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Soil water stress impacts on the stomatal limitation of photosynthesis: a meta-analysis

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Coupling carbon and water cycles

- Atmospheric aridity and drought impacting physiological function in plant leaves
- However, their relative contributions on changes in **ratio of leaf-internal (c_i) to ambient (c_a) partial pressure of CO_2 (also known as χ)** still difficult to disentangle



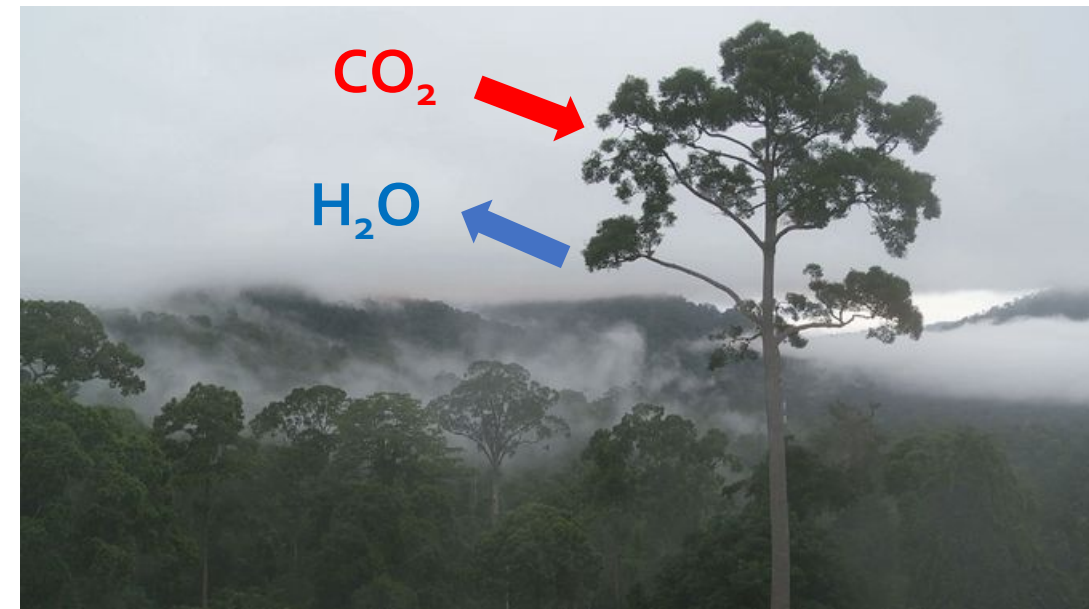
Many stomatal models predicting χ include the effect of only one of these drivers

χ = index of adjustments in both leaf stomatal conductance and photosynthetic rate to environmental conditions

- Key variable for the study of **carbon uptake**
- Provides insight into **(intrinsic) WUE**

$$\text{WUE} = \frac{\text{CO}_2}{\text{H}_2\text{O}}$$

Water use efficiency



Least-cost optimality hypothesis: leaves minimize the summed unit costs of transpiration (a_E) and carboxylation (b_V):

$$a_E \frac{\partial(E/A)}{\partial\chi} + b_V \frac{\partial(V_{cmax}/A)}{\partial\chi} = 0$$

Prentice et al. (2014) *Ecol. Lett.*
 Wang et al. (2017) *Nature Plants*
 Stocker et al. (2020) *Geosc. Mod. Dev.*

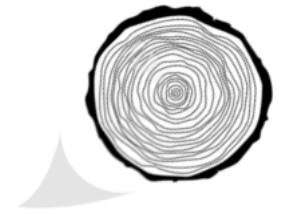
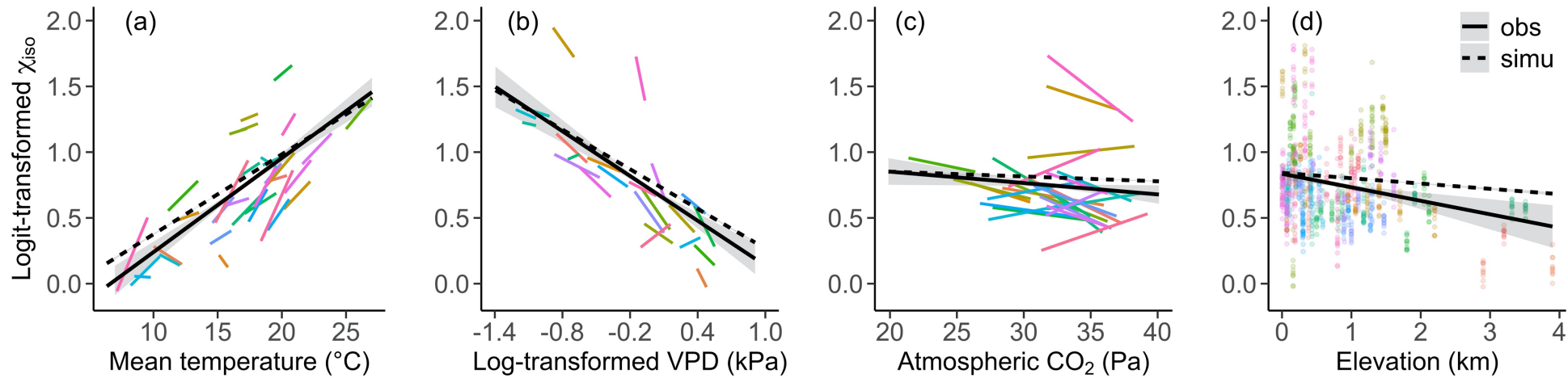


