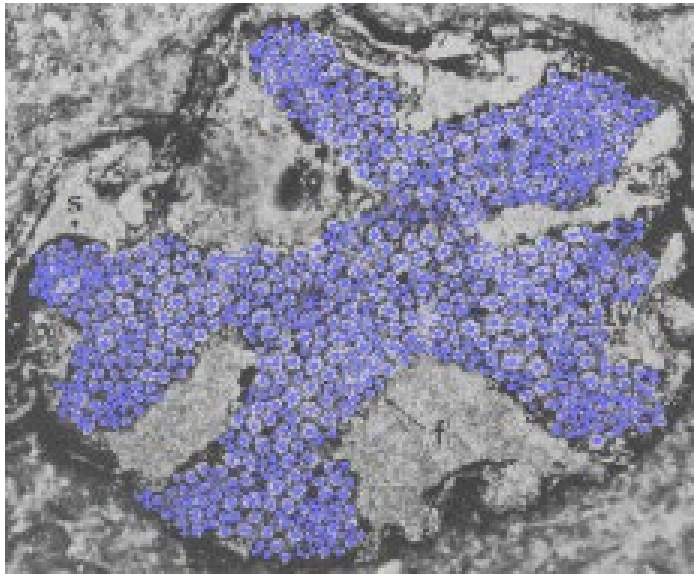
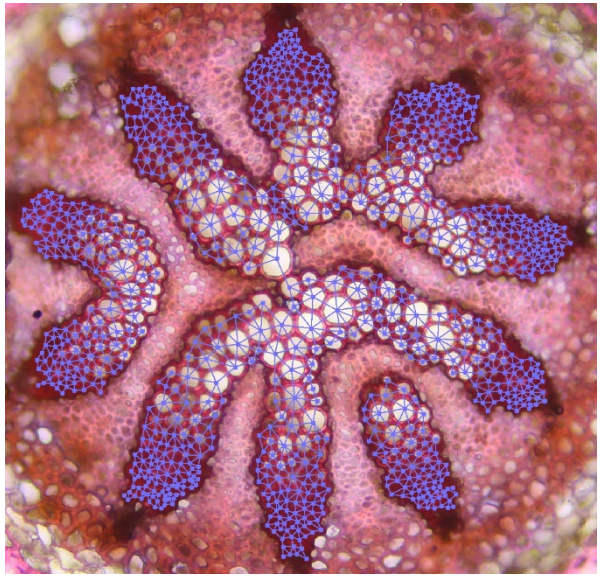
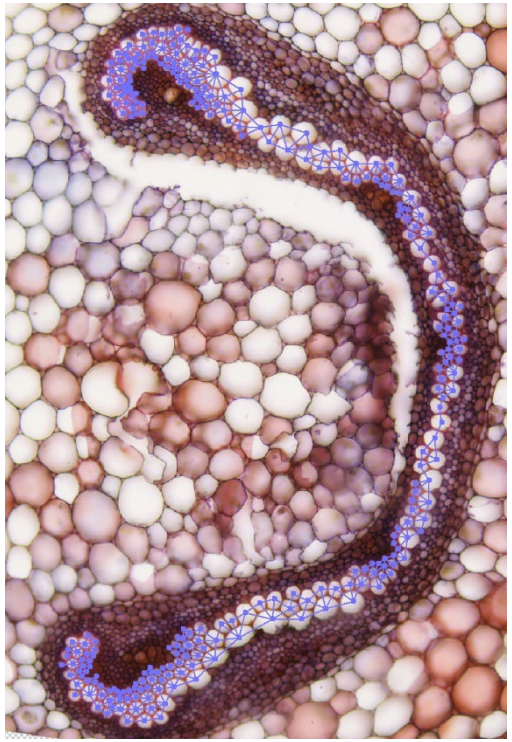
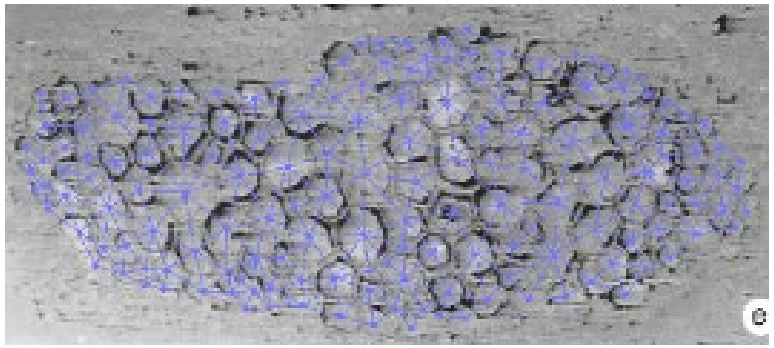
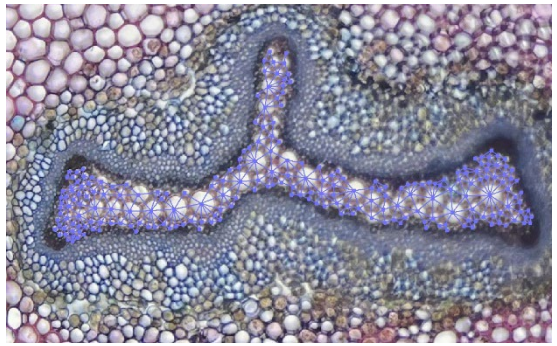
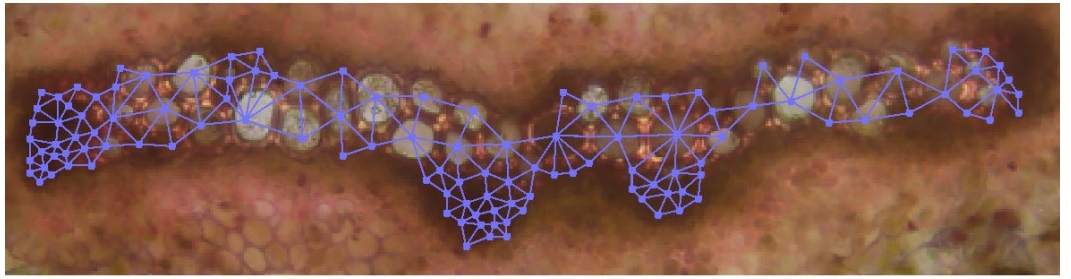
Morphological diversification but functionally parallel evolution: increasingly “complex” shapes show higher drought resistance





Bouda et al. (2022) *Science* 378:642-646.

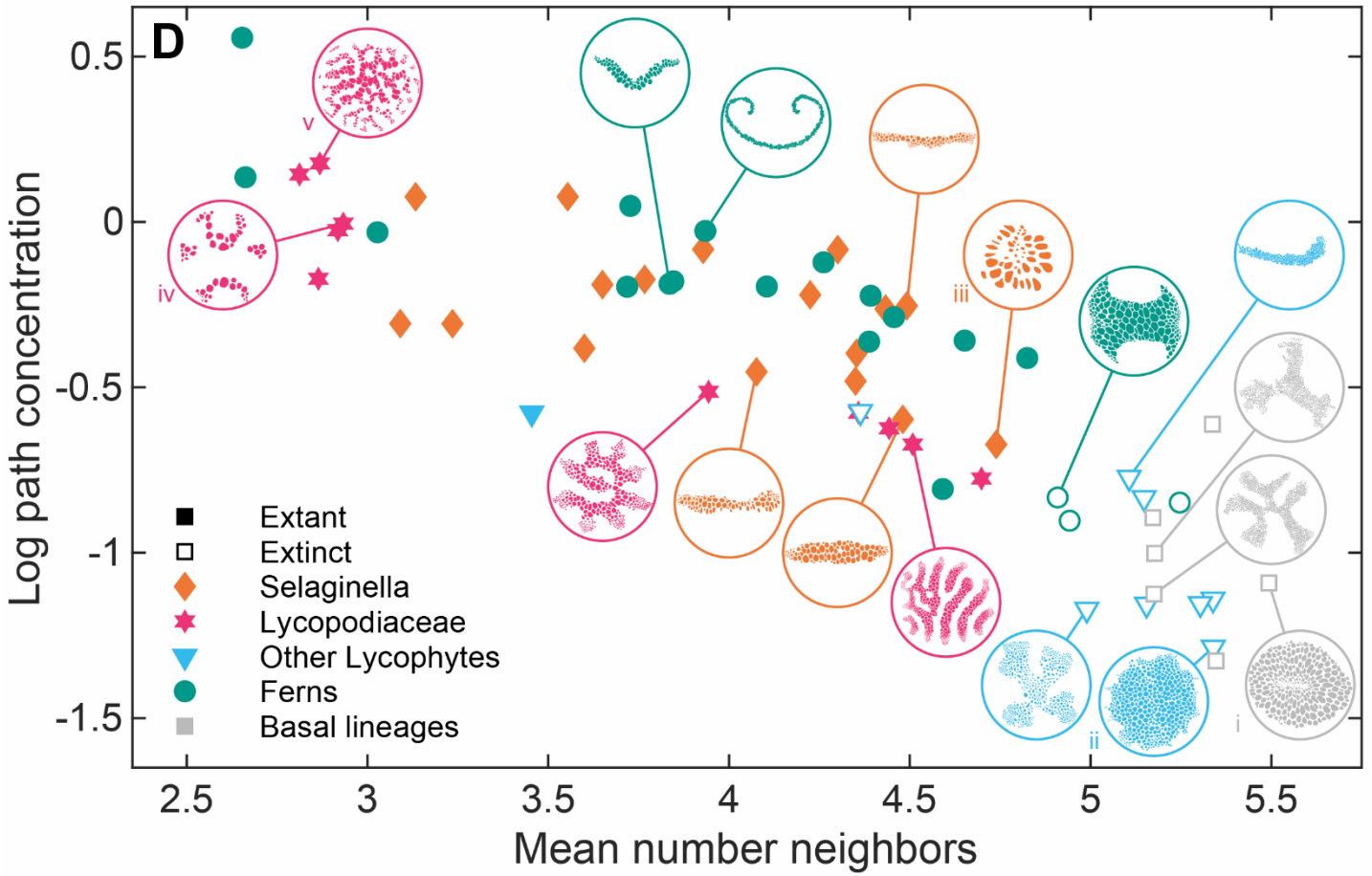
Data: conduit networks from cross sections of 60 species

44 Extant pteridophytes (light microscopy)
16 Devonian/Carboniferous fossils (from literature)

Top Left: *Aglaophyton majus*, Edwards (2003) Earth Environ Sci Trans R Soc Edinb 94:397-410.
Left : *Gosslingia breconensis*, Kenrick & Edwards (1988) Bot J Linn Soc 97: 95-123.
Top: *Drepanophycus spinaeformis*, Rayner (1984) Earth Environ Sci Trans R Soc Edinb 75:353-363.
Extant taxa & network reconstructions: Bouda et al. (2022) *Science* 378:642-646.

