

Linking hydraulic stress with tree mortality

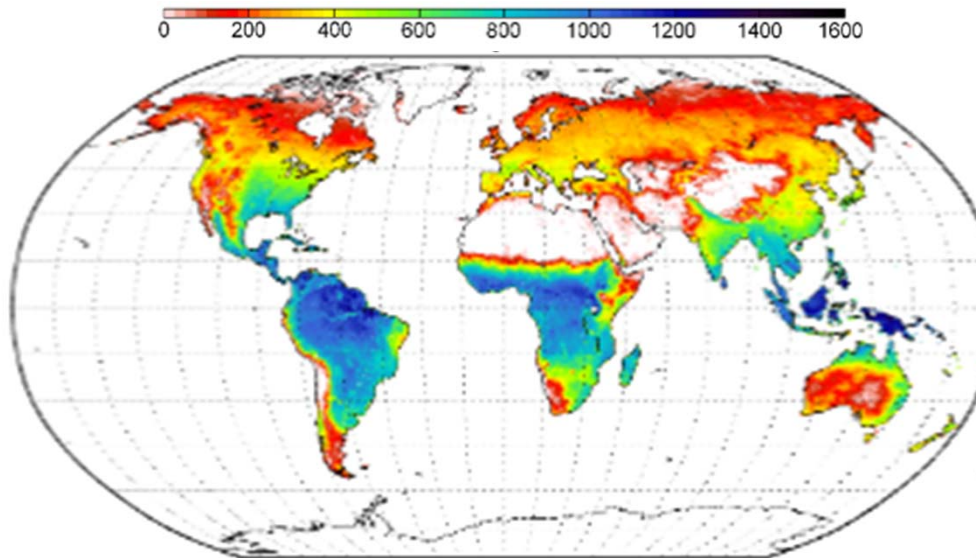
Patrick Meir

Australian National University



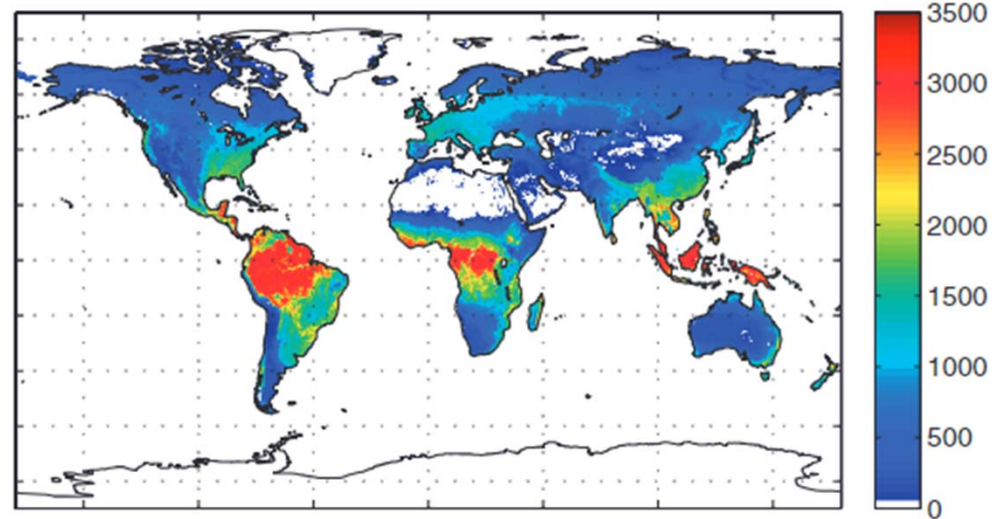
Global carbon and water cycles

Transpiration (mm yr⁻¹)



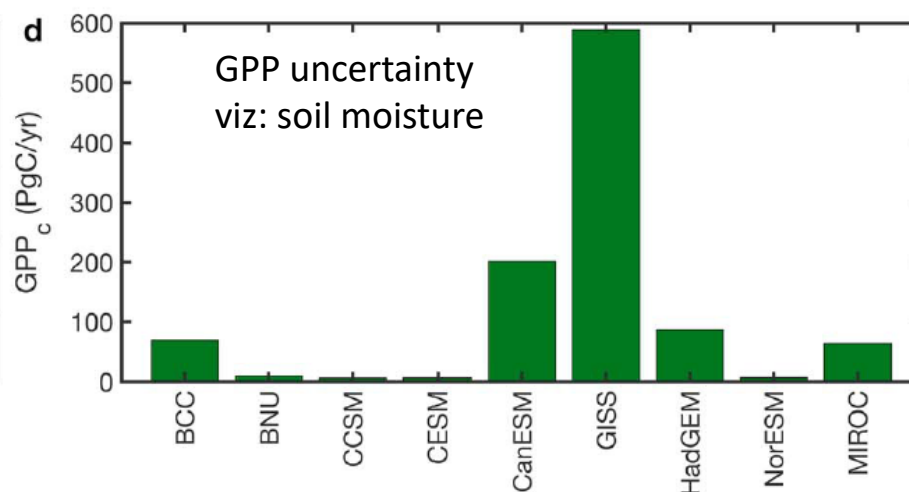
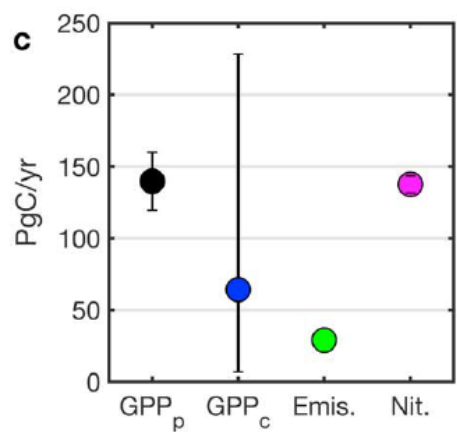
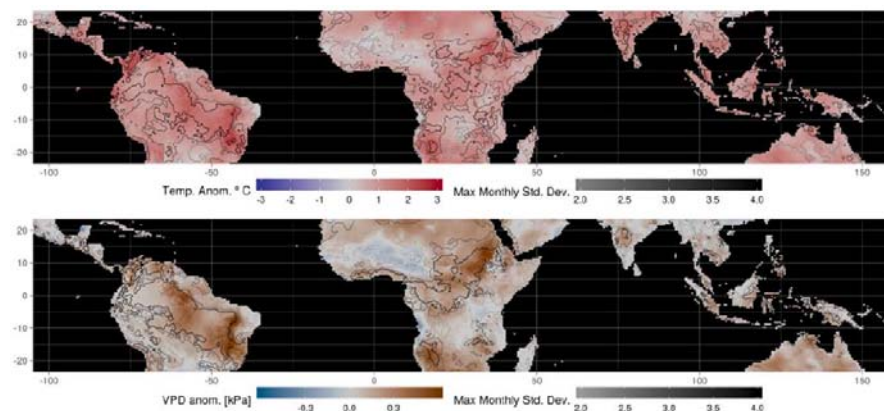
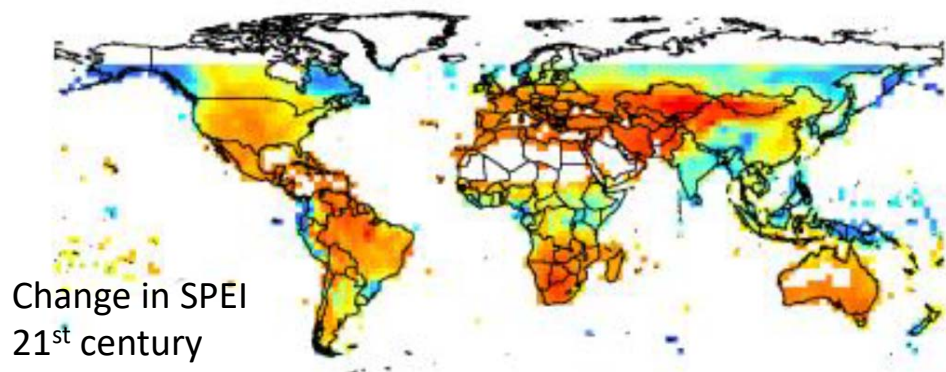
Miralles et al (2011) Hydrol. Earth Syst. Sci.

GPP (gC m⁻² yr⁻¹)



Beer et al (2010) Science

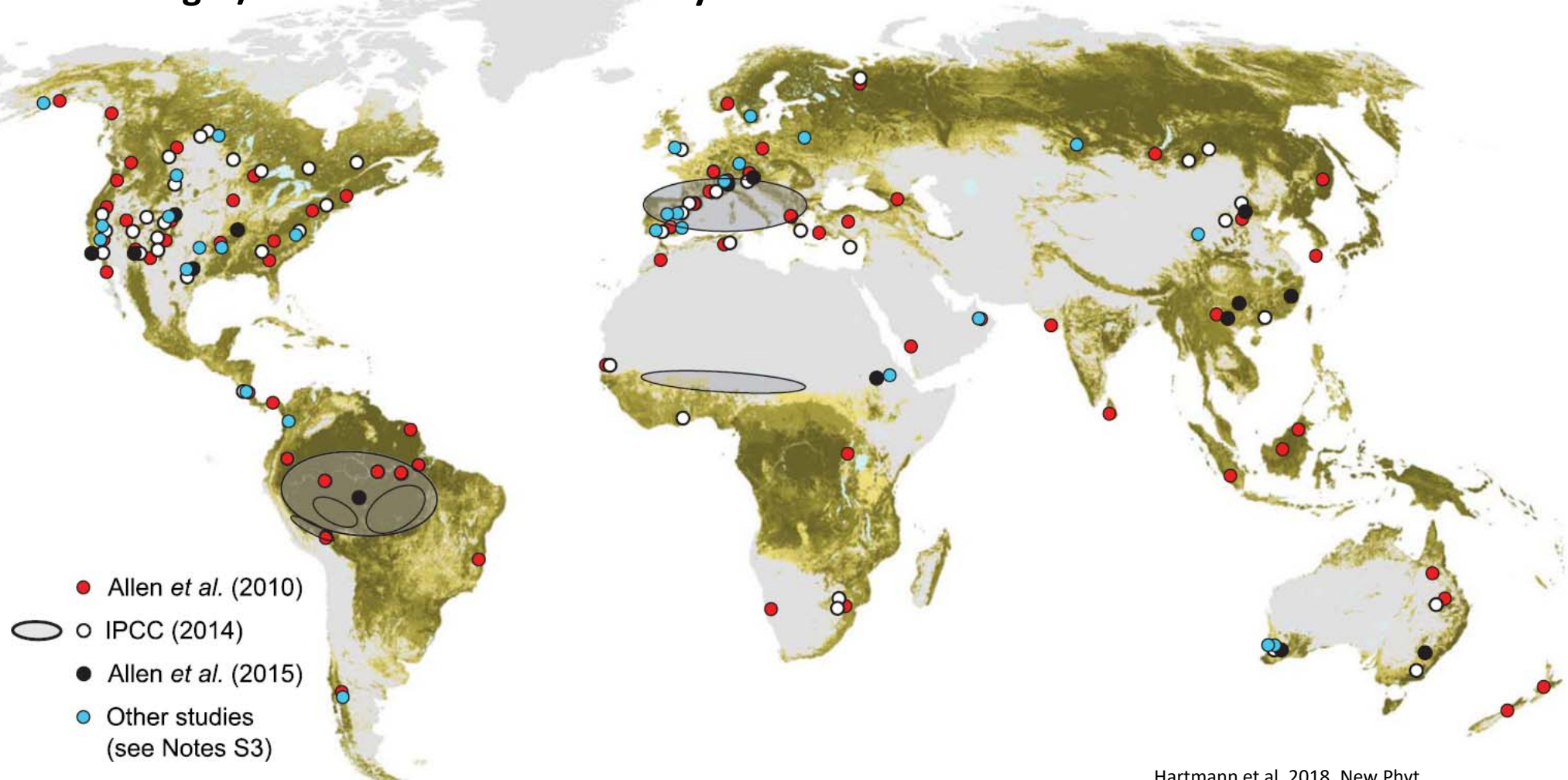
Climate risk, extreme events. Model uncertainty, soil water limitation.