$$\chi = \frac{\Gamma^*}{c_a} + \left(1 - \frac{\Gamma^*}{c_a}\right) \frac{\xi}{\xi + \sqrt{D}}$$

$$\xi = \sqrt{\beta \frac{K + \Gamma^*}{1.6\eta^*}}$$

E : transpiration ($\text{mol m}^{-2} \text{s}^{-1}$), A : net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
 V_{cmax} : photosynthetic capacity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
 D : leaf-to-air vapour pressure deficit (Pa)
 η^* : viscosity of water relative to its value at 25°C (unitless)
 K : effective Michaelis constant for Rubisco-limited photosynthesis (Pa)
 Γ^* : CO_2 photorespiratory compensation point (Pa)
 β = ratio of b_V and (a_E/η^*)

χ depends on temperature, vapor pressure, atmospheric CO_2 and atmospheric pressure (indexed by elevation)

Optimal χ : consequences on trends in iWUE

> 100 $\delta^{13}\text{C}_{\text{tree-ring}}$
chronologies

Lavergne et al. (2020)
New Phytol.

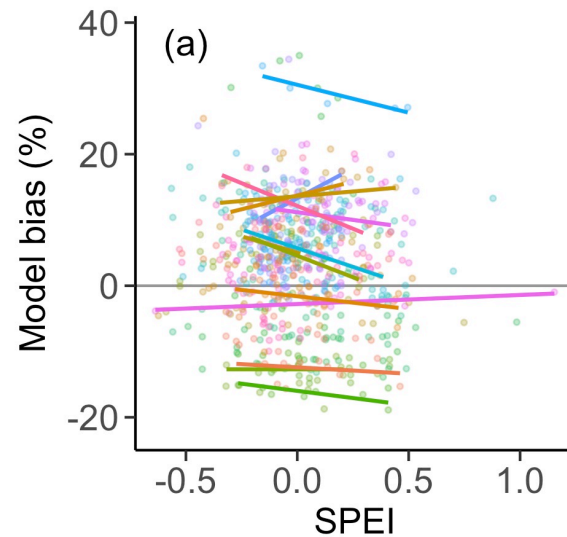
→ Broadly constant χ over long timescales after integrating environmental effects

Implications for iWUE:

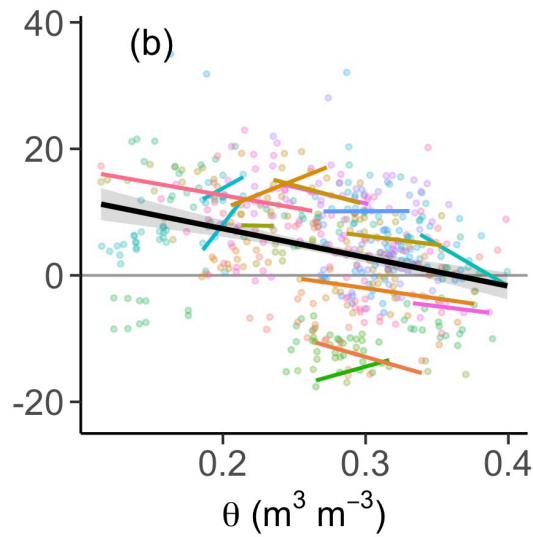
1. increase in iWUE with rising c_a **can be offset** by increasing mean T and decreasing VPD
2. for the same increase in CO_2 , iWUE increase with decreasing P_{atm} (increasing elevation)

But LC model **does not predict** how dry soils with reduced soil water availability **further influence** χ