Topology of real xylem networks

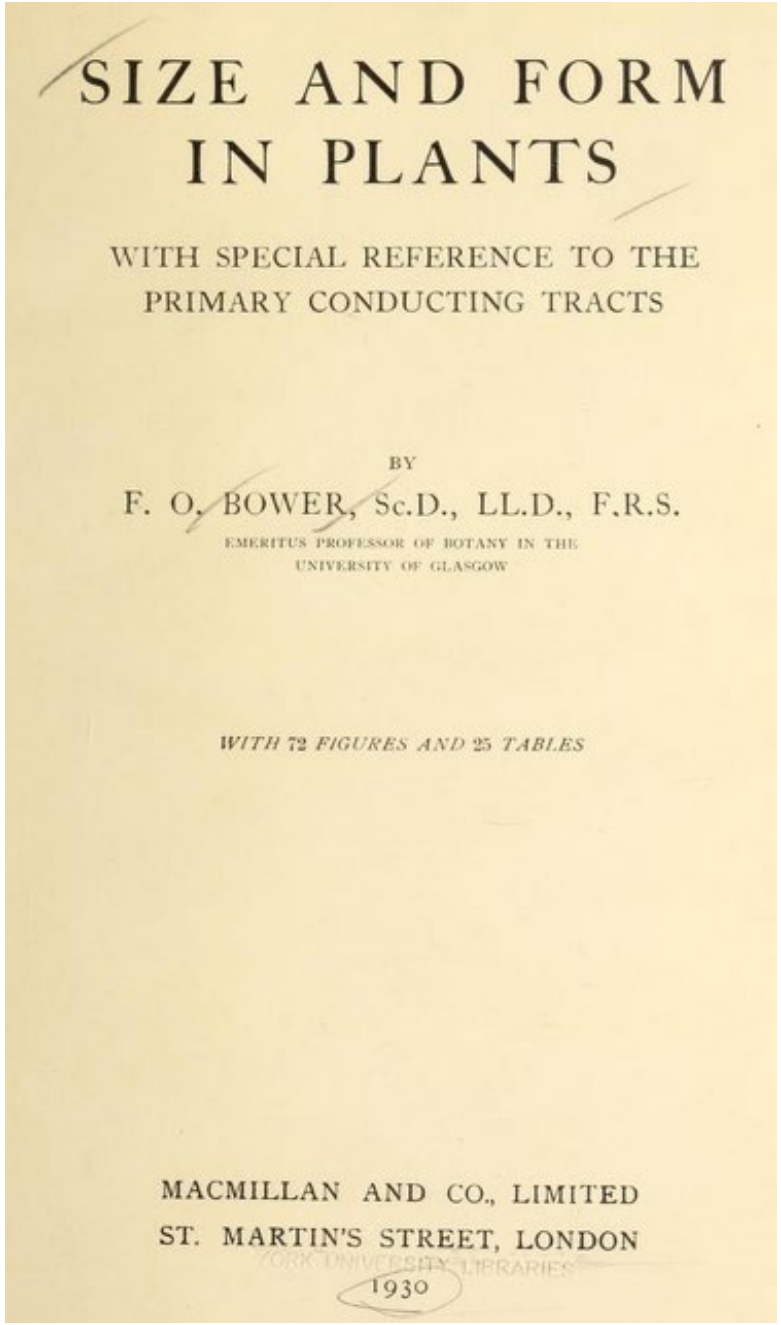


- Real plants cover nearly the whole theoretical space
- Early tracheophytes cluster in vulnerable part of space
- No extant xerophytes found with vulnerable topologies

i *Psilophyton dawsonii*
ii *Haskinsia colophylla*
iii *Selaginella selaginoides*
iv *Huperzia squarrosa*
v *Huperzia obtusifolia*

Bouda et al. (2022) *Science* 378:642-646.

What is the effect of size?



SIZE AND FORM IN PLANTS

WITH SPECIAL REFERENCE TO THE PRIMARY CONDUCTING TRACTS

BY

F. O. BOWER, Sc.D., LL.D., F.R.S.

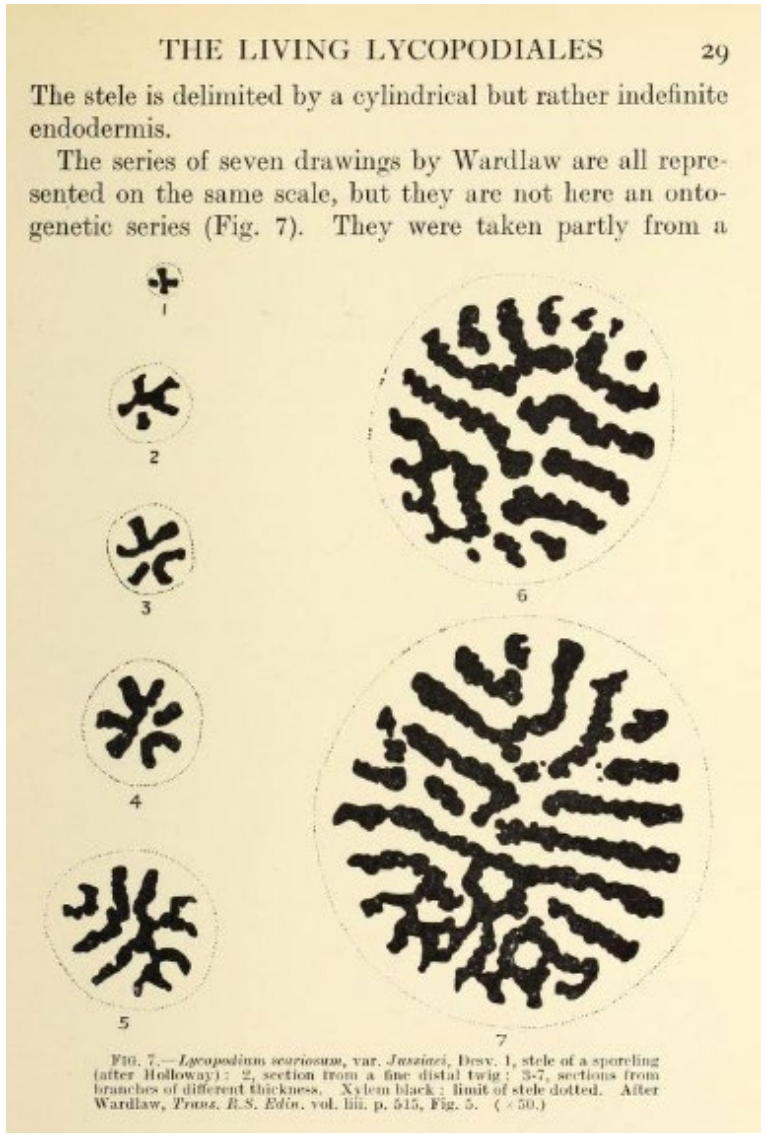
EMERITUS PROFESSOR OF BOTANY IN THE UNIVERSITY OF GLASGOW

WITH 72 FIGURES AND 25 TABLES

MACMILLAN AND CO., LIMITED

ST. MARTIN'S STREET, LONDON

1930



The stele is delimited by a cylindrical but rather indefinite endodermis.