El Niño 2015/16
anomalies: T, VPD
Increasing frequency?

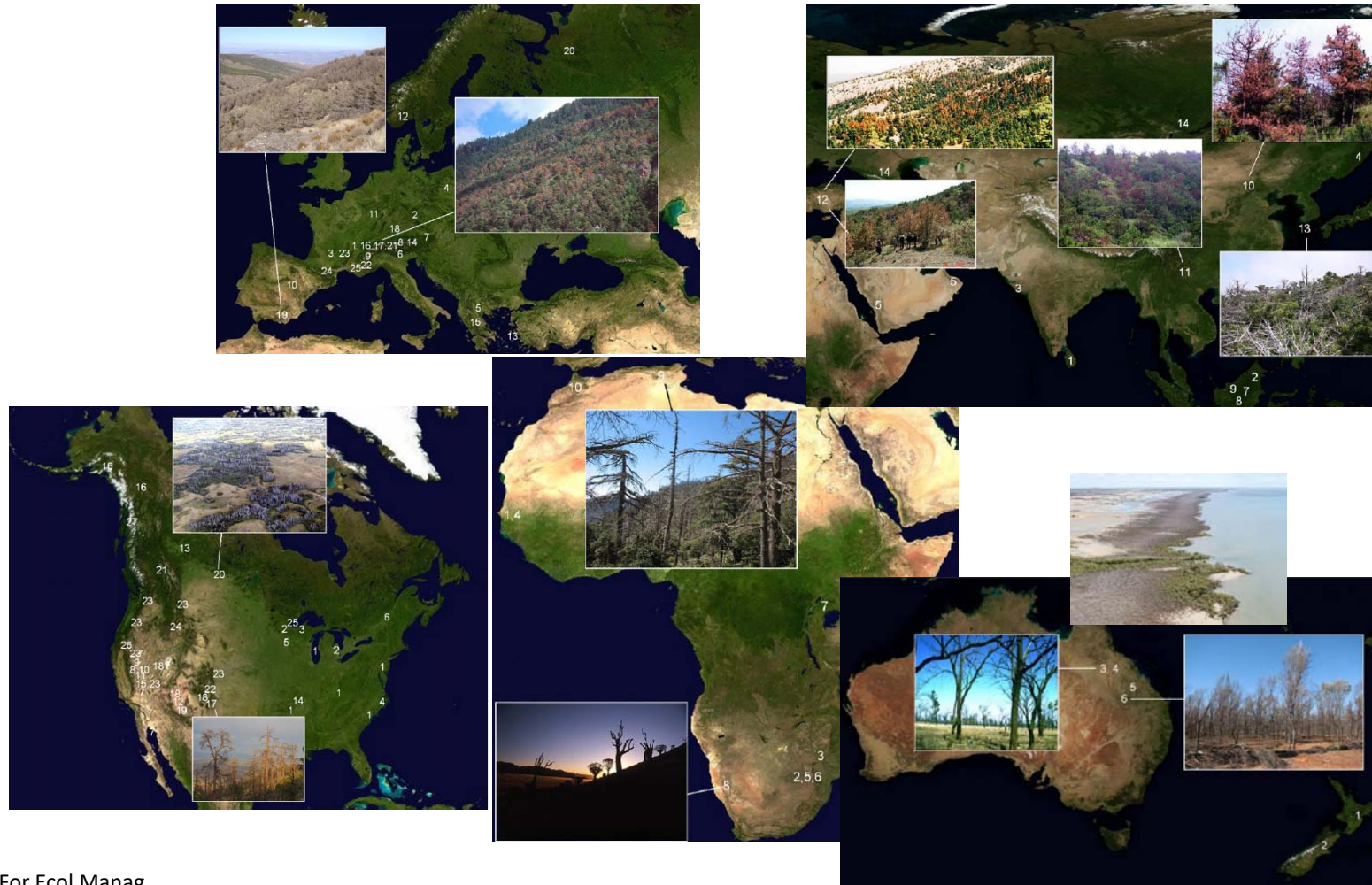
Vicente Serrano 2019, Earth Sci Rev
Rifai et al. 2019, ERL
Trugman et al., 2018 GRL
Cai et al. 2014, NCC

Drought/heat-related tree mortality 1970-



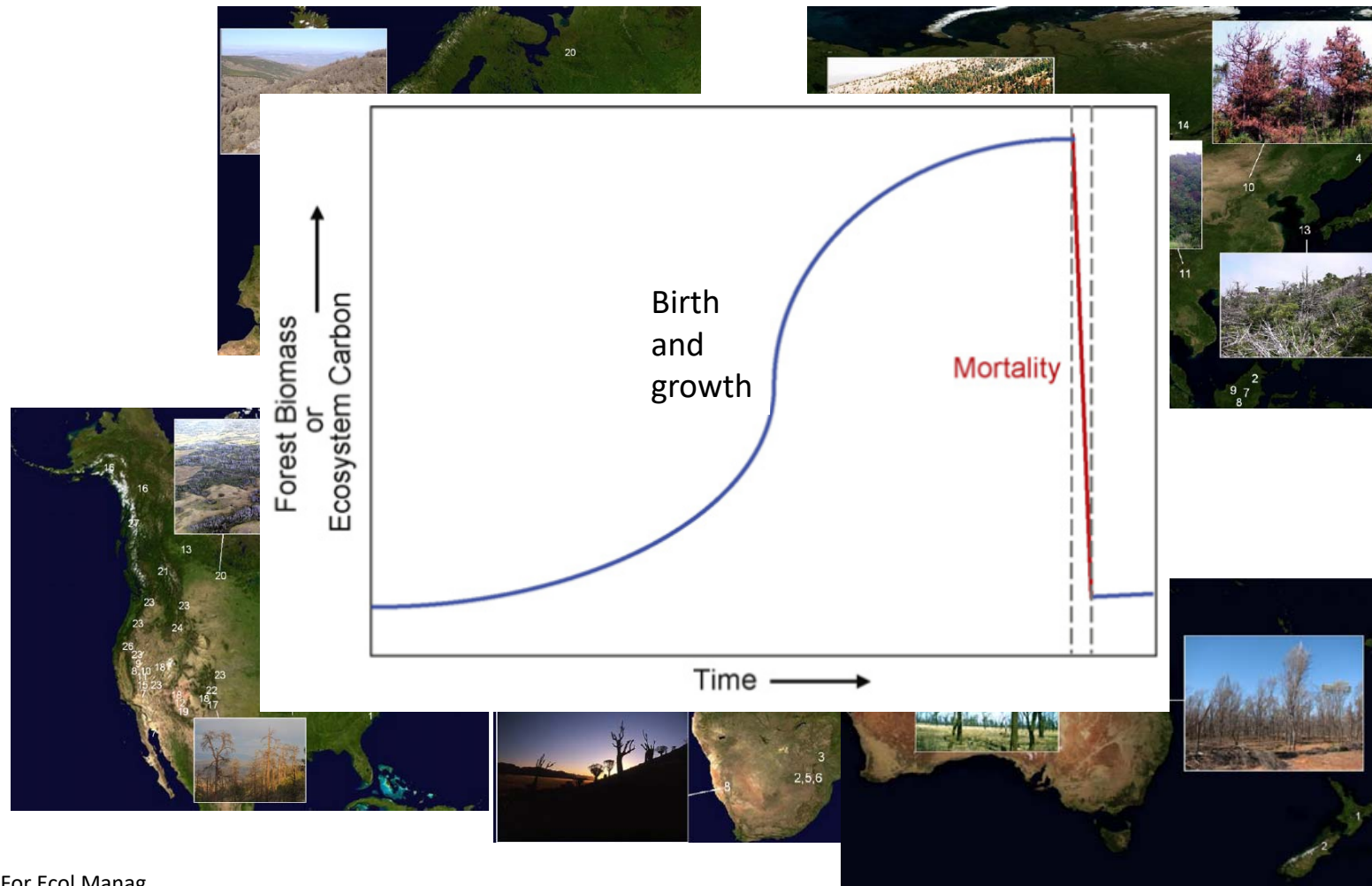
Hartmann *et al.* 2018, New Phyt
Allen *et al.* 2010, IPCC 2014

Tree mortality. Stress, temp, drought. Global

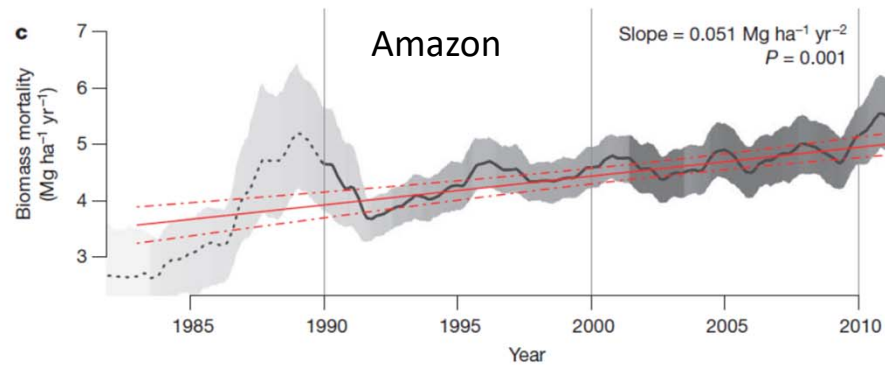
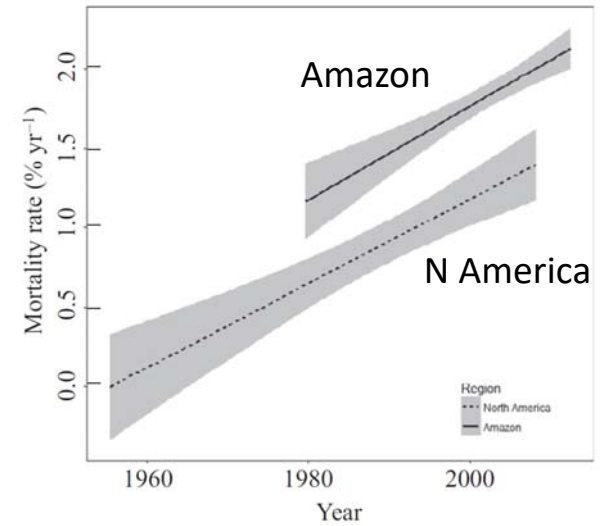
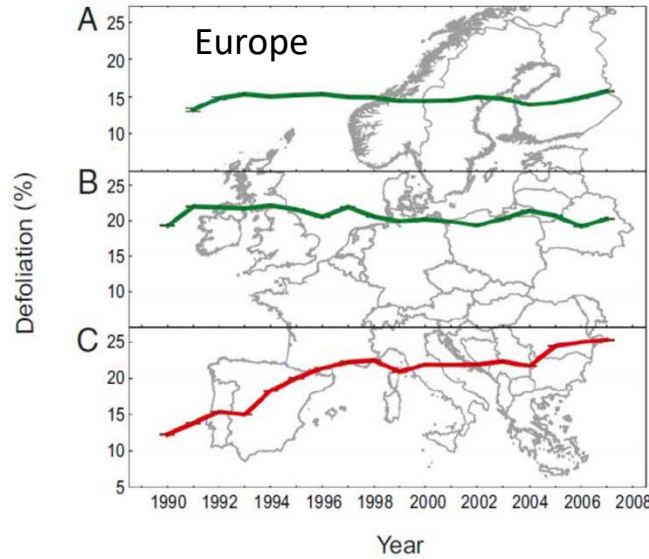
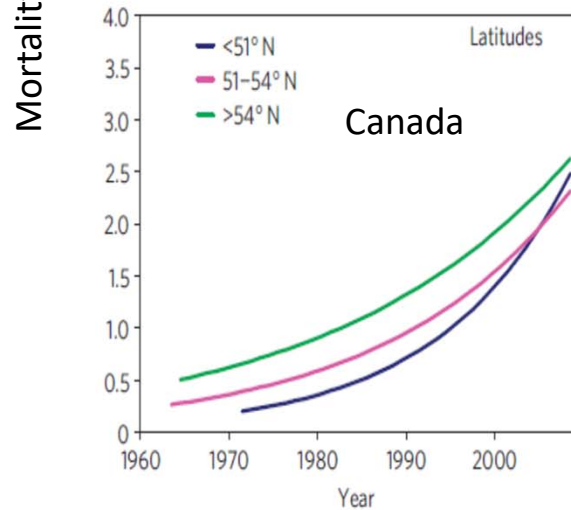
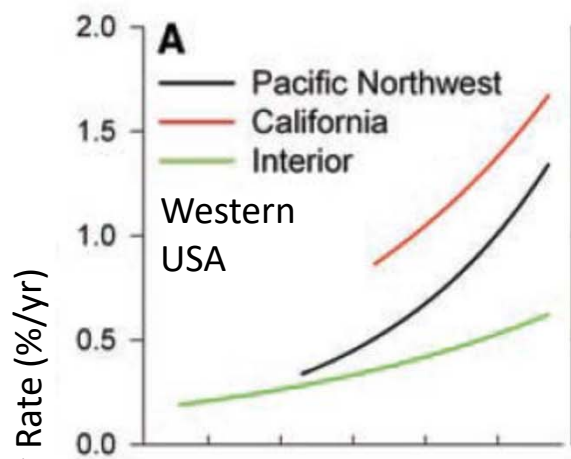