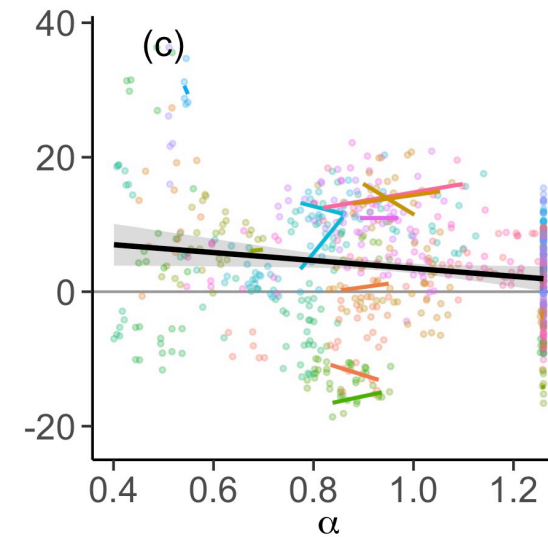
→ overestimation of χ under dry conditions and underestimation of χ under moist conditions (Lavergne et al. 2020 *New Phytol.*)



Standardized Precipitation-
Evapotranspiration Index



ESA CCI v4.4
volumetric soil
moisture



SPLASH model
AET/PET*

*AET/PET = ratio of actual to potential evapotranspiration

Is β sensitive to soil water availability?

β = unit costs of carboxylation and transpiration modulated by water viscosity

Standard model: β constant (~ 170 - 190 for full model vs ~ 200 - 240 for simple model)

Questions

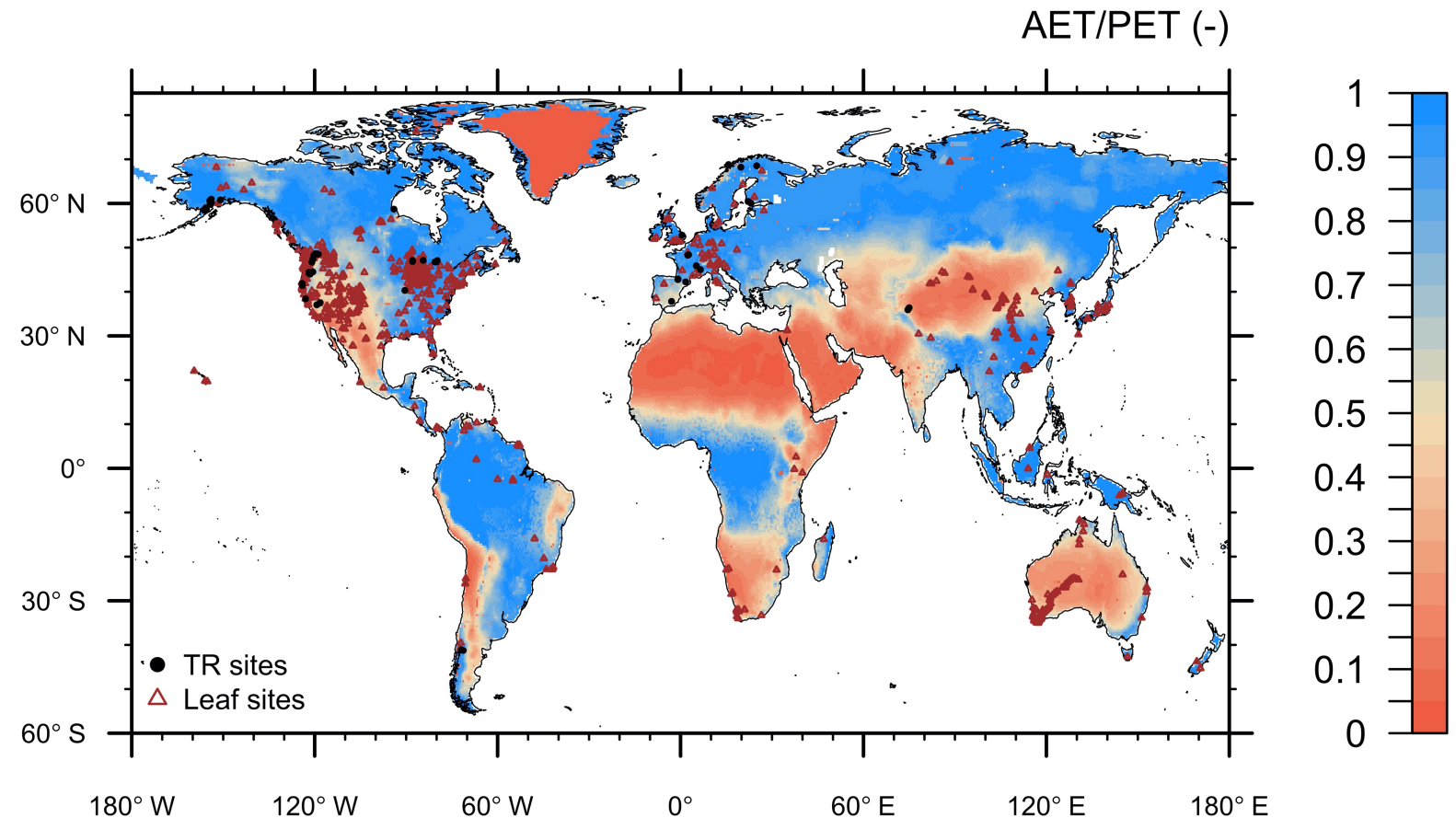
- 1) Is there any difference in the response of β to soil water between angiosperms and gymnosperms? [s10](#)
- 2) Can β be predicted from soil moisture data? [s11](#)
- 3) Does the inclusion of β as a function of soil moisture improve χ predictions compared to those from the original LC model? [s12](#)-[s13](#)