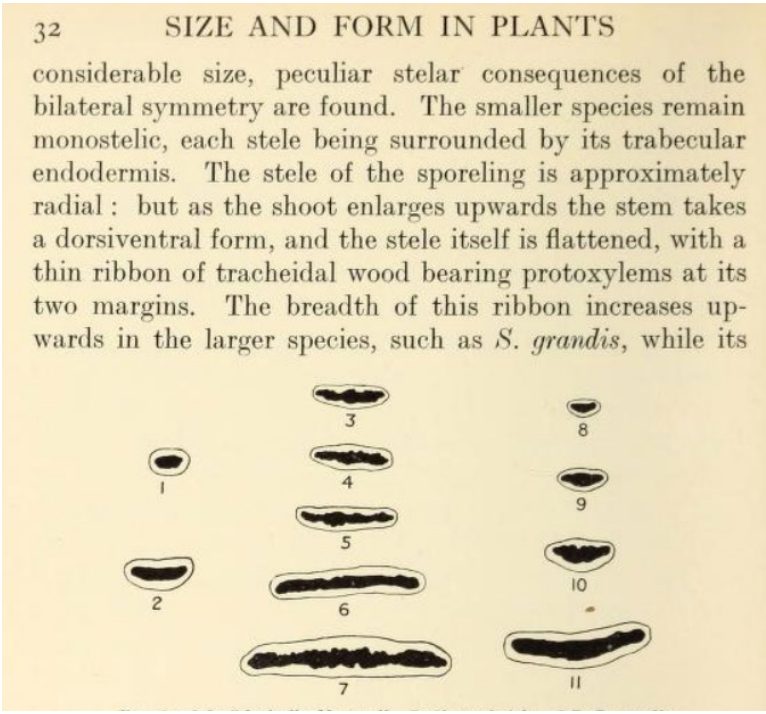
The series of seven drawings by Wardlaw are all represented on the same scale, but they are not here an ontogenetic series (Fig. 7). They were taken partly from a

1 2 3 4 5 6 7

FIG. 7.—*Lycopodium scariosum*, var. *Jussiaei*, Desv. 1, stele of a sporeling (after Holloway): 2, section from a fine distal twig: 3-7, sections from branches of different thickness. Xylem black: limit of stele dotted. After Wardlaw, *Trans. R.S. Edin.* vol. liii. p. 515, Fig. 5. (×50.)

Bower & Wardlaw found that organ size correlates with vascular complexity over 100 years ago.

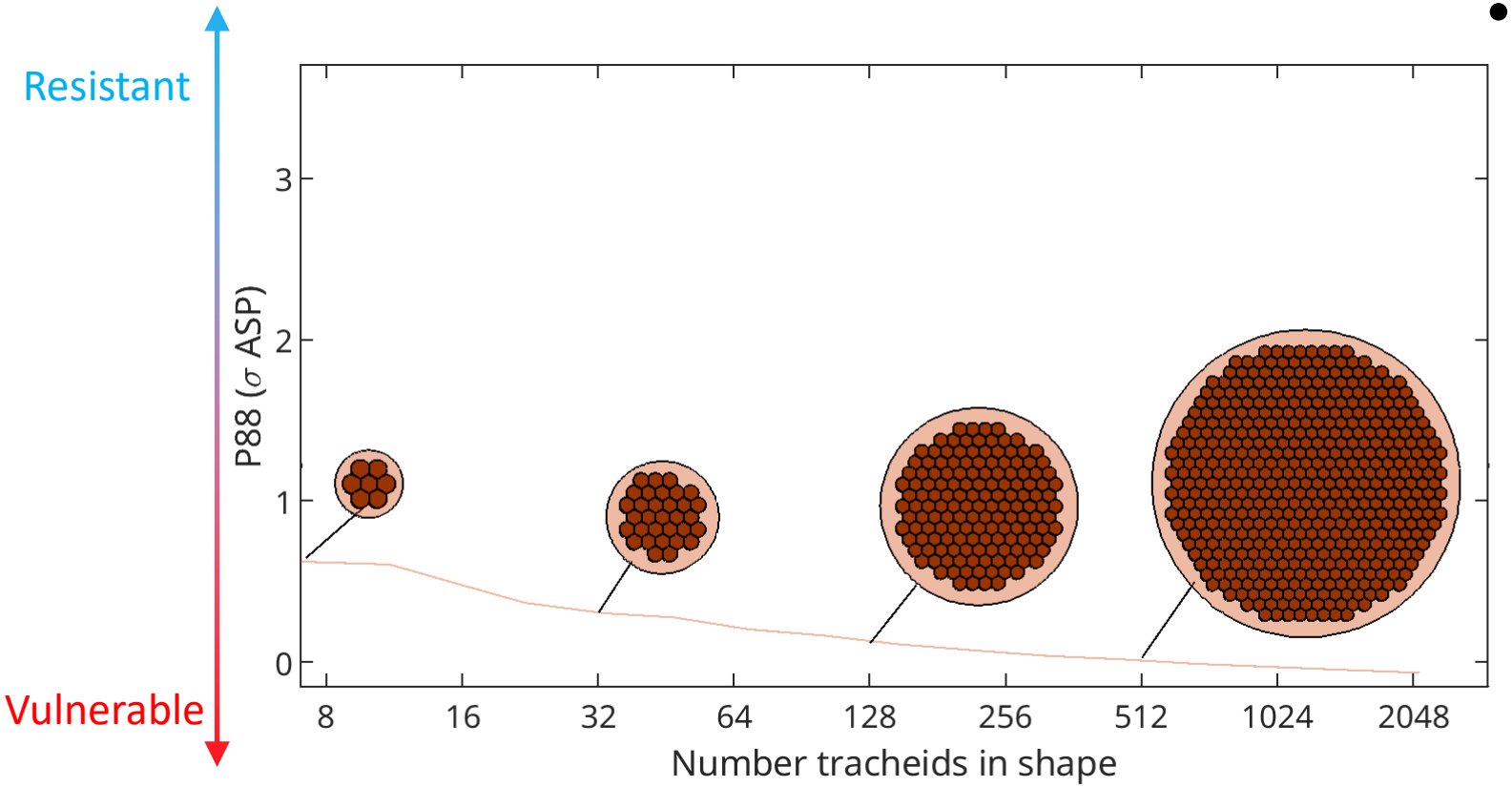
But why?



considerable size, peculiar stelar consequences of the bilateral symmetry are found. The smaller species remain monostelic, each stele being surrounded by its trabecular endodermis. The stele of the sporeling is approximately radial: but as the shoot enlarges upwards the stem takes a dorsiventral form, and the stele itself is flattened, with a thin ribbon of tracheidal wood bearing protoxylems at its two margins. The breadth of this ribbon increases upwards in the larger species, such as *S. grandis*, while its

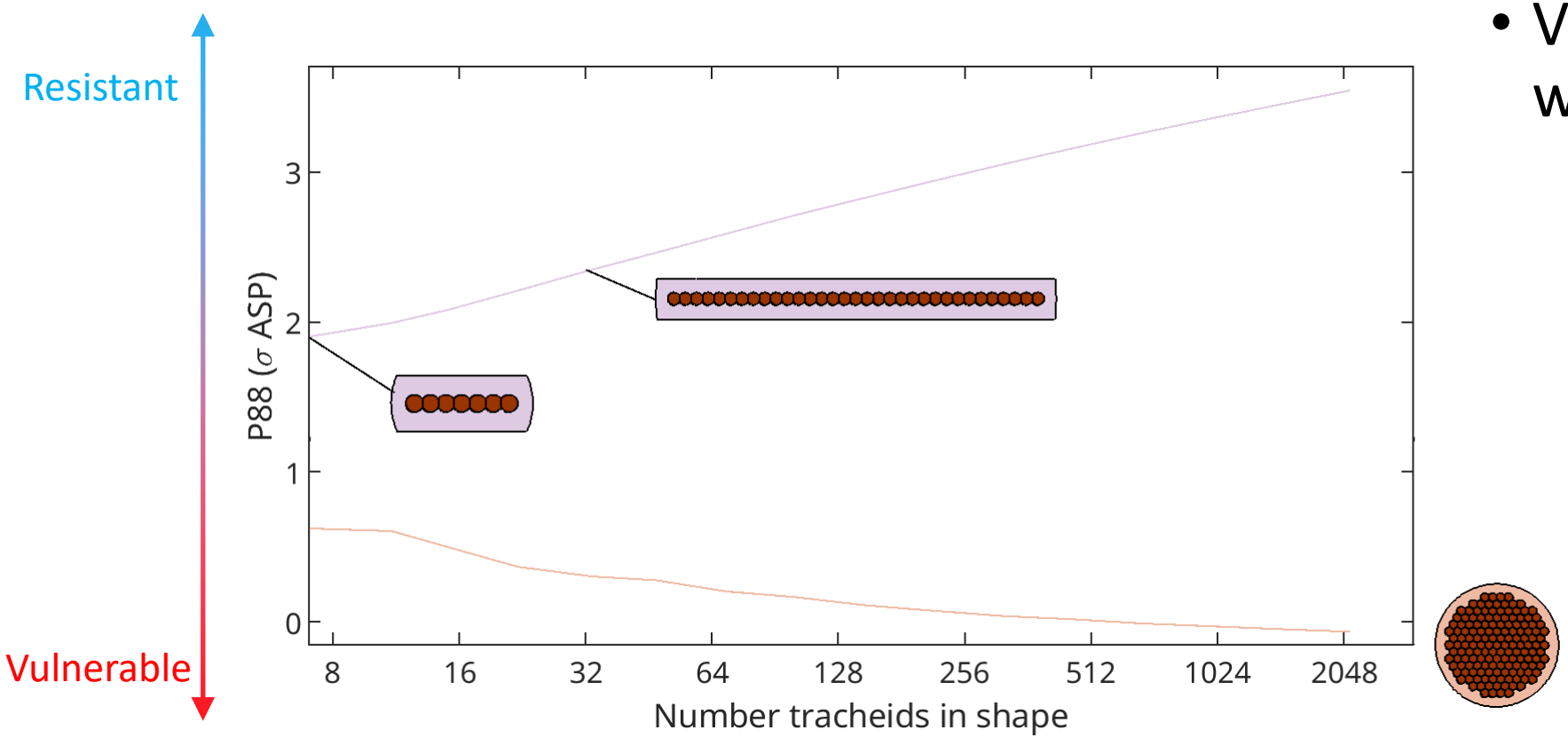
1 2 3 4 5 6 7 8 9 10 11

Vulnerability of growing xylem strand: (1) Cylinder (terete form)