Allen et al. 2010, For Ecol Manag

Tree mortality. Stress, temp, drought; global



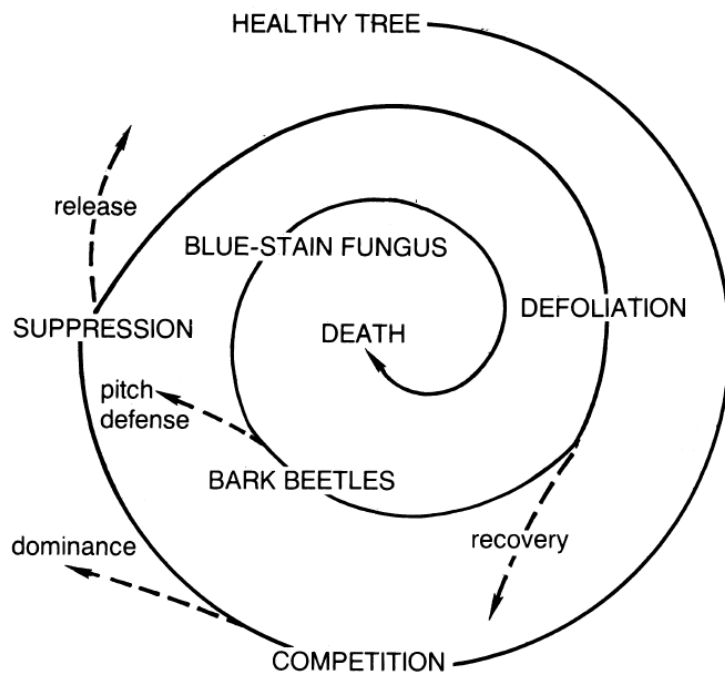
Mortality rates rising globally



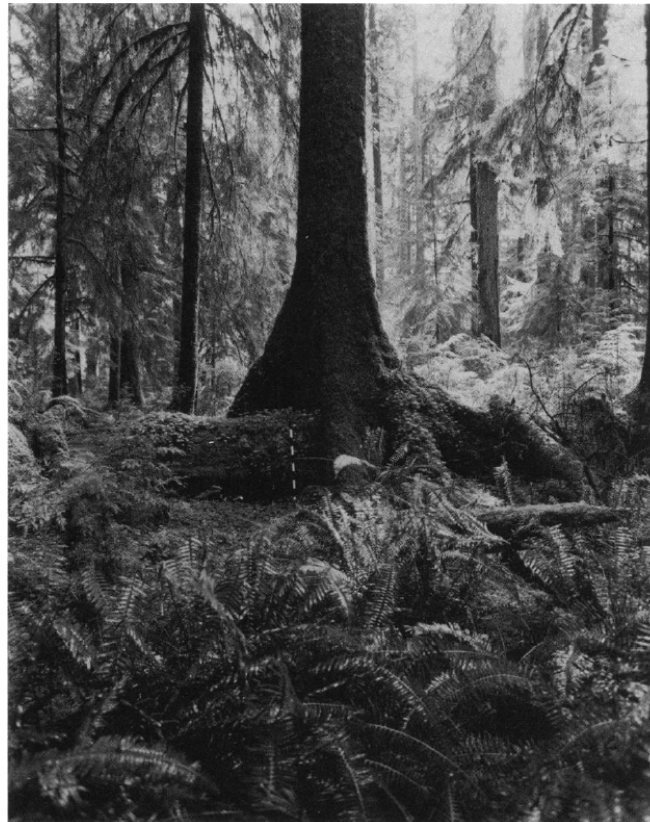
Brienen et al. 2015 Nature
McDowell et al. 2018 New Phytologist
Van Mantgen et al. 2009, Science
Peng et al. 2011, NCC
Carnicer et al. 2011, PNAS

Early frameworks for understanding tree mortality

Combination of stress from adverse environment, competition/suppression + pest or pathogen attack (& fire)
How to define death? Physical, physiological?



'Mortality spiral', Douglas Fir

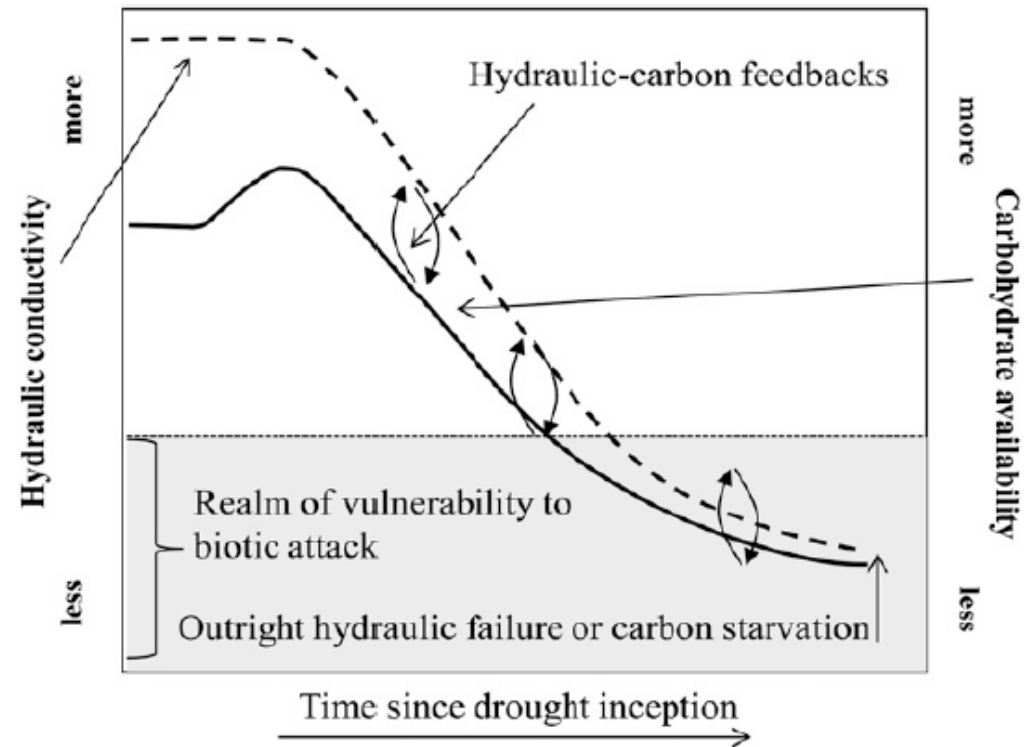
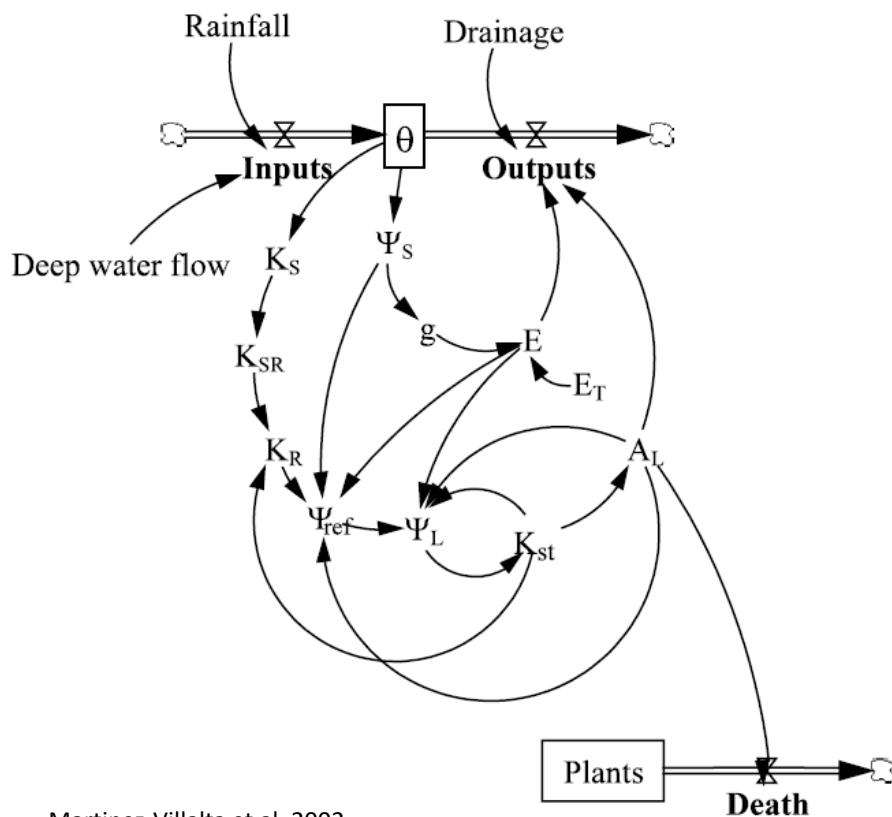


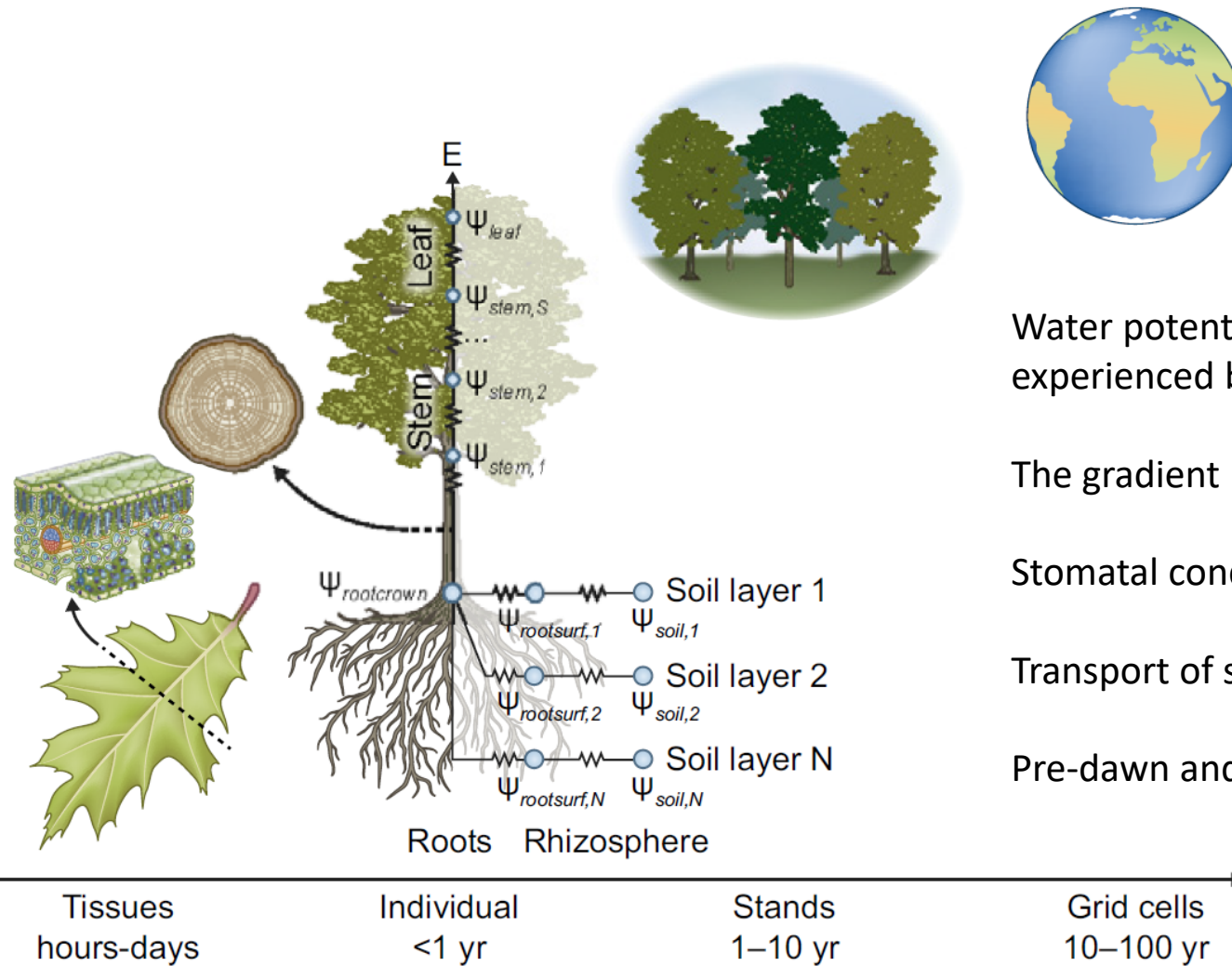
Trees die when they
cannot acquire or
mobilize sufficient
resources to heal injuries
or otherwise sustain life