We hypothesize that:

1. $\beta_{\text{angio}} > \beta_{\text{gymno}}$ ($\chi_{\text{angio}} > \chi_{\text{gymno}}$) due to higher sapwood permeability in angiosperms
2. β decrease with reduction in soil moisture due to changes in whole plant hydraulic conductivity \rightarrow decrease of χ

1. Compiling stable carbon isotopes ($\delta^{13}\text{C}_{\text{plant}}$) data

- **leaf level:** $\delta^{13}\text{C}_{\text{leaf}}$ for C_3 woody plants from Diefendorf et al. (2010) *PNAS* + Cornwell et al. (2018) *Global Ecol. Biogeo.* + Sheldon et al. (2020) *Global Plan. Change*
- **plant level:** tree-rings $\delta^{13}\text{C}_{\text{TR}}$ at 75 sites from Lavergne et al. (2020) *New Phytol.*



*AET/PET = ratio of actual to potential evapotranspiration

2. Predicting β from χ and environmental data

χ inferred from $\delta^{13}C_{\text{plant}}$ assuming
infinite mesophyll conductance:

$$\chi_{iso} = \frac{\left(\frac{\delta^{13}CO_2 - (\delta^{13}C_{\text{plant}} - d)}{1 + (\delta^{13}C_{\text{plant}} - d)/1000} \right) + f \frac{\Gamma^*}{c_a}}{b - a_s}$$

$a_s = 4.4$ ‰ fractionation due to diffusion of CO₂ in air
 $b = 28$ ‰ fractionation due to carboxylation
 $f = 12$ ‰ fractionation due to photorespiration
 $d = 2.1$ ‰ post-photosynthetic fractionation (for TR only)
 Γ^* and K : calculated from temperature and atmospheric pressure using parameter values at 25°C derived from Bernacchi et al. (2001) *Plant, Cell & Env.*

LC optimality model

$$\chi = \frac{c_i}{c_a} = \frac{\Gamma^*}{c_a} + \left(1 - \frac{\Gamma^*}{c_a}\right) \frac{\xi}{\xi + \sqrt{D}} \quad (1)$$

$$\xi = \sqrt{\beta \frac{K + \Gamma^*}{1.6\eta^*}} \quad (2)$$

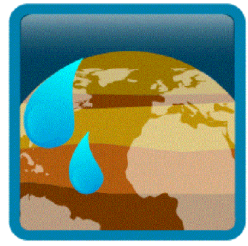
Expected β



$$\beta = 1.6\eta^* D \frac{\left(\chi_{iso} - \frac{\Gamma^*}{c_a}\right)^2}{(1 - \chi_{iso})^2 (K + \Gamma^*)}$$

- + CRU climate dataset as input: 0.5 x 0.5 spatial resolution over 1901-2018
- + Atmospheric CO₂ from SCRIPPS
- + $\delta^{13}CO_2$ from Graven et al. (2017) *Geosc. Mod. Dev.*

3. Comparing inferred β values with soil water data



soil moisture

cci

~ 0.5 cm soil depth

[ESA CCI v4.4 product](#) (1979-2018)

Dorigo et al. (2017) *Rem. Sens. Env.*



~ 1 m soil depth

[GLEAM v3.3a product](#) (1980-2018)