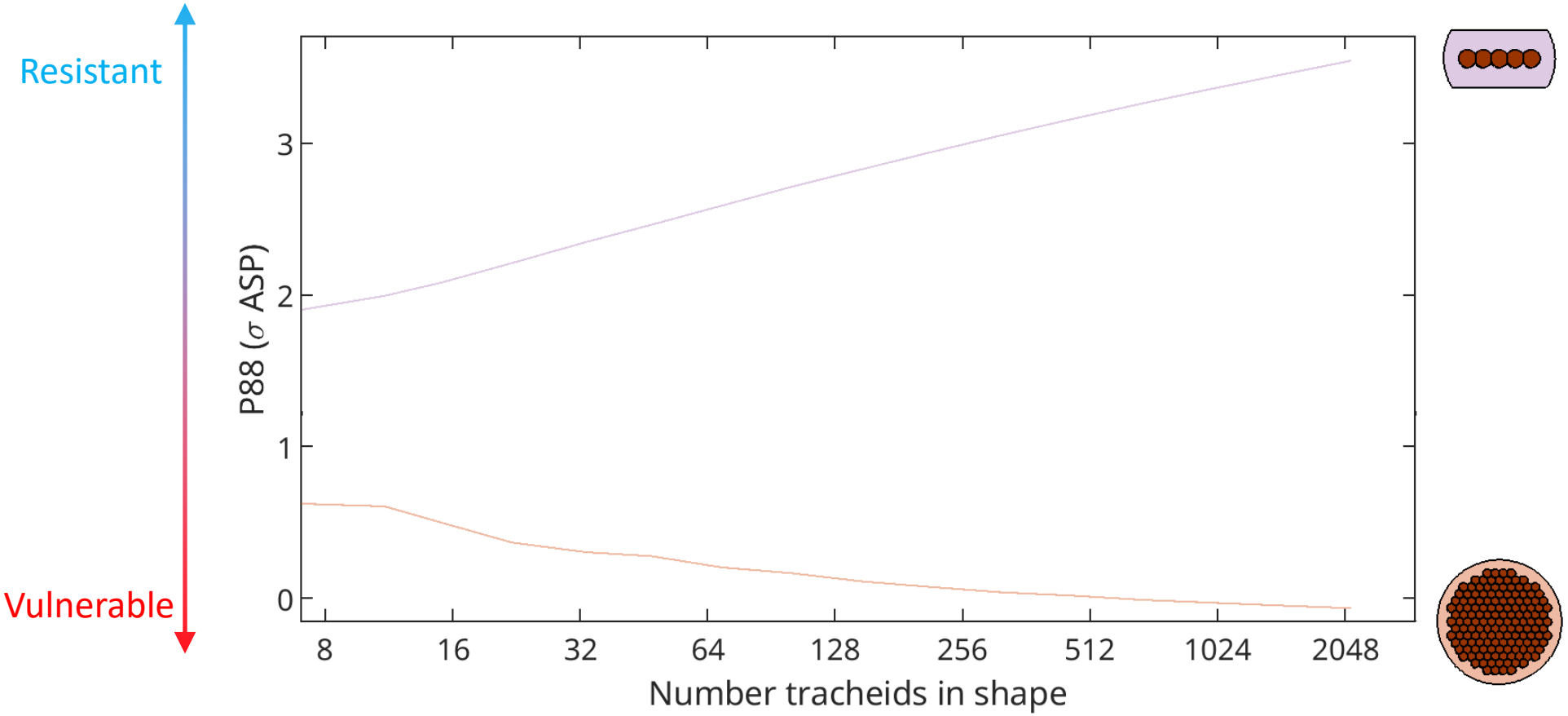
- Vulnerability increases with size:
  - Number of neighbours tends toward 6
  - Parallel pathways multiply

Vulnerability of growing xylem strand: (2) Linear strand



- Vulnerability decreases with size:
  - Number of neighbours tends towards 2
  - No parallel paths, increasing path concentration

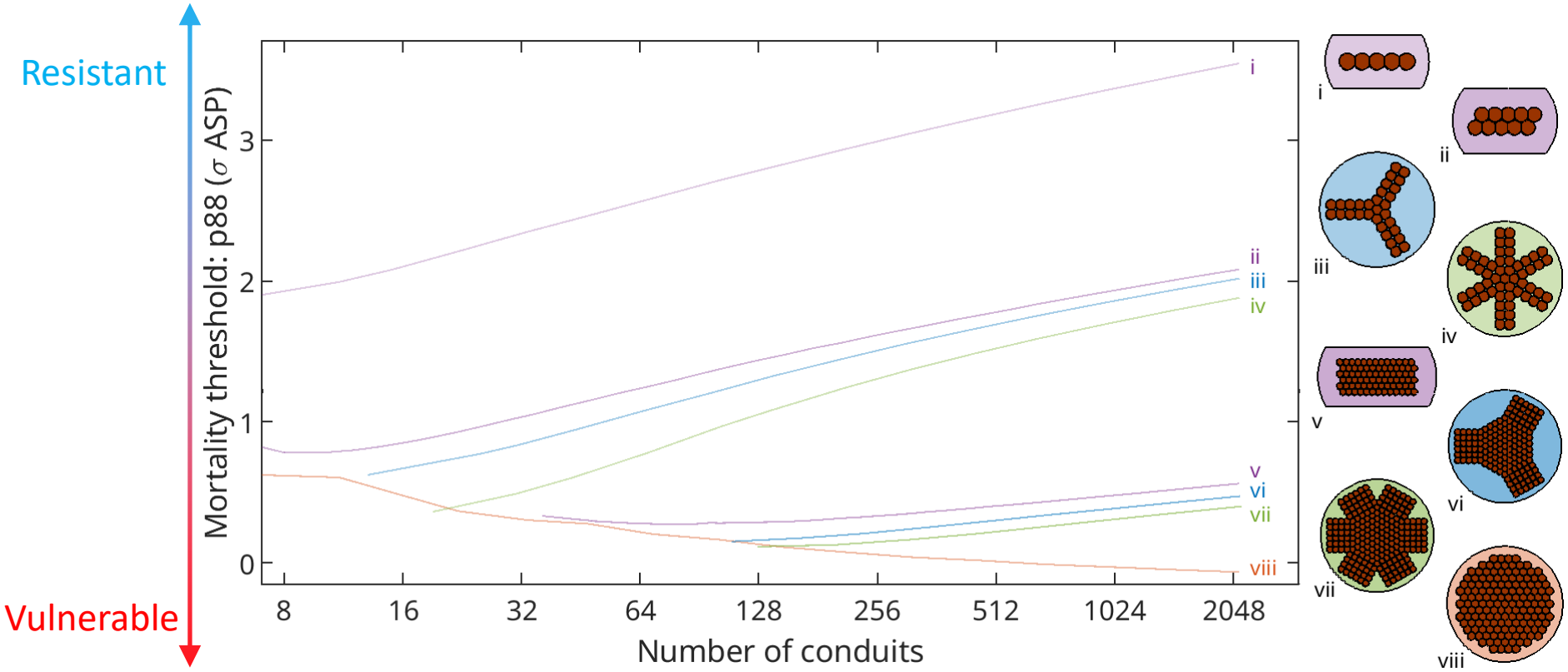
Terete and linear limits of theoretical space



(1) All other shapes must fall between these two

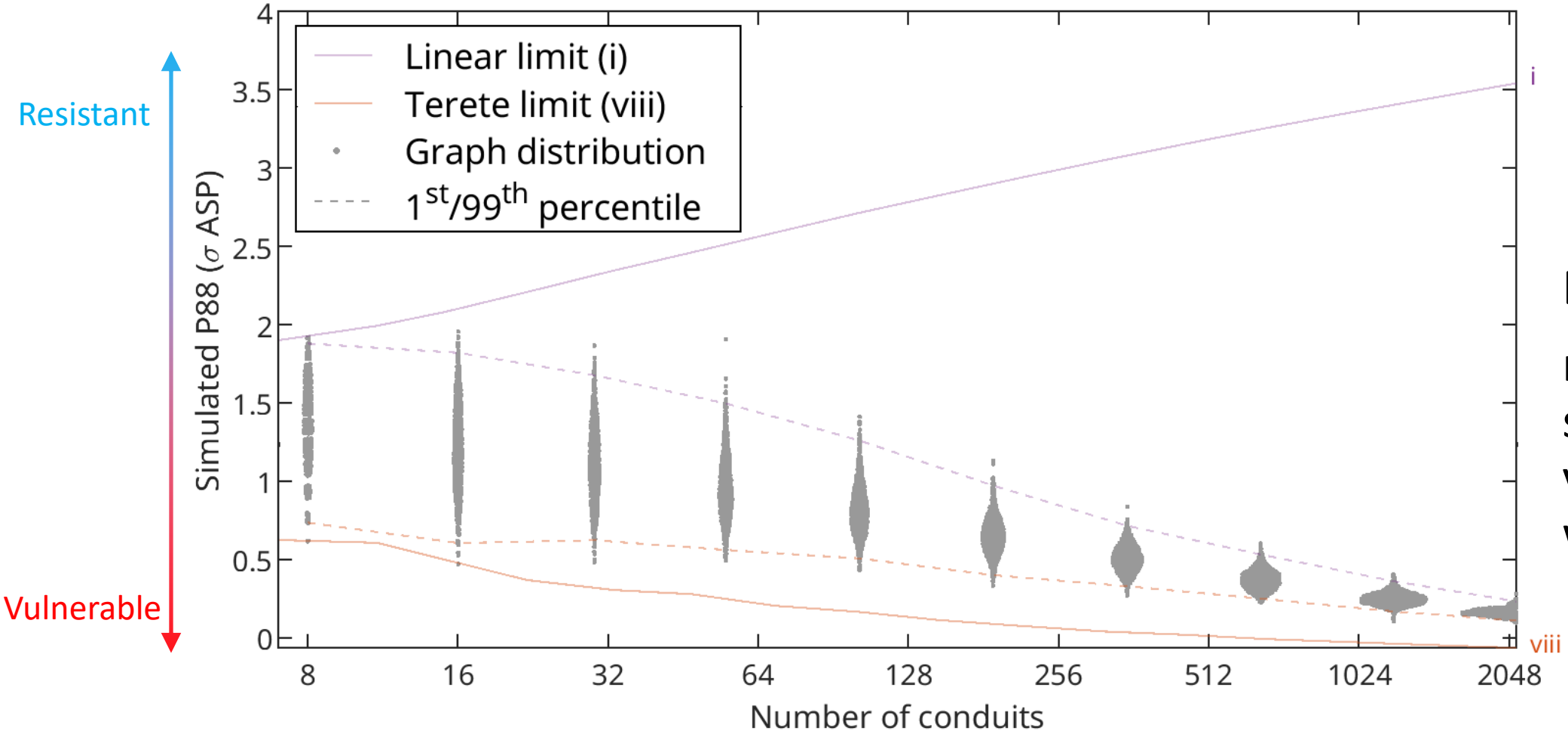
(2) Some network properties are extensive, not intensive