Franklin et al. 1987, Bioscience
Manion 1981, Tree Disease Concepts

Extending the framework, water stress focus

- Improved accounting for water stress: altered tissue water potential, hydraulic conductivity, leaf area
- Interactive combination of: (i) hydraulic conductivity, (ii) carbon availability and (iii) pests/pathogens





Water potential, ψ determines the moisture stress experienced by a plant

The gradient in ψ determines flow to the canopy

Stomatal conductance - leaf ψ

Transport of sugars in phloem

Pre-dawn and midday leaf ψ

Multiple tree traits reflecting or influencing transpiration

Physiological traits (leaf)

- Stomatal regulation
- Turgor loss point
- Cuticular conductance

Physiological traits (common)

- Vulnerability to cavitation (Ψ_{12} , Ψ_{50} , Ψ_{88})
- Maximum hydraulic conductance
- Capacitance and water storage
- Cell membrane permeability (aquaporin regulation)

Physiological traits (root)

- Cortical lacunae formation
- Root shrinkage/hydraulic isolation
- Soil-root hydraulic conductance

Morphological traits (shoot)

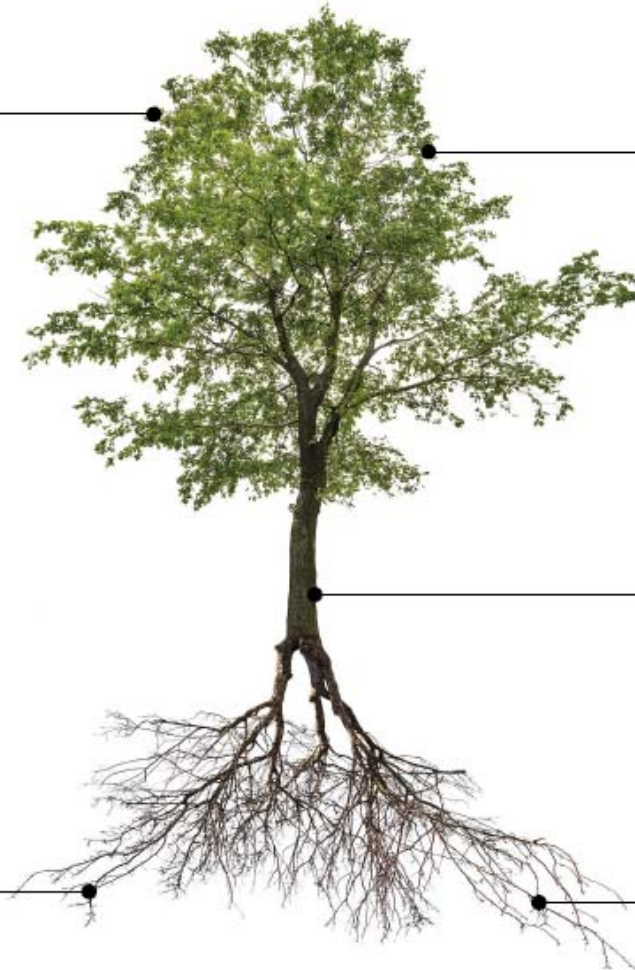
- Stomatal anatomy
- Leaf vein density
- Total leaf area
- Leaf shedding/drought deciduous
- Leaf to sapwood area ratio

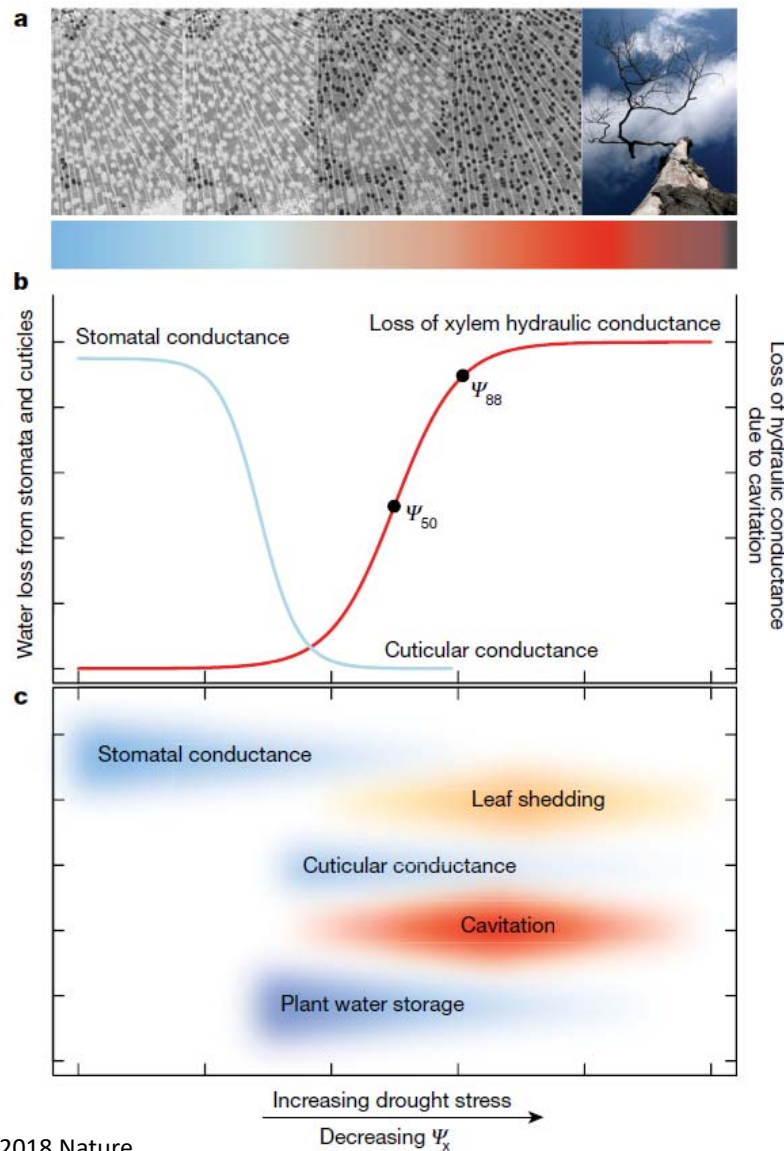
Xylem anatomical traits

- Xylem conduit size, number and connectivity
- Pit membrane thickness/porosity
- Wood density

Morphological traits (root)

- Root to shoot ratio
- Rooting depth
- Fine root loss





Choat et al. 2018 Nature

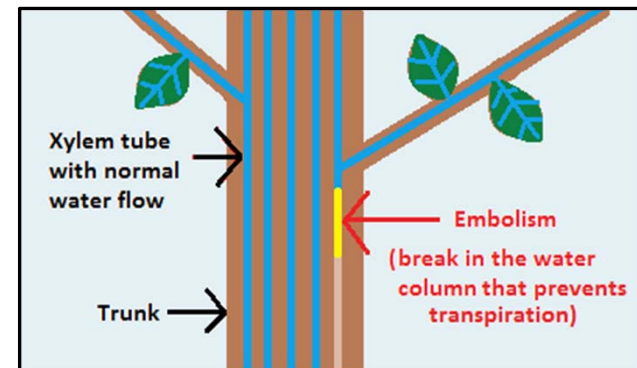
Increasing moisture stress

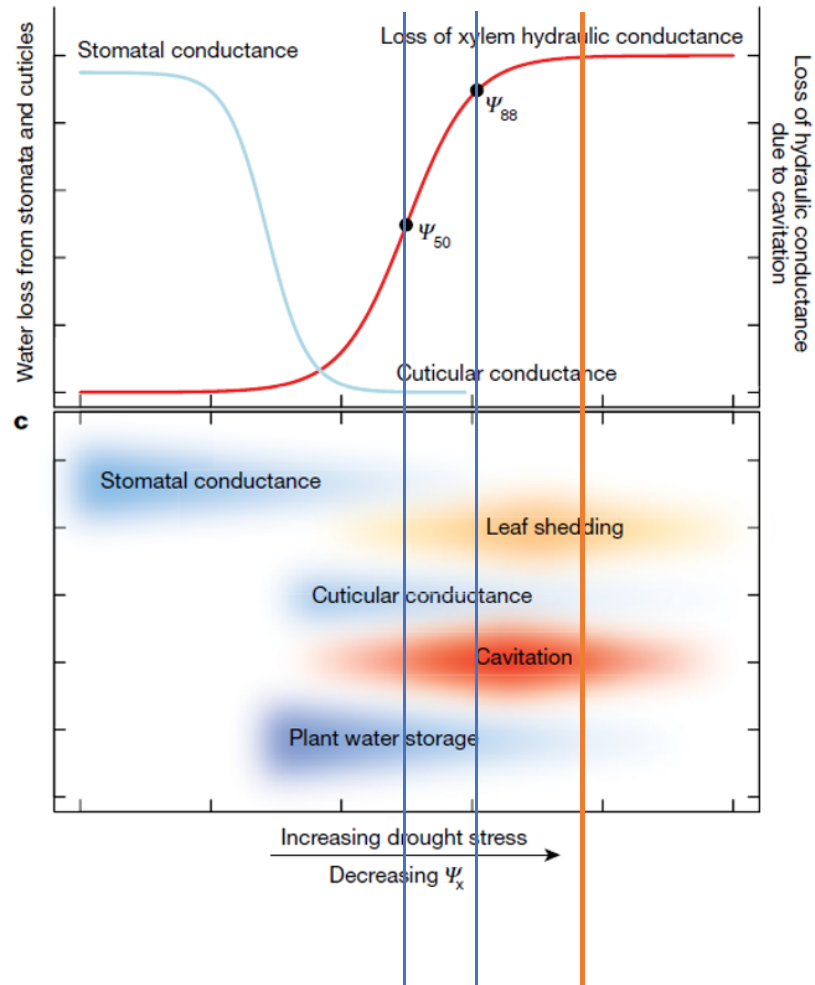
Reduced xylem water potential, ψ_x (leaf, wood)

Stomatal conductance, g_s , declines to control water loss (...water storage, cuticular conductance, leaf area).