Martens et al. (2017) *Geosci. Mod. Dev.*

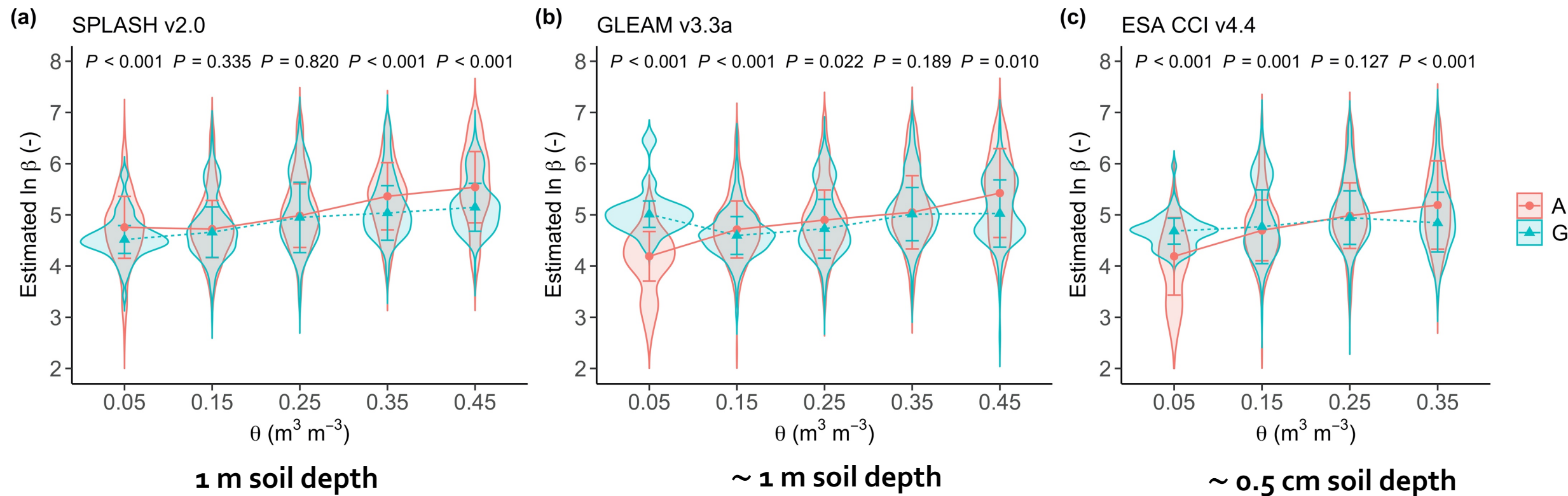
SPLASH model **1 m soil depth**

Davis et al. (2017) *Geosc. Mod. Dev.*

v2.0 from Sandoval et al. (in prep)*

<https://github.com/dsval/rsplash>

*see Session HS2.2.1 - 5073: <https://meetingorganizer.copernicus.org/EGU2020/EGU2020-5073.html>

Sensitivity of β to soil water: across plant groups