Vulnerability of growing xylem strand: (3) straps & lobed shapes



- Width is the key explanatory variable
- Increasing number of lobes is a disadvantage
- Lowest vulnerability region only available to extreme shapes (width < 2)

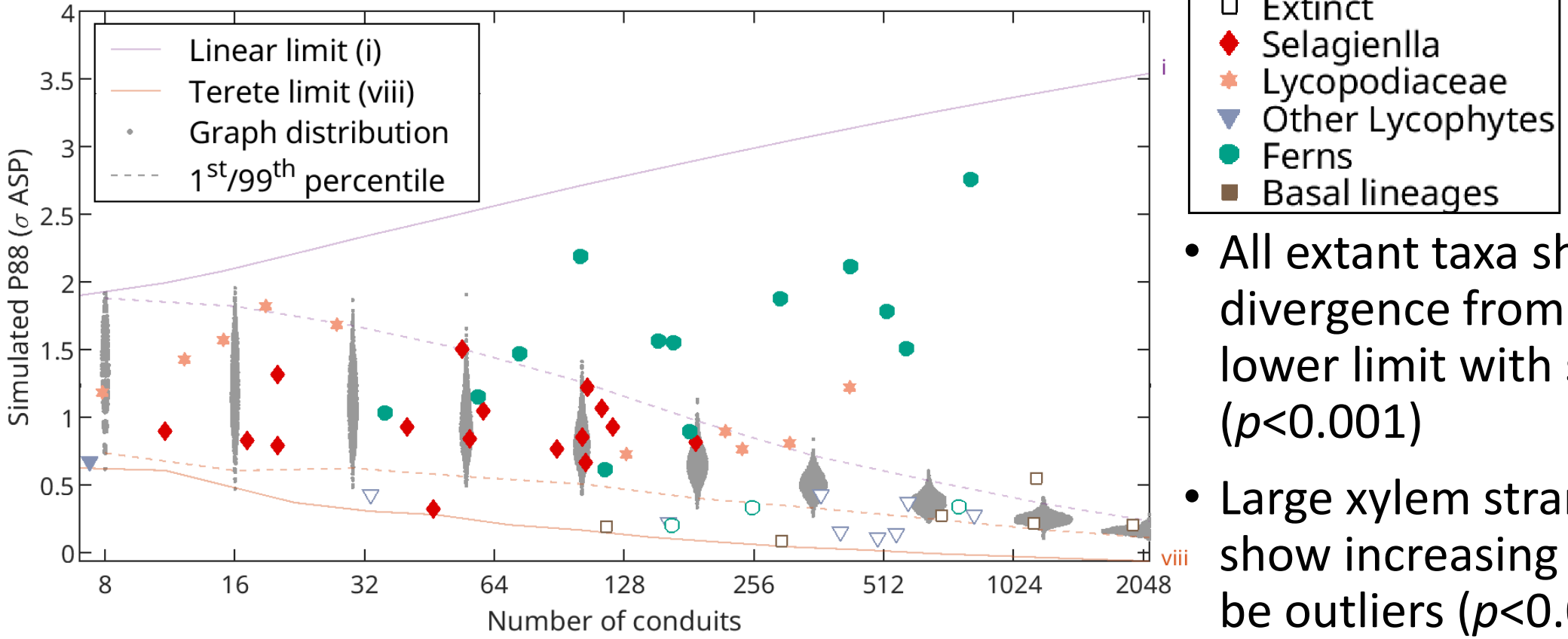
Null hypothesis construction:
Randomly sample graphs over range of sizes



Expectation:

random graphs show increased vulnerability with size

Observed xylem strands are non-random

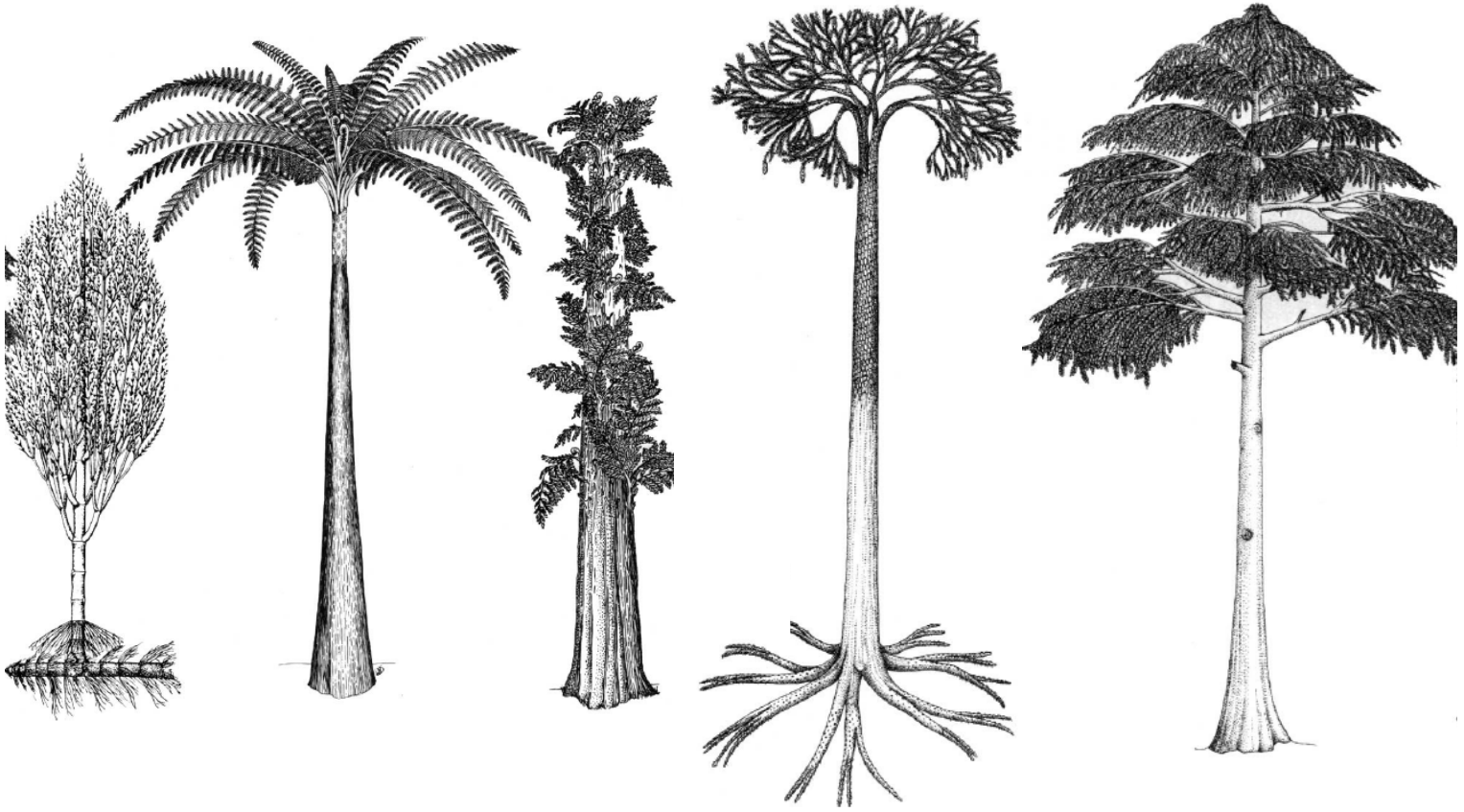


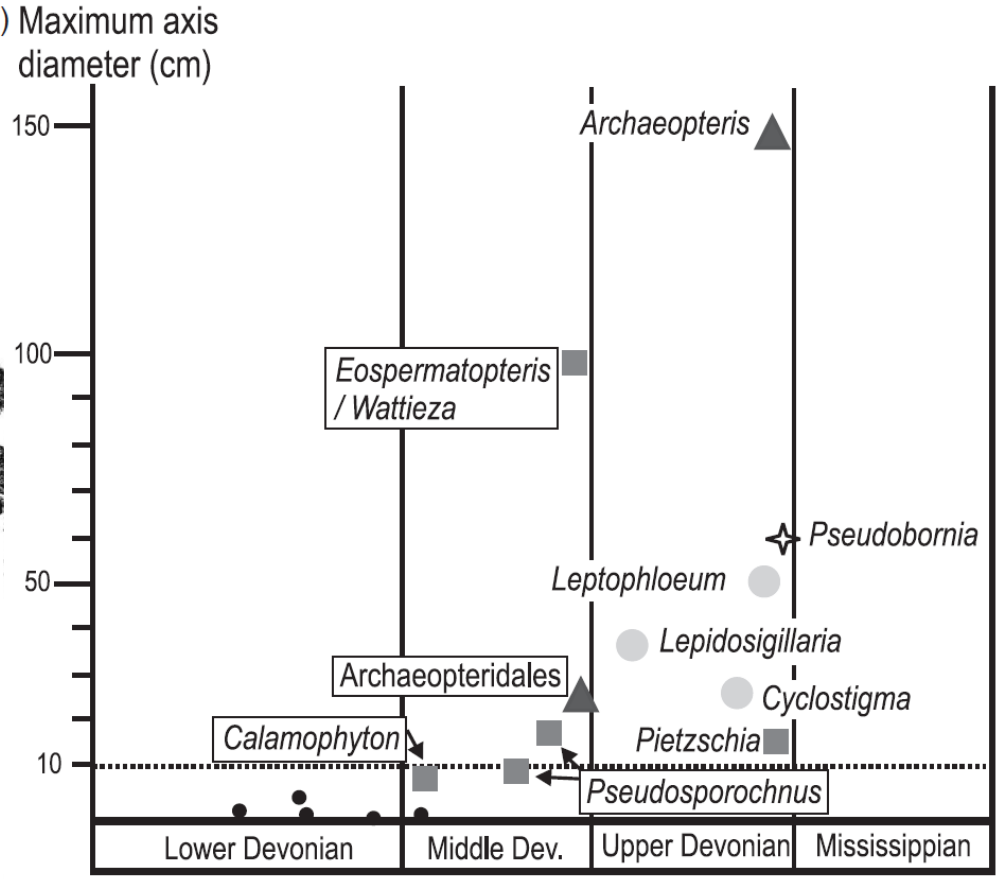
- All extant taxa show divergence from terete lower limit with size (p<0.001)
- Large xylem strands ($n_{cond} > 130$) show increasing tendency to be outliers (p<0.001)
- Taking fossils as 1 group, same tendencies, but weaker (p<0.001)

Bouda et al. (2022) *Science* 378:642-646.

No large cylinders, eh?

Was there Parallel Evolution of Anatomy Towards Trees?

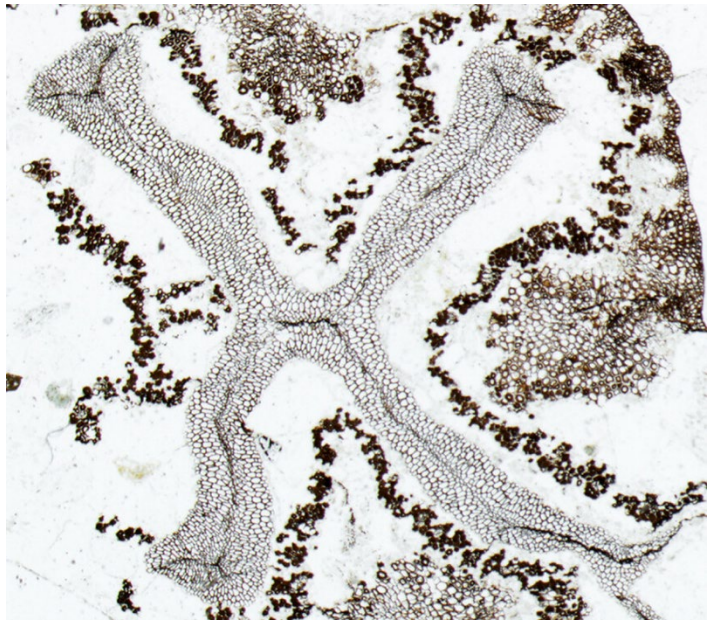


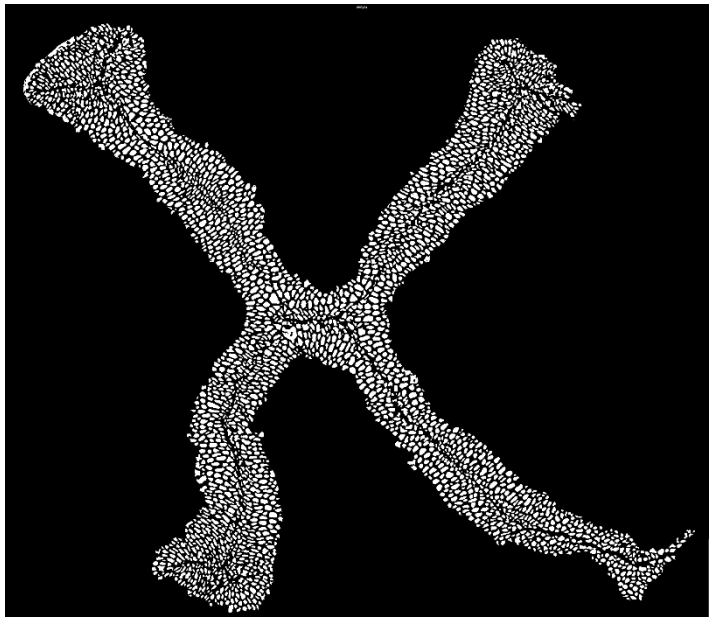


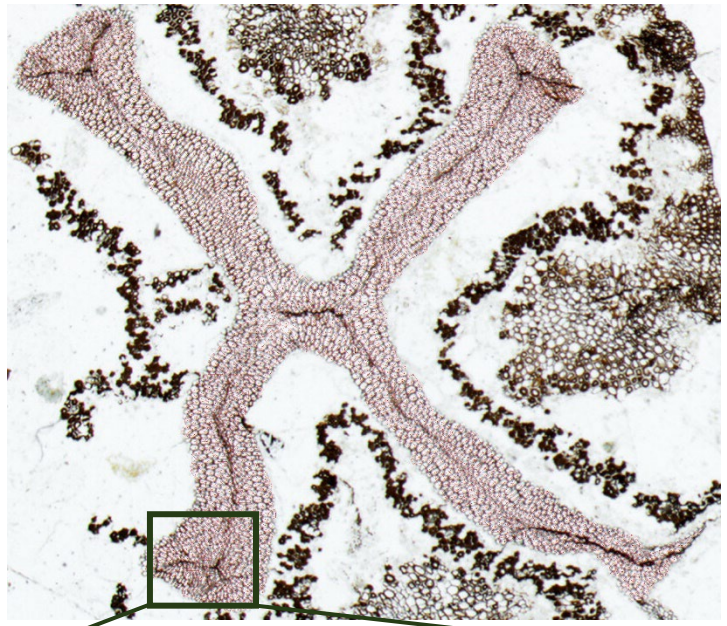
Donaghue (2005) *Paleobiology* 31(2):77-93.

Meyer-Bertaud et al. (2010) Geological Society, London, Special Publications 339:59 – 70.

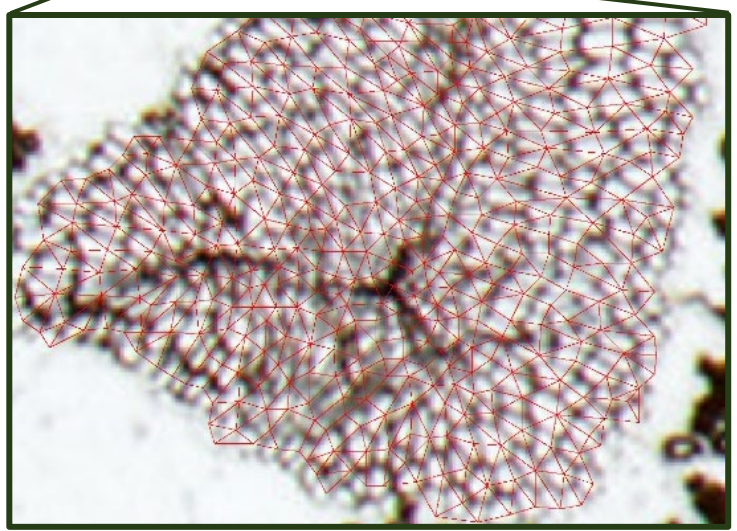
Image Processing Pipeline







Kenricrana bivena (Battery Pt. Fm., 402-397 MYA); Toledo *et al.* (2018) *New Phytol.* **232**:914-927.