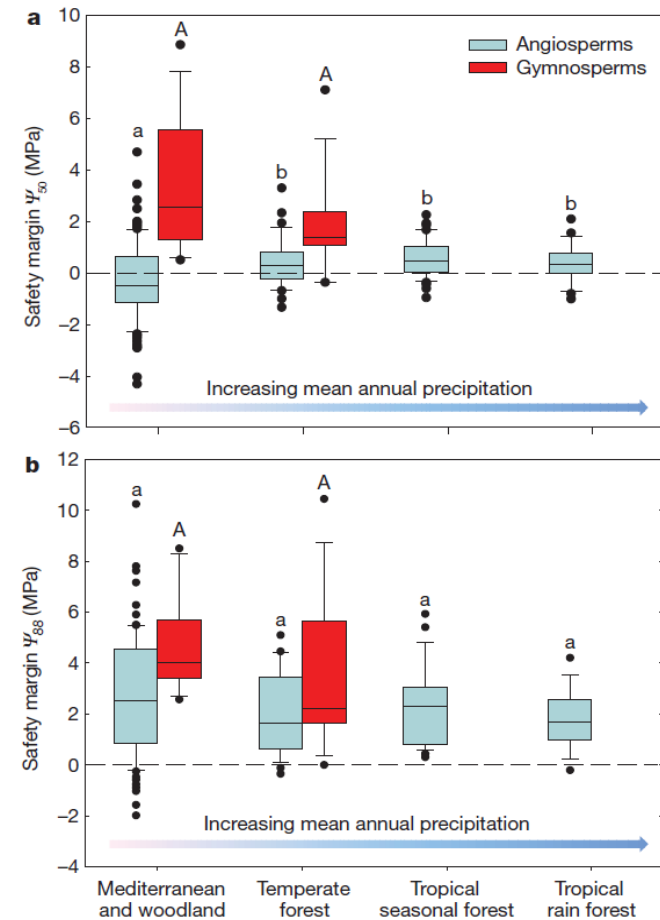
Photosynthesis declines: less carbon for osmoregulation, defence, metabolism

Large negative pressure leads to air seeding into xylem: cavitation....reduced hydraulic conductance
50% (P50, ψ_{50}), 88% (P88, ψ_{88})

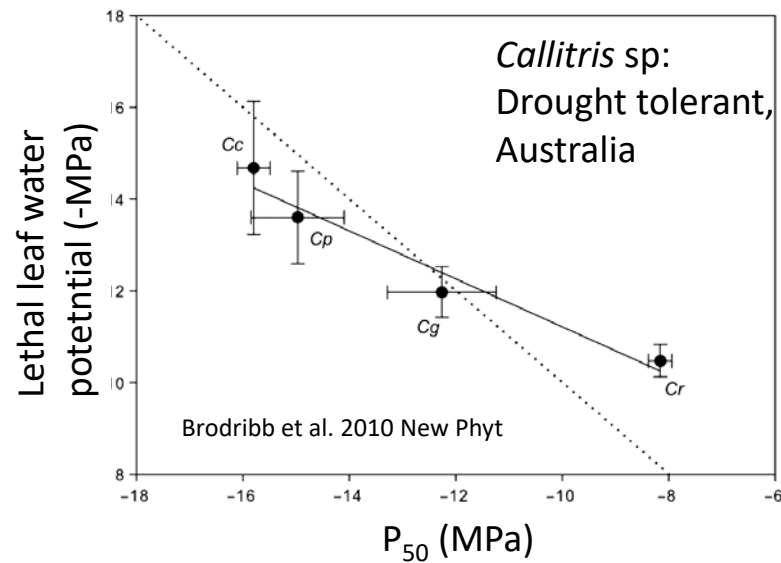




**Wide global variation (eg to -14 MPa for P50) ,
but conserved hydraulic safety margin**
 $[\psi \text{ at P50}] - [\text{min } \psi \text{ experienced}]$



Metrics associated with drought-mortality: Hydraulic? Carbon?

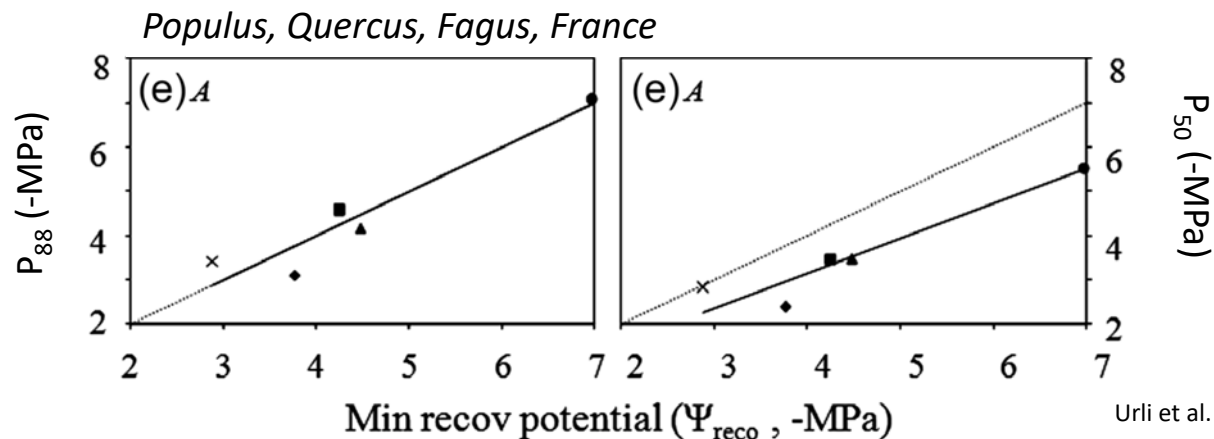


Seedling experiments linking mortality with hydraulic vulnerability

Seedlings dried down and then re-watered to determine limit for recovery

Lethal water potential determined by physiological recovery

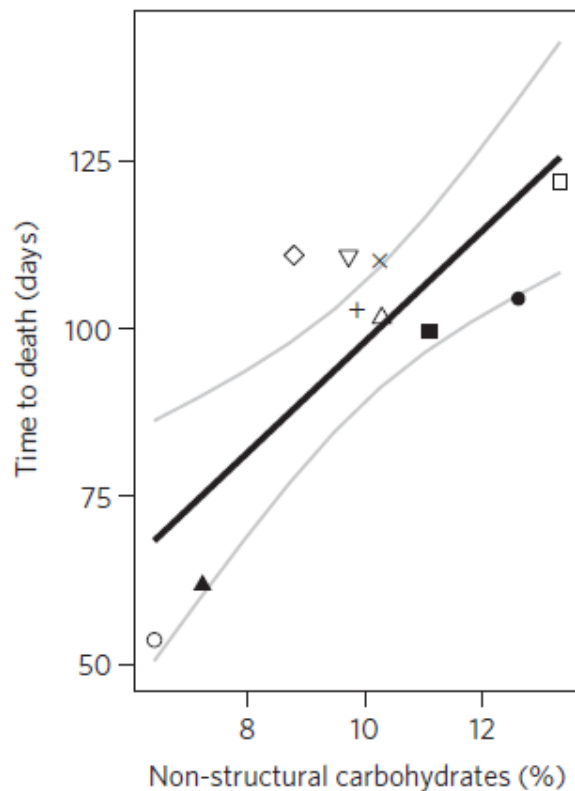
Mortality associated with P_{50} and P_{88} in woody tissue xylem



Urli et al. 2013 Tree Phys

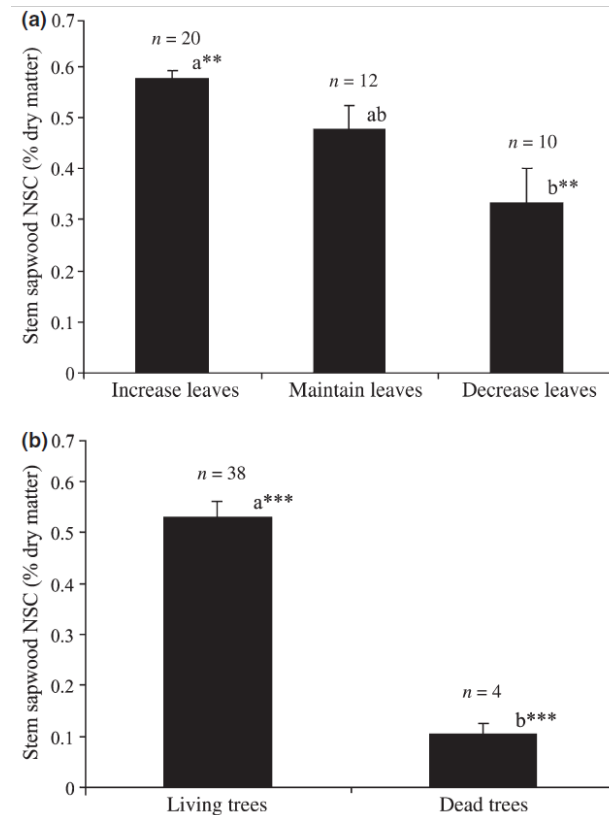
Metrics associated with drought-mortality: Hydraulic? Carbon?

Tropical seedlings, multiple species: non-structural carbohydrates (NSC) extend period before death.



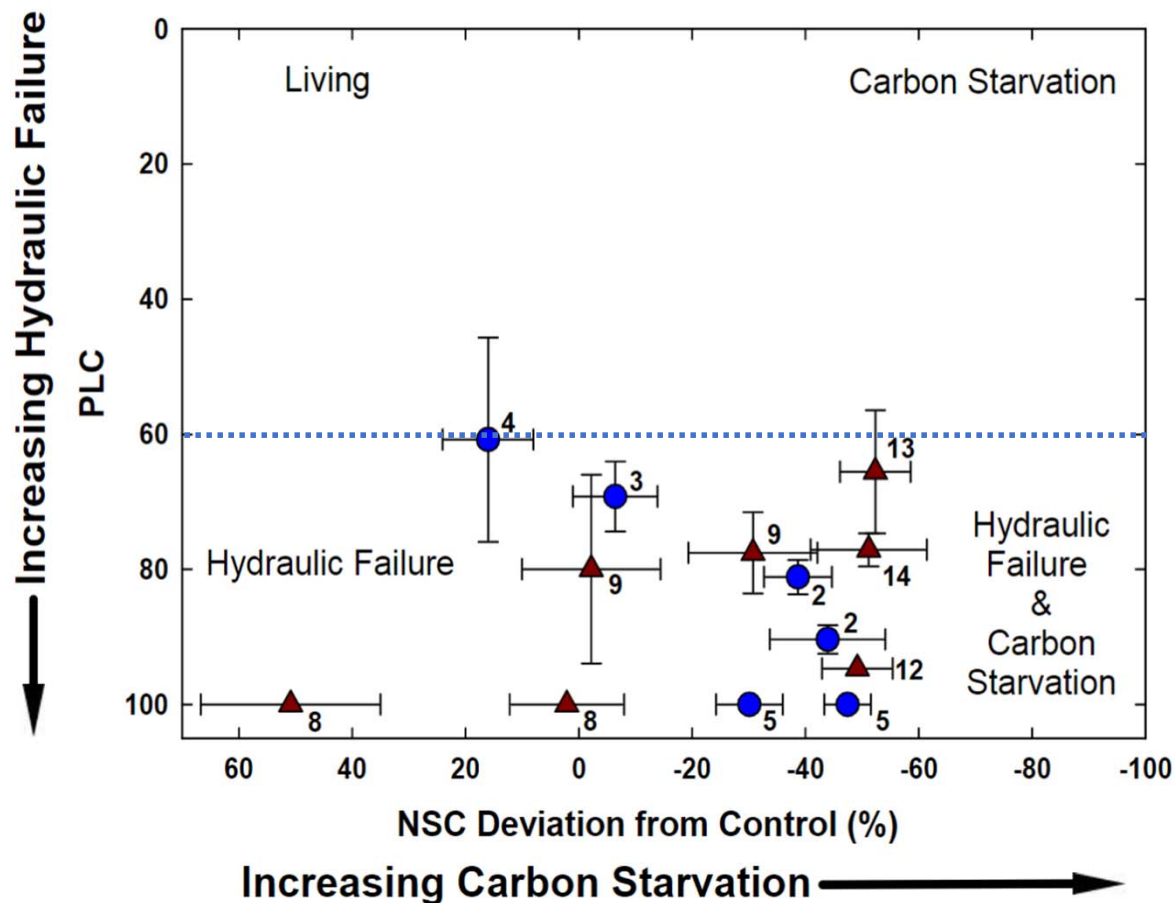
O'Brian et al. 2014, Nat CC

Mediterranean trees (*Pinus sylvestris*): low NSC associated with low leaf area & mortality



Galiano et al. 2011, New Phyt

Metrics associated with drought-mortality: Hydraulic? Carbon?
Both important – but is there a dominant signal?