> 4,050 measures
over 1980-2018

→ Higher sensitivity of β to changes in soil water content for angiosperms than for gymnosperms

→ Crossover at around $0.35 \pm 0.05 \text{ m}^3 \text{m}^{-3}$

A: angiosperm
G: gymnosperm

Sensitivity of β to soil water: within & across bins

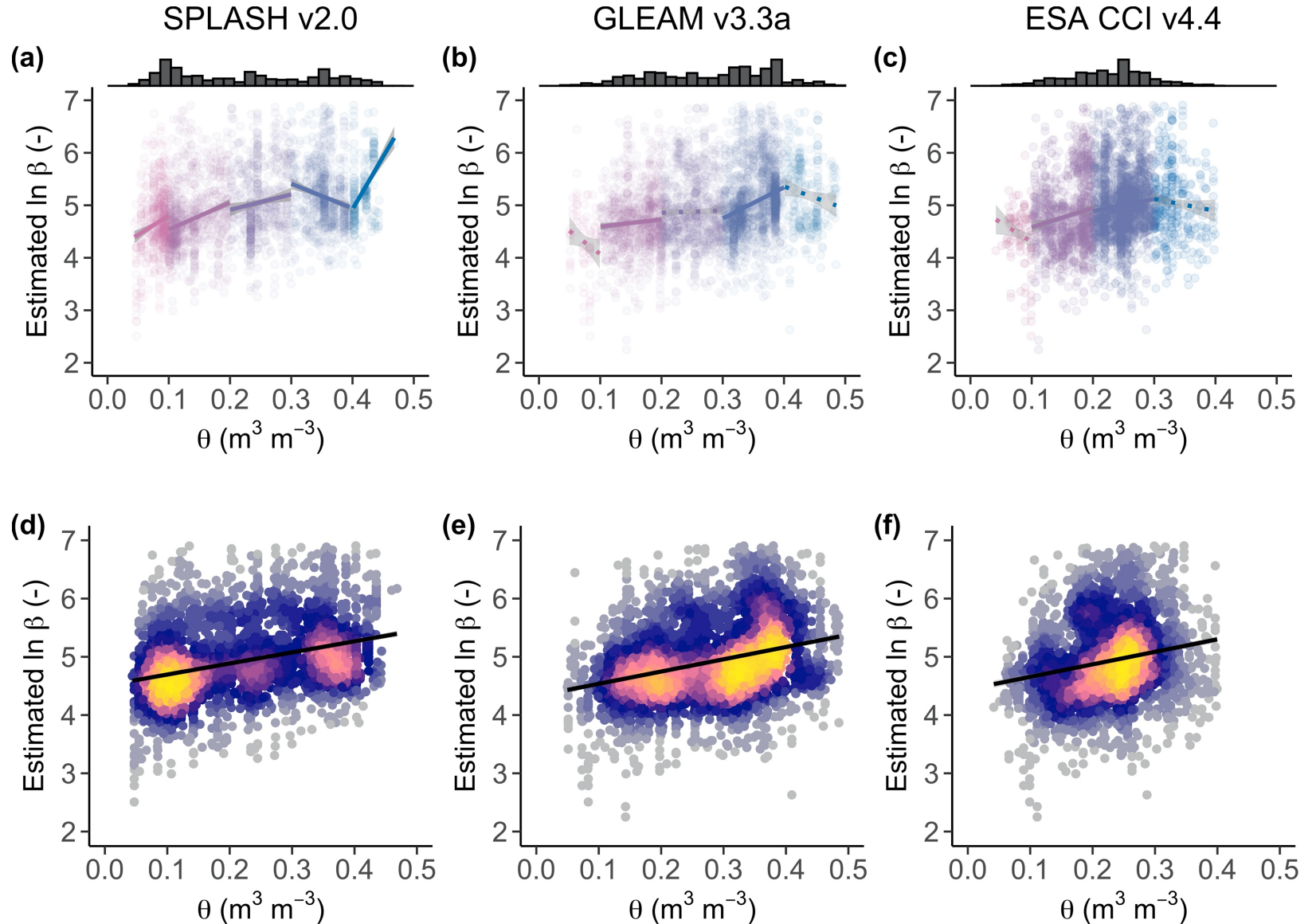
→ Increase of β within bins of soil water
Saturation at high soil moisture?