Step 1: Binarisation [Fiji]

Step 2: Network extraction[Custom Matlab code]
Semi-automated, UI-based,
working towards releasing v1.0

Fossil xylem database

Current State:

>120 fossils processed

>100 Lower Devonian (420-390 MYA)

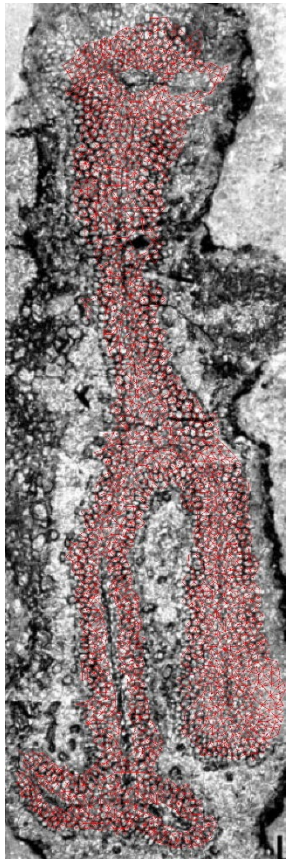
> 20 “woody”

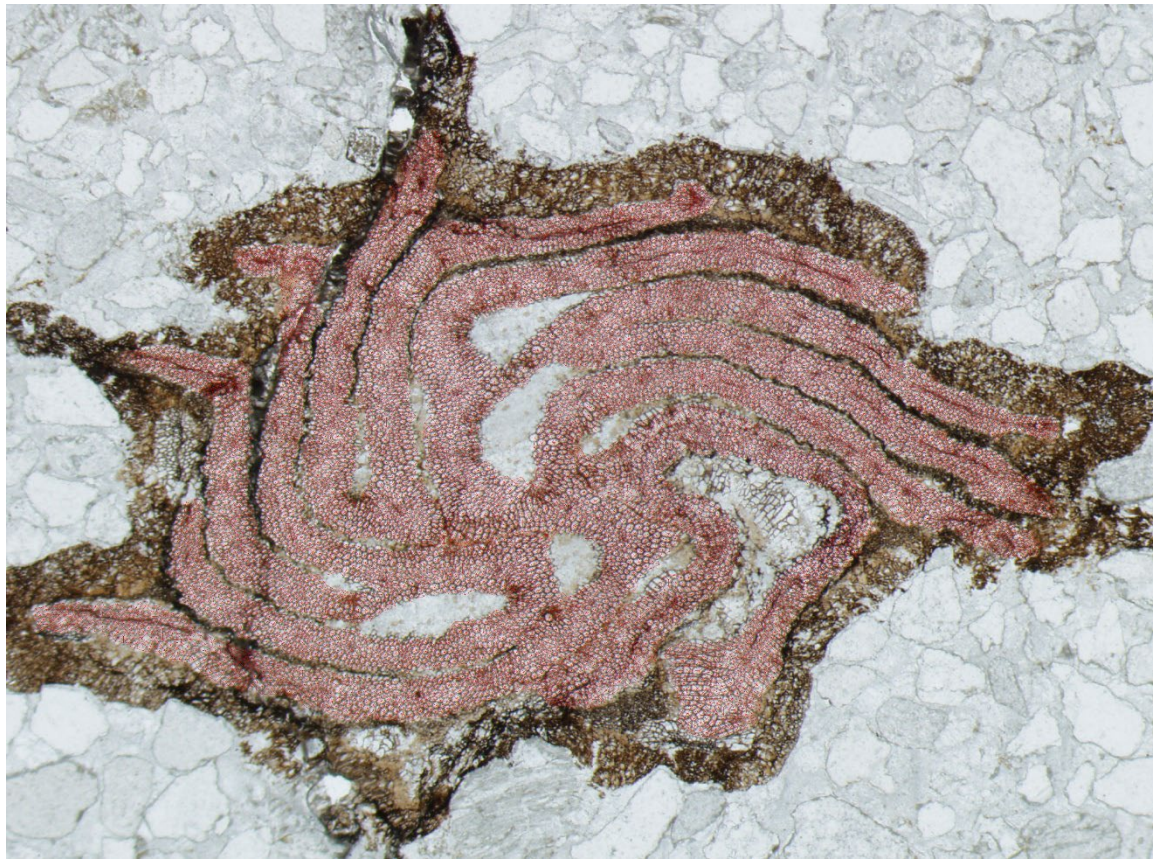
> 80 non-woody

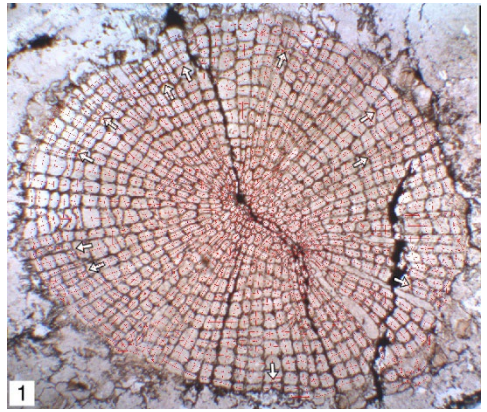
> 100.000 conduits

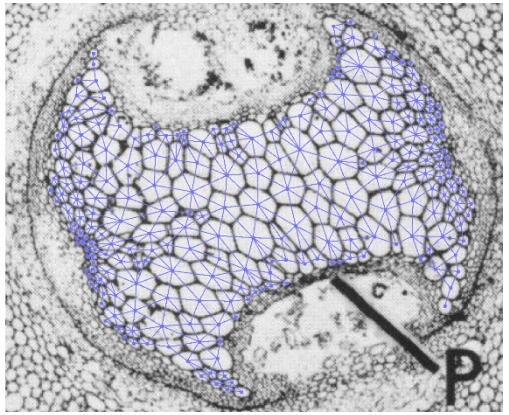
Becoming a unique record of plant vascular evolution

Will need curation…







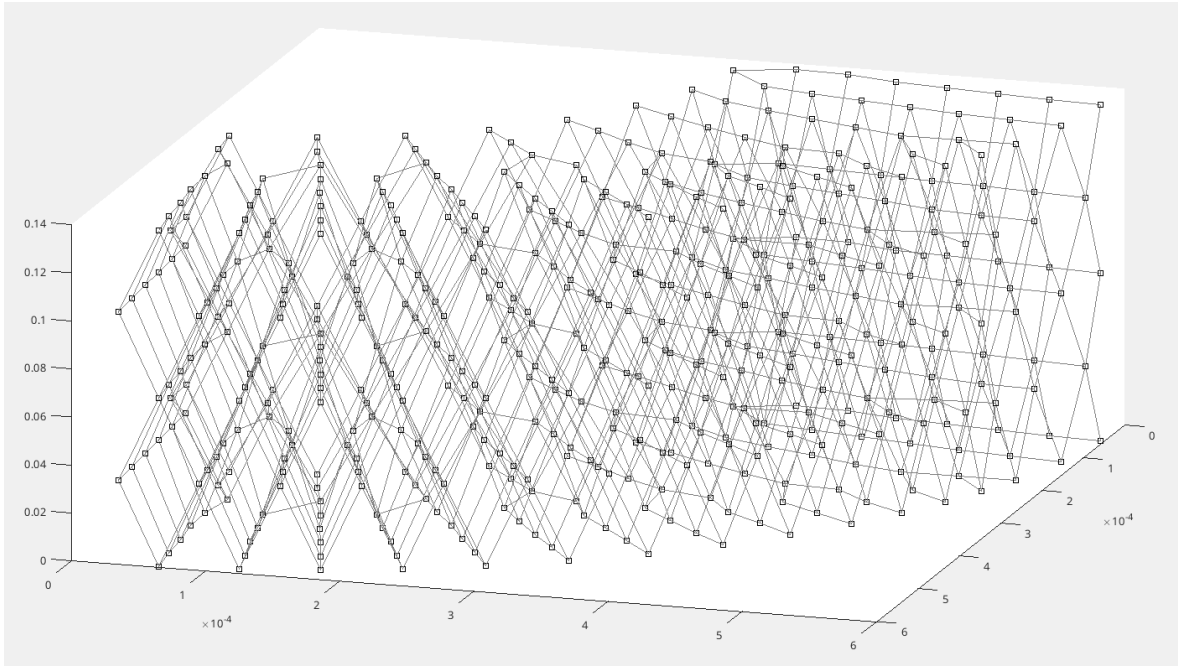


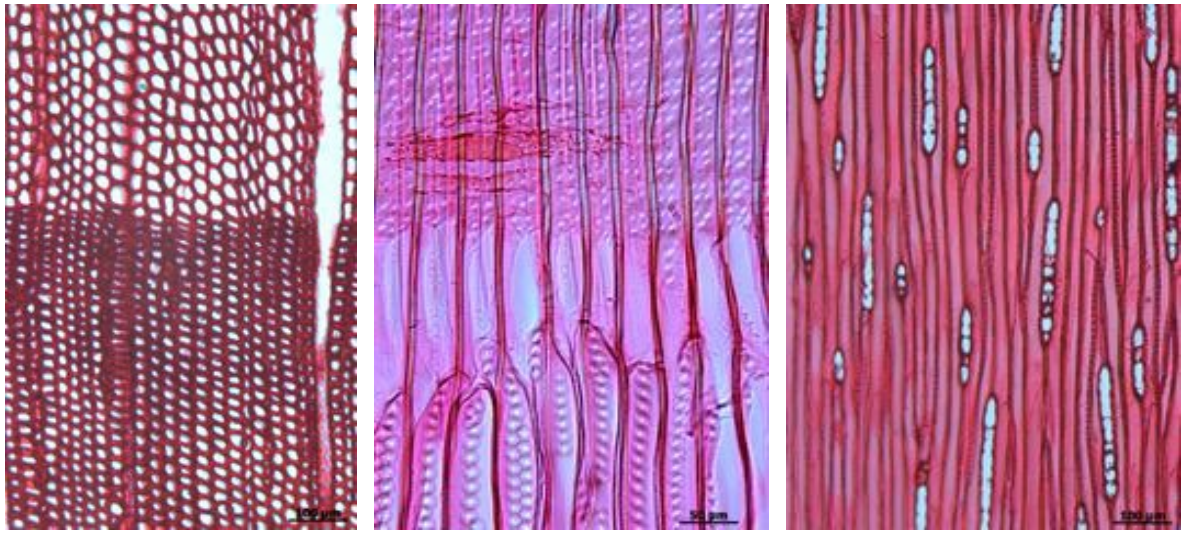
3D Models of Wood & Growth

Wood is anisotropic & has 3D structure

Inherently 3D networks derived from images (fossil & modern wood)