Synthesis of >30 studies

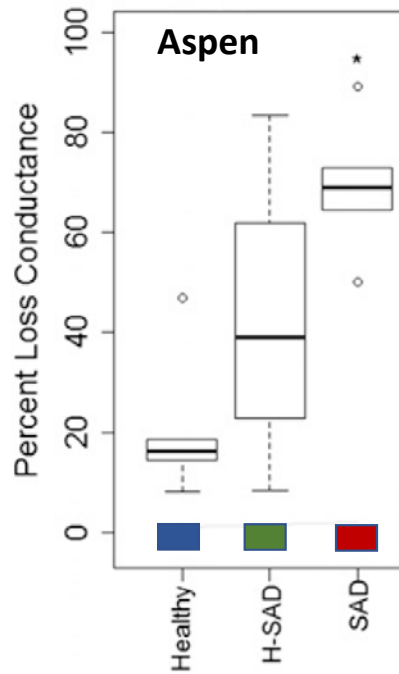
Variable NSC change

Loss in conductivity is $\geq 60\%$

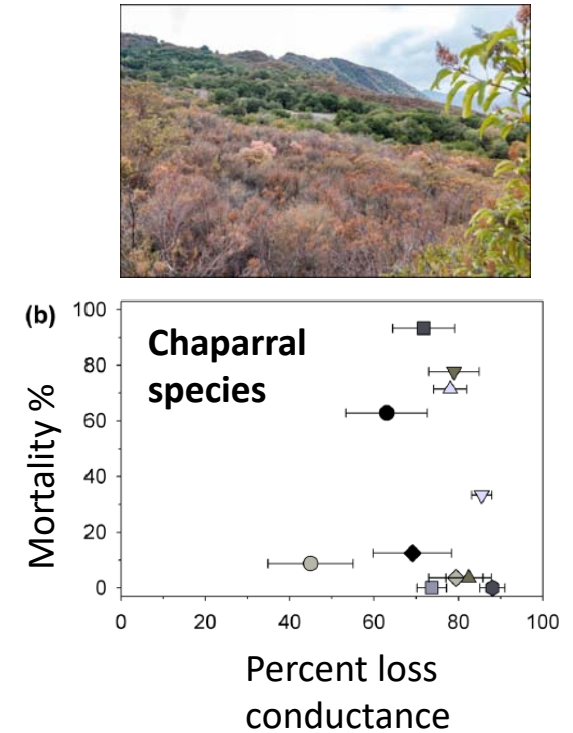
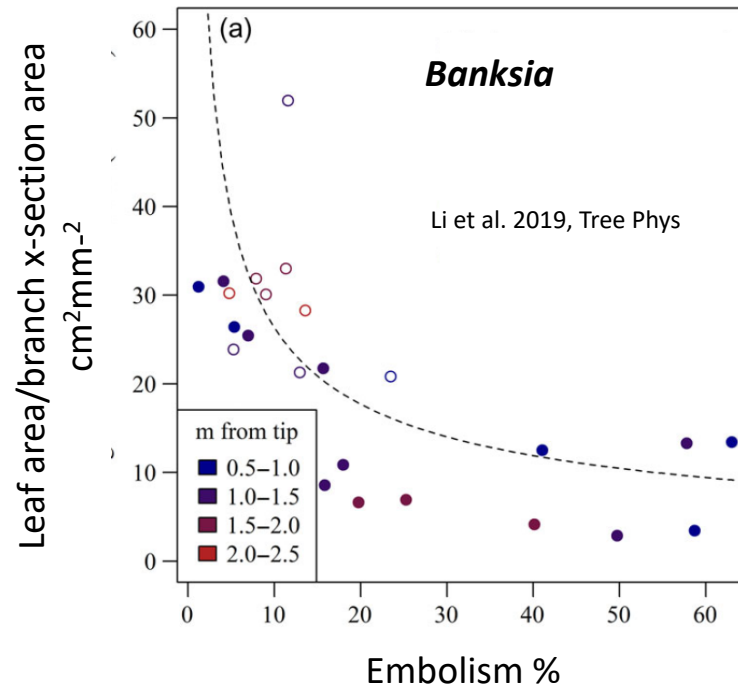
[Nearly all seedling studies...]

Metrics associated with drought-mortality

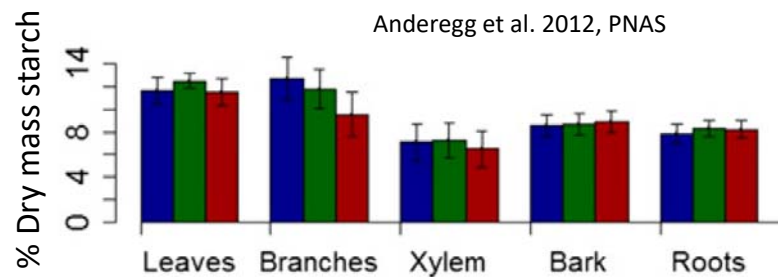
Evidence from natural drought/tree branches



Anderegg et al. 2012, PNAS

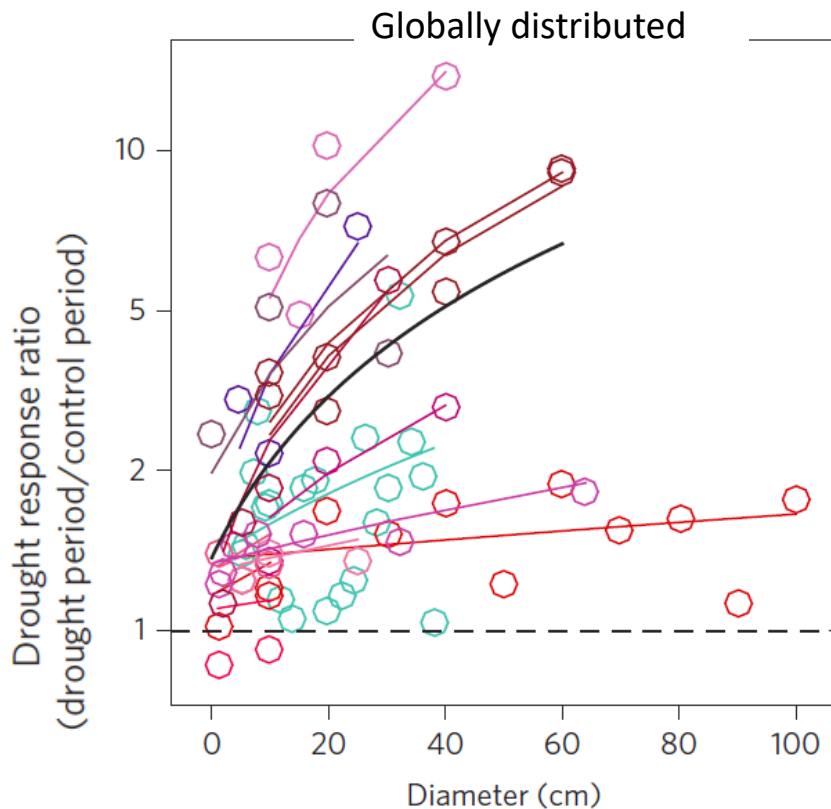


Venturas et al. 2016, PLoS1

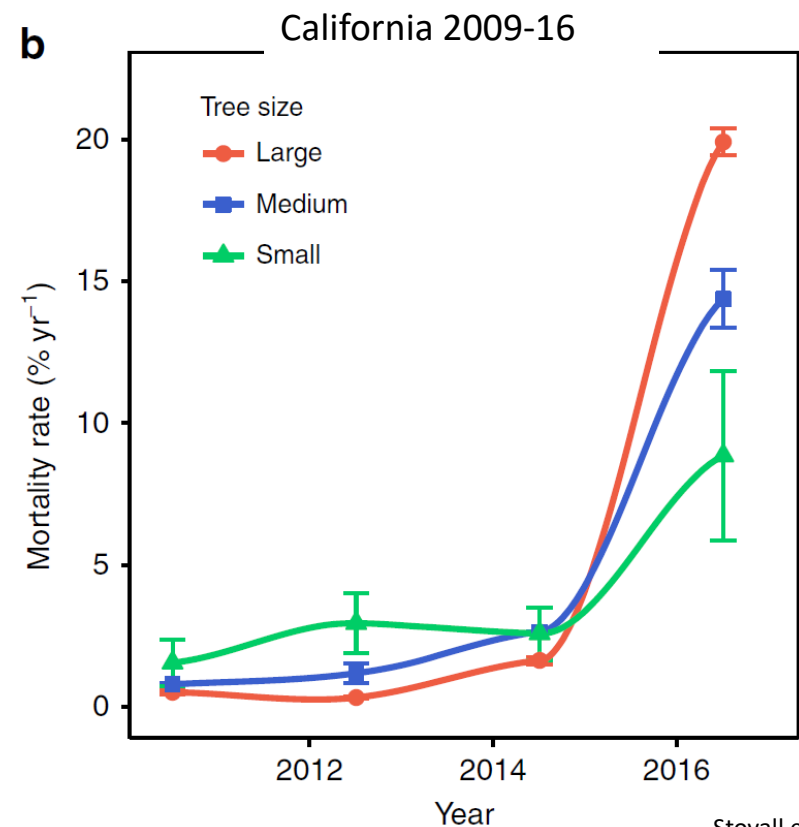


Branches of drought-damaged trees: highly visible
Loss in conductance & leaf area
NSC signal unclear