→ β increase relatively linearly over the whole range of soil water conditions

$$\ln \beta = a_{\beta} \theta + b_{\beta}$$

$$a_{\beta} = 2.0 \pm 0.1$$

$$b_{\beta} = 4.4 \pm 0.1$$



Predicting β with soil moisture: calibration

Cross-validation tests:
100 training/testing subsets

Bootstrapping (100 replicates)

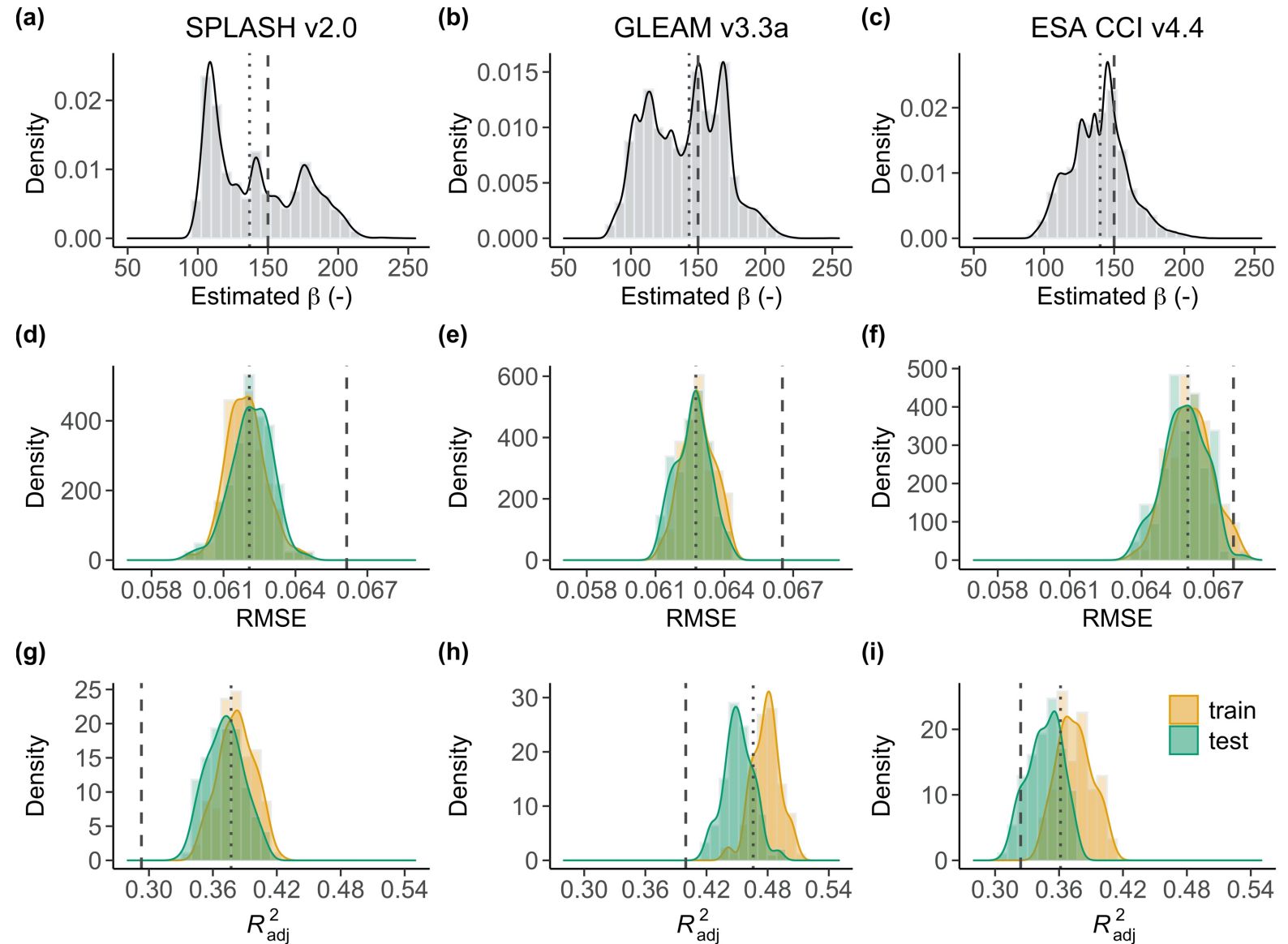
..... Median values for modified model

- - - Original model

RMSE = root mean square error

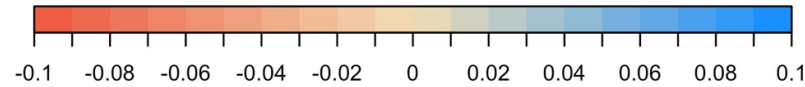
R^2_{adj} = adjusted R^2

→ Higher predictive skill
for the modified than for
the original models



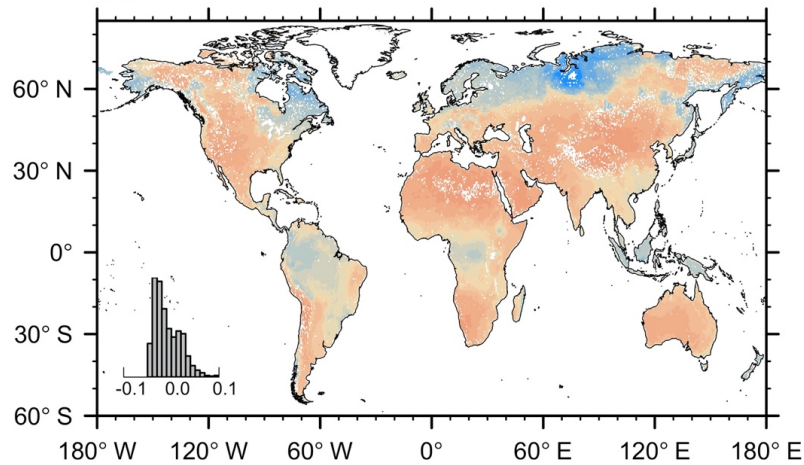
Optimal χ : modified versus original LC model

Absolute difference of predicted χ between models (-)