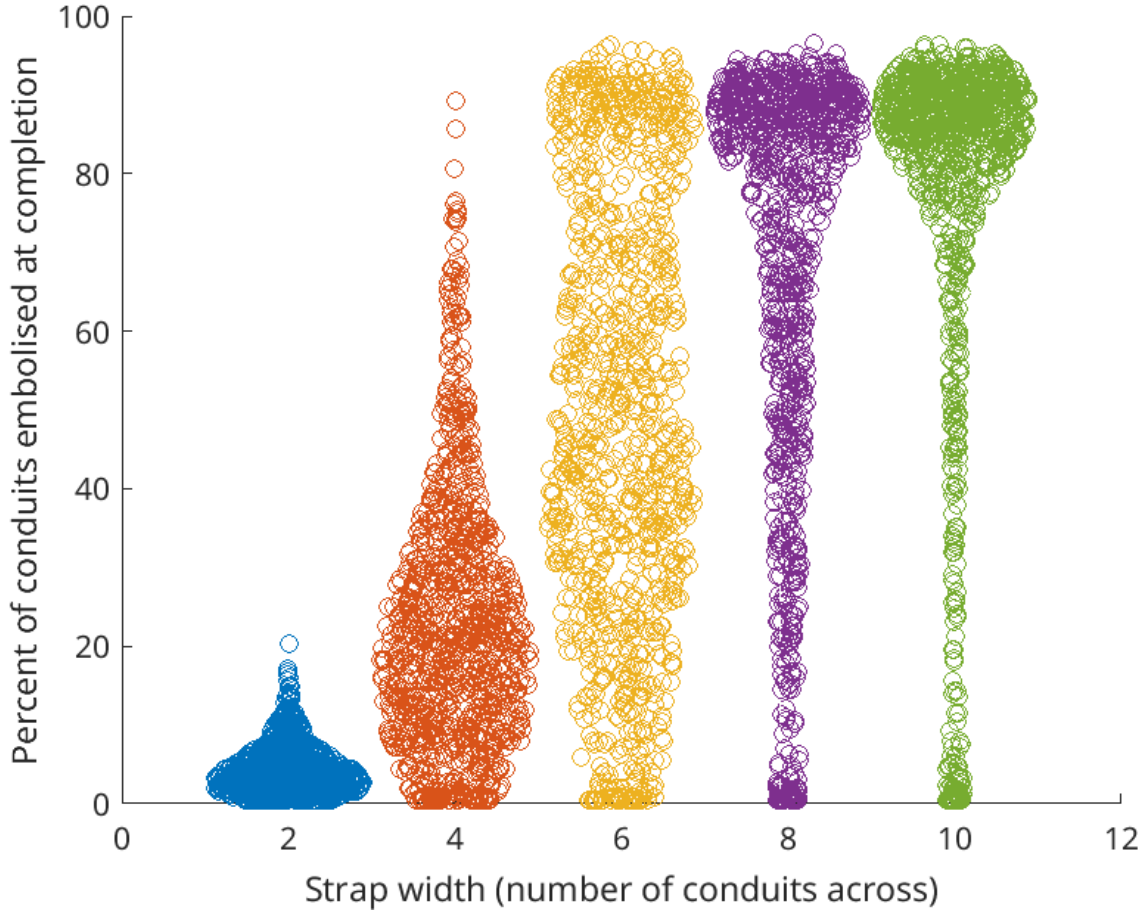
Questions:
Does wood anatomy change percolation threshold?
Does percolation constrain possible anatomies for trees? (large plants)

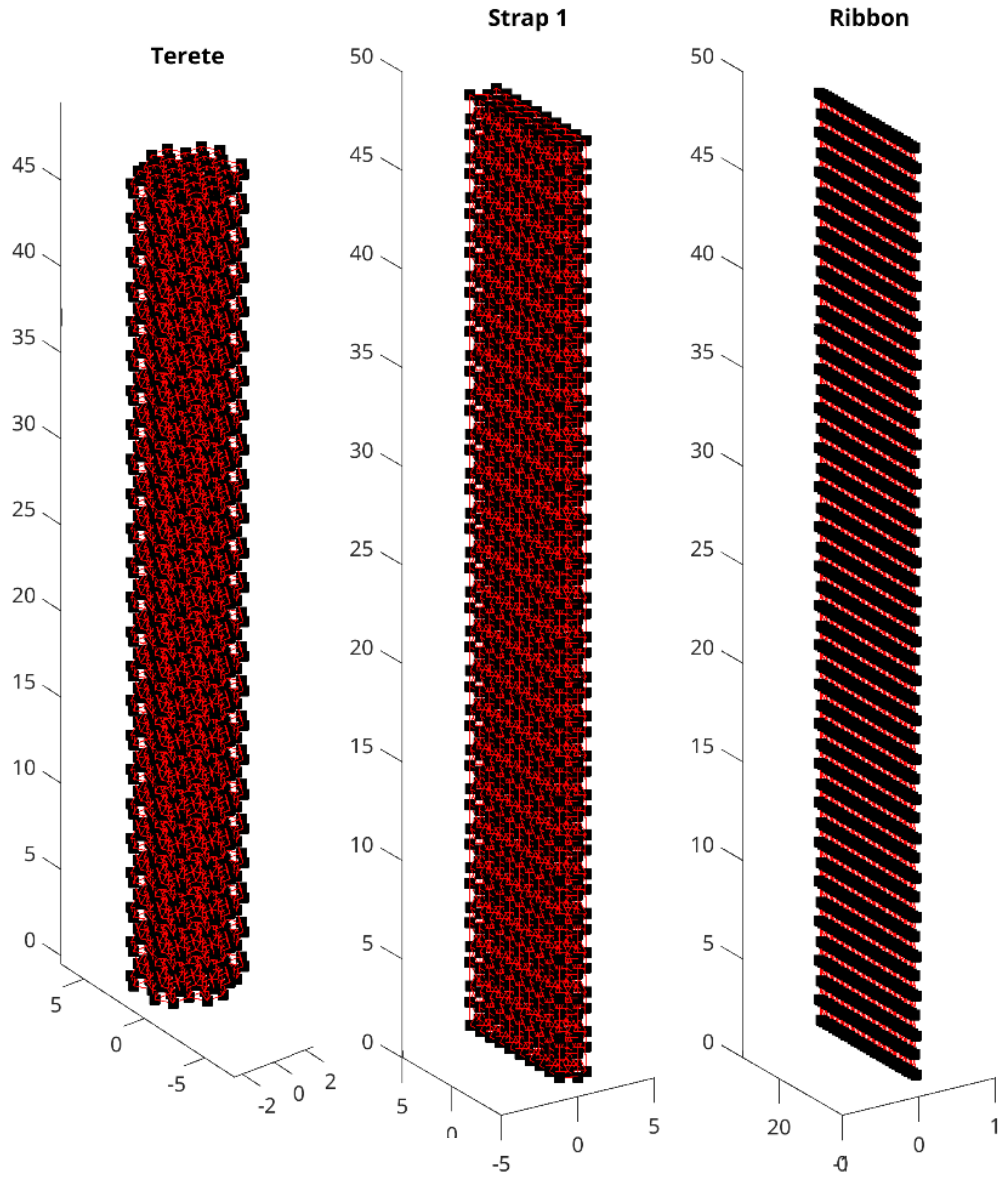


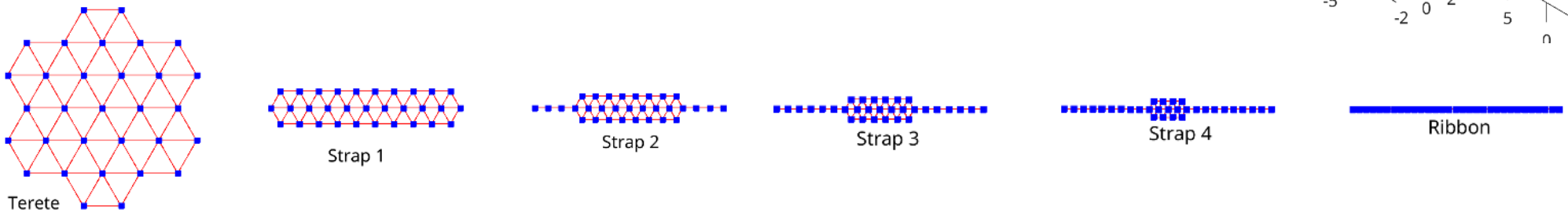


Top: Conduit network of a wood sector
Bottom: 3 planes of Araucaroid wood (InsideWood Database)

3D Embolism (Percolation) Simulations







Research Questions

How does drought constrain plant anatomy?

Did drought make plants branch?

How can there be trees?

Computational Techniques

Simulating flow & percolation on lattice graphs (xylem conduit networks)

Image analysis (network construction)

Simulating development (xylem)

Constrained optimization

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THANK YOU FOR YOUR ATTENTION!