Drought-mortality: large trees tend to be most at risk

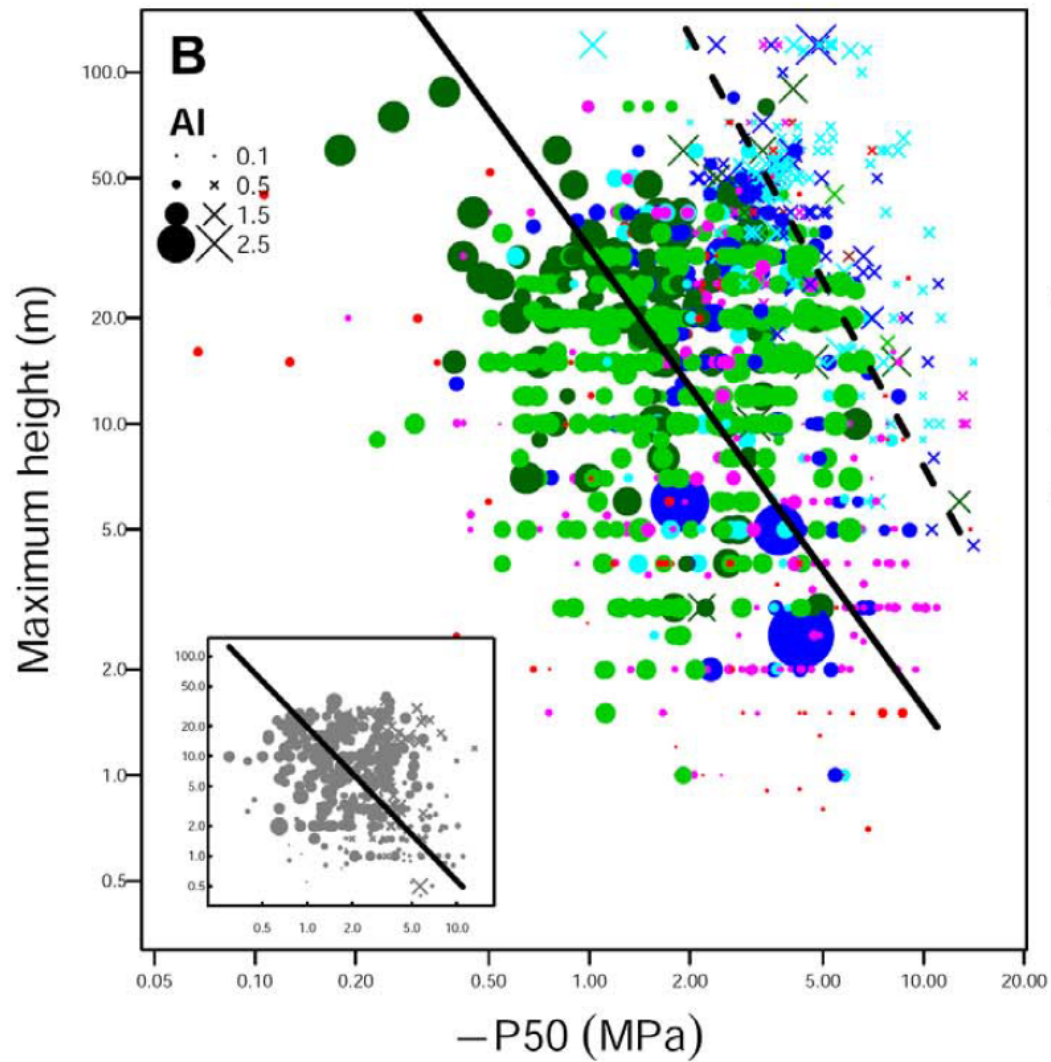


Bennett et al. 2015 Nature Plants



Stovall et al. 2019
Nature Comms

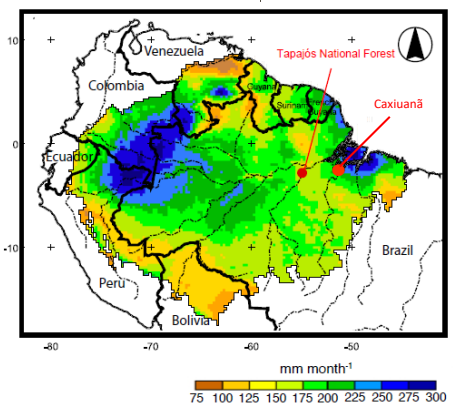
Higher mortality rate; increases over extended drought
Environmental exposure: ht, VPD, soil water storage
Metabolism, incomplete recovery



Taller trees more hydraulically vulnerable (P50 closer to zero)

How does these patterns hold out at high diversity?

Liu et al. 2019
Science Advances



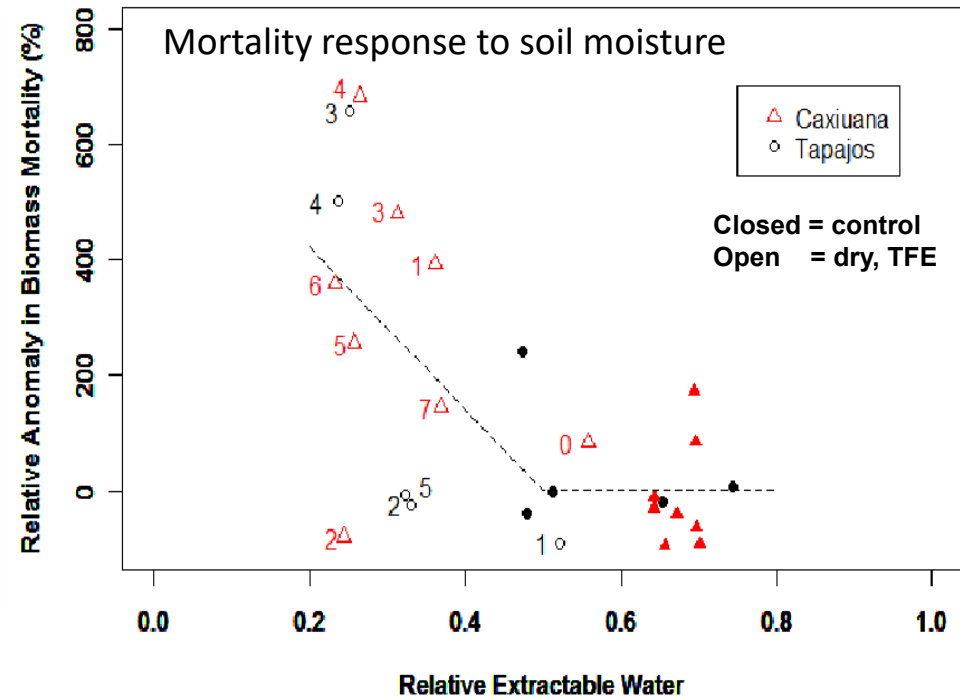
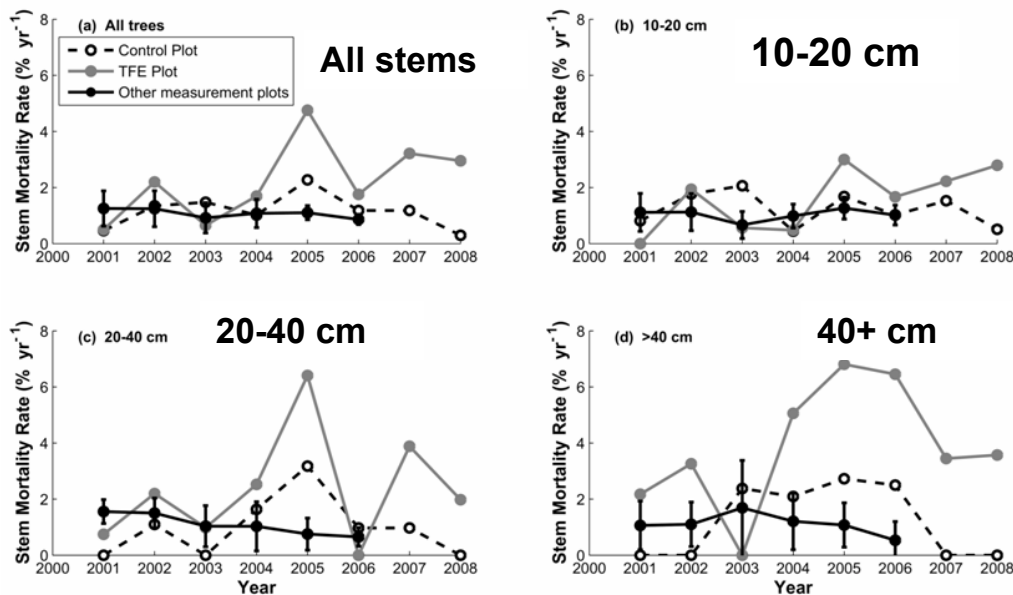
Amazon throughfall exclusion (TFE) experiments. 1 ha forest plots – control and TFE; 50% exclusion



7 yr effects of drought treatment

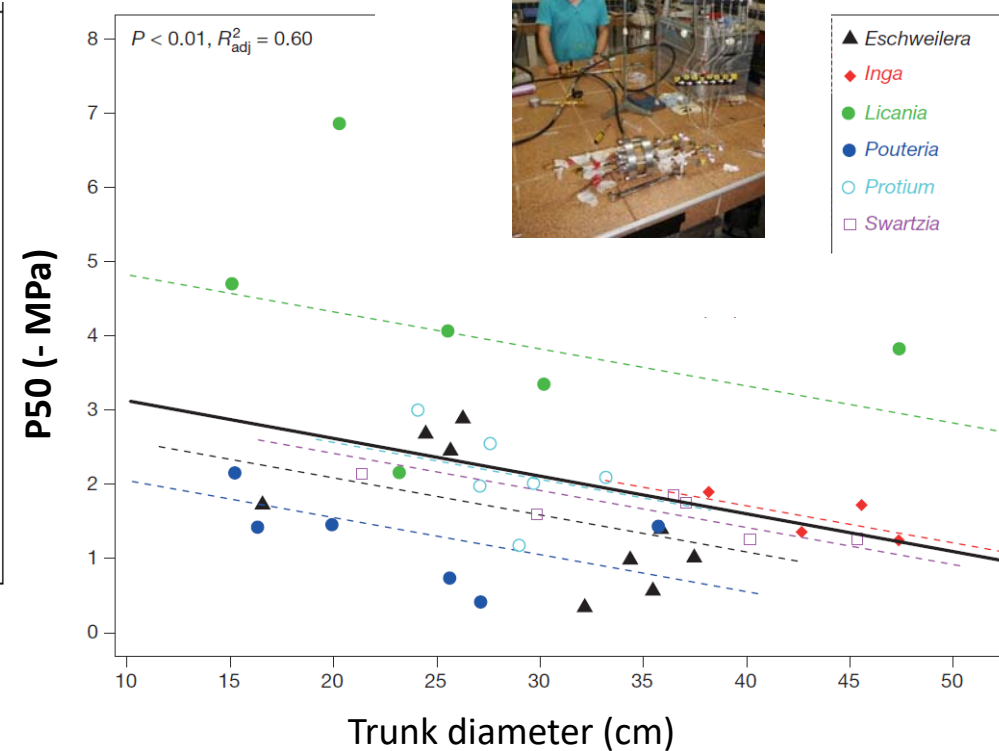
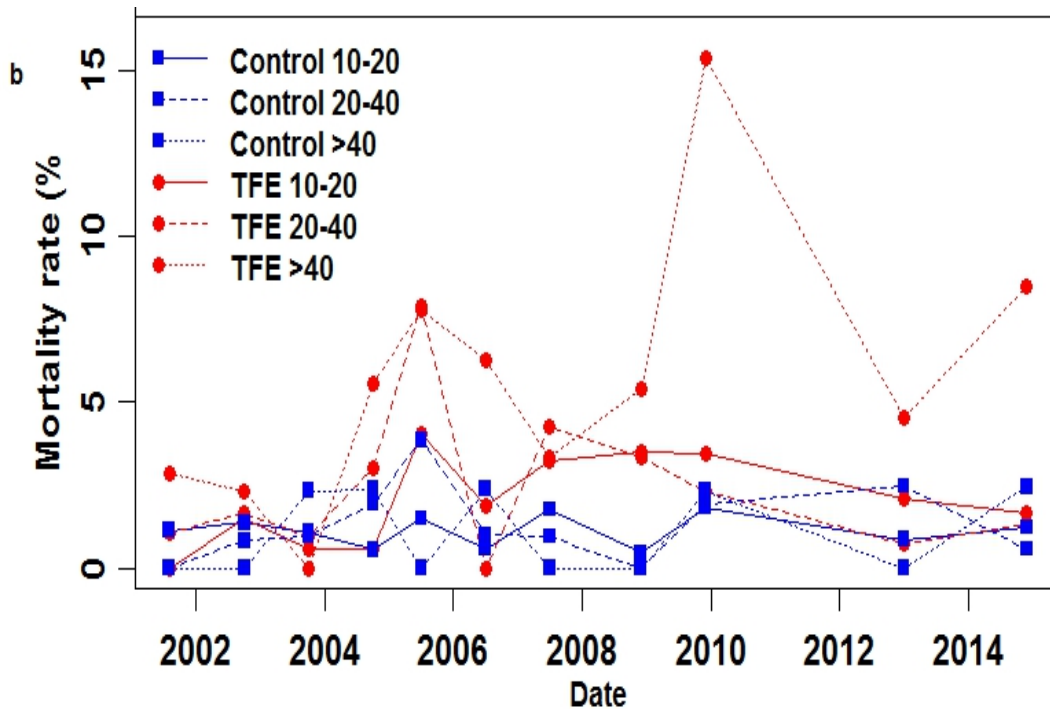
~20% biomass loss after 7 years; lag for first 3 years

Mortality (%)