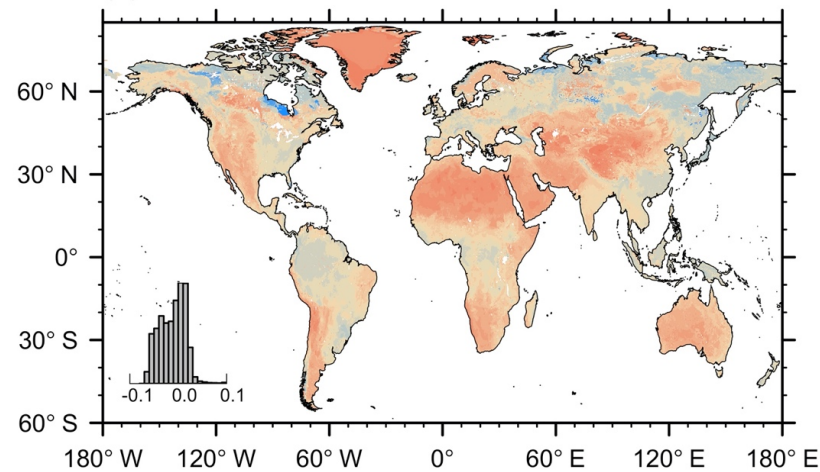


Modified - original model

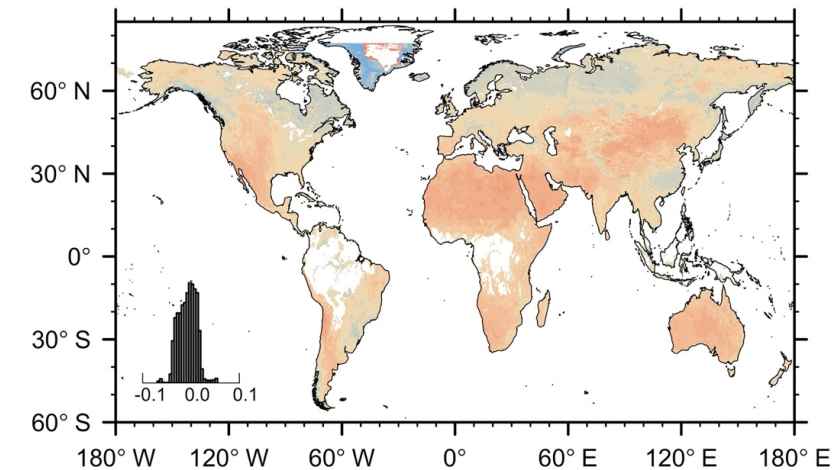
(a) SPLASH v2.0



(b) GLEAM v3.3a



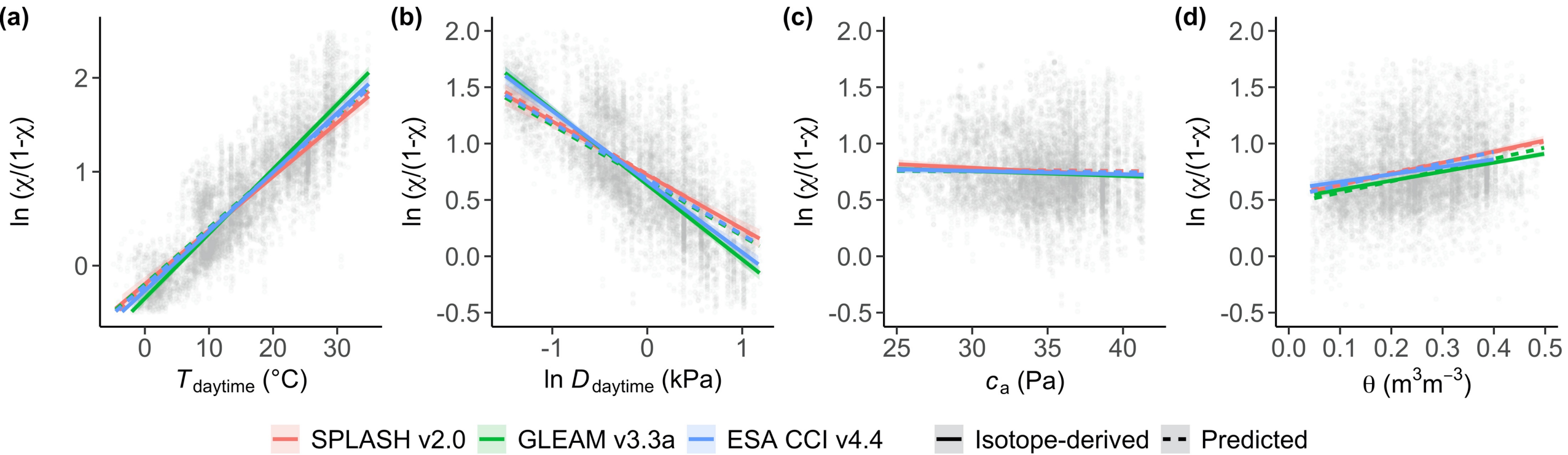
(c) ESA CCI v4.4



- Soil moisture effect reducing on average predicted χ values by $1.4 \pm 3.9\%$ over the globe
- **But** higher predicted χ values in modified than in original model in dense vegetation areas (e.g., boreal or tropical rainforests)

Optimal χ : environmental dependencies

Partial residual regressions of isotope-derived and predicted χ with environmental drivers



- Good predictions of environmental dependencies from LC model
- Larger effects of temperature and vapor pressure deficit on χ

- Only **partial support for our first hypothesis**: $\beta_{angio} > \beta_{gymno}$ solely under well-watered upper- to mid-soil conditions
- Higher sensitivity of β to soil water for angiosperms than for gymnosperms
→ **contrasting trait-based hydraulic strategies** for the two plant vascular groups:
larger diameter of xylem conduits / narrower hydraulic safety margins / lower water potential for angiosperms than for gymnosperms **maximizing hydraulic conductance of angiosperms**
- Simple empirical function for β to represent χ responses to soil drought improving predictions by $6.2 \pm 2.4\%$ (mean \pm sd of adjusted R^2) over 1980-2018
- **But approach** does not provide insights into underlying processes → need to incorporate plant hydraulics and information about trait-environment dependencies into the model*

*see Jadeep Joshi presentation beyond the 'β approach' Session BG3.6:
<https://meetingorganizer.copernicus.org/EGU2020/EGU2020-9687.html>

Thank you

BG3.13

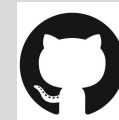
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from analysis and modelling of stable carbon ISOtope data

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<https://prenticeclimategroup.wordpress.com/lab-members/>



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