14 years of drought treatment at Caxiuanã

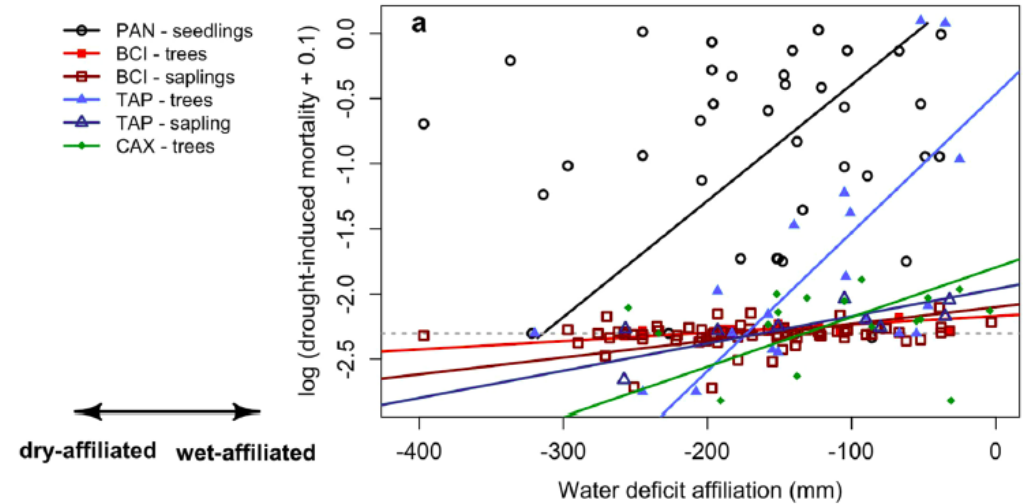
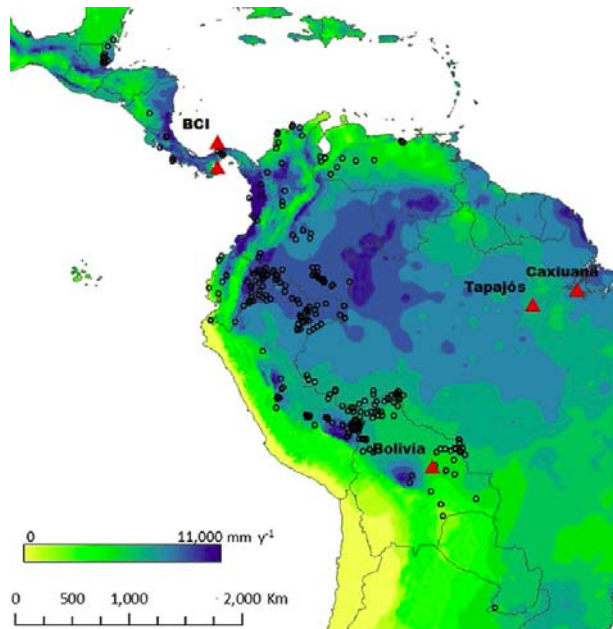
Mortality increases to 40%; large trees



Large trees - highest mortality; greater hydraulic vulnerability (big trees: P50 closer to zero)
BUT: ONLY 6 taxa considered....biodiversity?

Regional context?

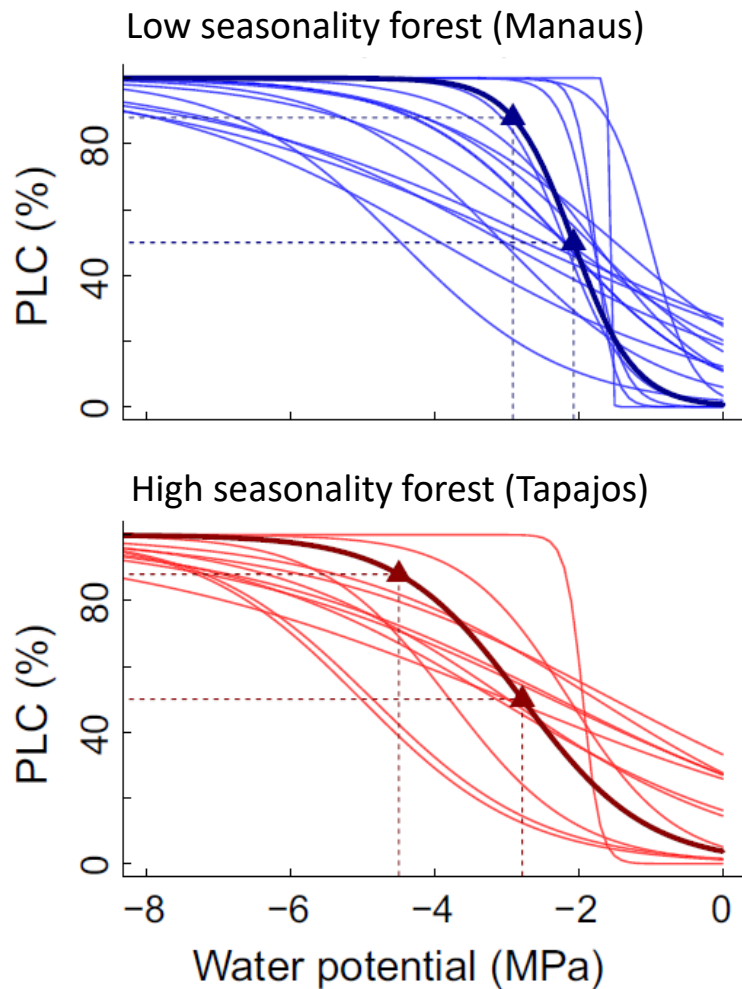
Compared with climate-affiliations across S. America



Wet-affiliated species have higher mortality risk
Physiological signal?

Esquivel-Muelbert et al. 2017 Sci Reps

If P50 is quantified for many species, what is the community-level signal?



Low seasonality vs high seasonality Amazon forests

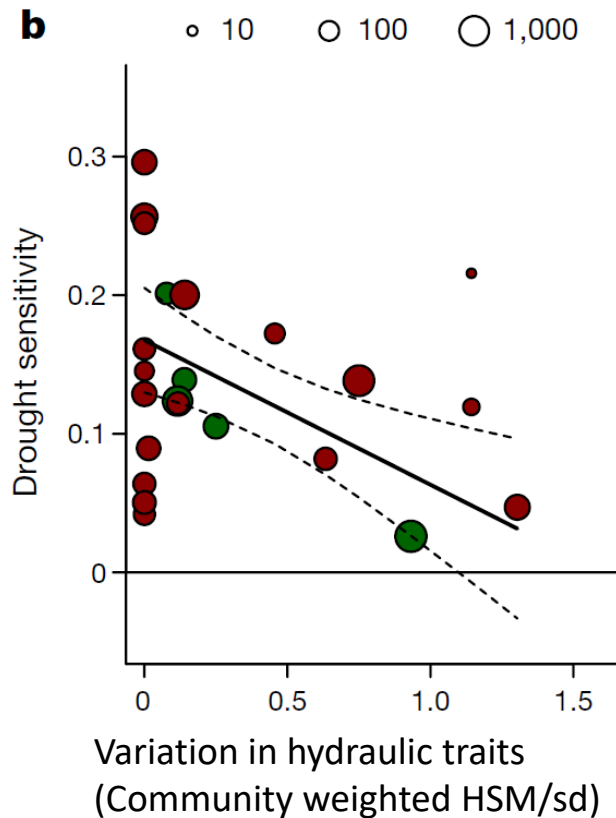
Tapajos: more drought-stressed than Manaus

- More dry affiliated species at Tapajos
- Community weighted P88 lower (drought tolerant)

- Similar canopy conductance response to VPD
...explained by species differences in hydraulic vulnerability

....P50/P88 traits contribute to species filtering during extreme or repeated droughts?

Effects of hydraulic diversity in other systems?



Eddy correlation LE fluxes and species hydraulics data [temperate and boreal forest]

Higher diversity in hydraulic traits leads to drought stability?

May be scale- or ecosystem-dependent (eg, Grossiord et al. 2014)

A rapidly evolving field; emerging issues

1. Relative water content (Martinez-Vilalta et al. 2019)

Potential to: integrate drought stress physiology

: link with remotely sensed water content

Issues of scaling and sensitivity

e.g., Kursar et al 2009, Sapes et al. 2019 – dry down experiments.

2. Cuticular conductance and membrane integrity

High temperature phase change to high cuticular conductance may cause rapid mortality (Cochard 2019)

Membrane failure/fluorescence signal (Guadagno et al. 2017)

3. Foliar water uptake

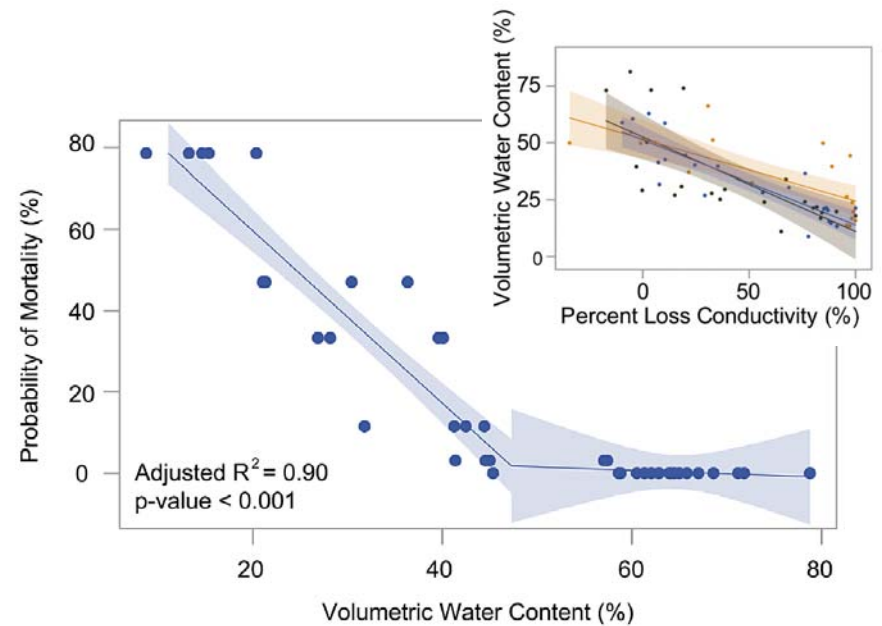
Wide occurrence; potentially large eg, Amazon (Binks et al. 2019)

Alleviate daily drought stress/reduce mortality risk?

4. Incorporating hydraulics into models

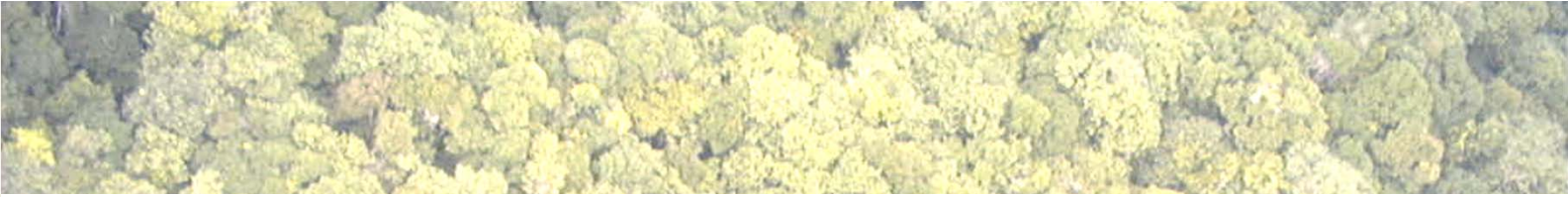
Linking soil moisture-water potential-transpiration (Eller et al. 2018)

New capacity to account for drought-recovery and mortality



Summary

1. Climate risk, secular and episodic: increased and repeated drought stress.
2. Evidence of increasing mortality related to drought, globally
3. Traits determining loss of hydraulic conductance related to moisture stress, water use and mortality risk
4. Focus on P50/P88 vs: size, species distribution, stability under drought
5. Immediate challenges
 - : scaling over space (trait diversity, soil moisture supply); time (response, recovery, plasticity), using new/expanding datasets (eg SAPFLUXNET)
 - : new modelling frameworks: soil-plant hydraulics, allocation, leaf phenology
 - : quantifying biotic attack thresholds
 - : connecting to remote sensing capability, including water and temp (VOD, Ecostress)



Thank you



