How well-tested eco-evolutionary optimality hypotheses can make land surface models more reliable and robust

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What is an EEO hypothesis?

- Hypothesis that an observable quantity tends to optimize some criterion of "success" (e.g. costs versus benefits).
- Many criteria are possible.
- **Must always be tested** against observations.

*1 Focus on **outcomes,** not **mechanisms.***

*2 Biological systems – huge diversity, but unity is **imposed by natural selection** – the "missing law" for LSMs.*

3 "Eco" vs "evo": plasticity (acclimation) vs adaptation

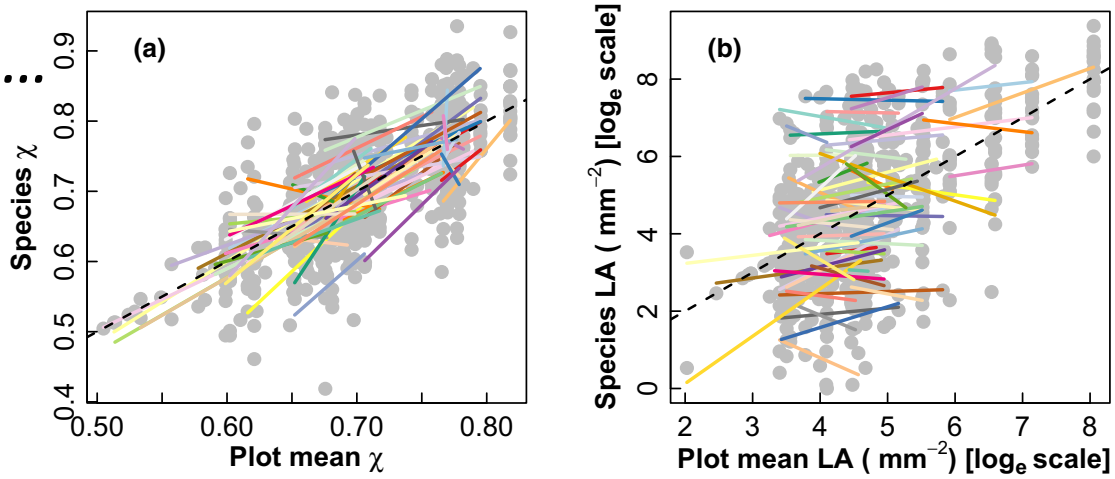
Time scales of EEO responses

- Instantaneous (minutes)
- Acclimation (weeks) – focus in this talk
- Competition (years)
- Migration (centuries)
- Evolution (longer)

1 Acclimation vs species replacement: traits vary in plasticity

2 Plastic: V_{cmax}, χ (= c_i/c_a)…

3 Less plastic: leaf area, LMA…



Dong et al. 2020 *New Phytologist*

Practical advantages of EEO

- Replace PFT-specific parameters with universal parameters (more realistic, and a **simplification**)
- Example: photosynthetic capacity (V_{cmax})…
  - Usual approach: fix PFT-specific values at 25˚C (V_{cmax25}) and apply the instantaneous temperature response
  - EEO approach: set 2-week moving average of V_{cmax25} *just large enough* to use available light (coordination hypothesis)
  - Temperature response over the seasonal cycle is less steep, and more realistic
  - Correct responses to vpd (increase) and eCO_2 (decline) follow automatically

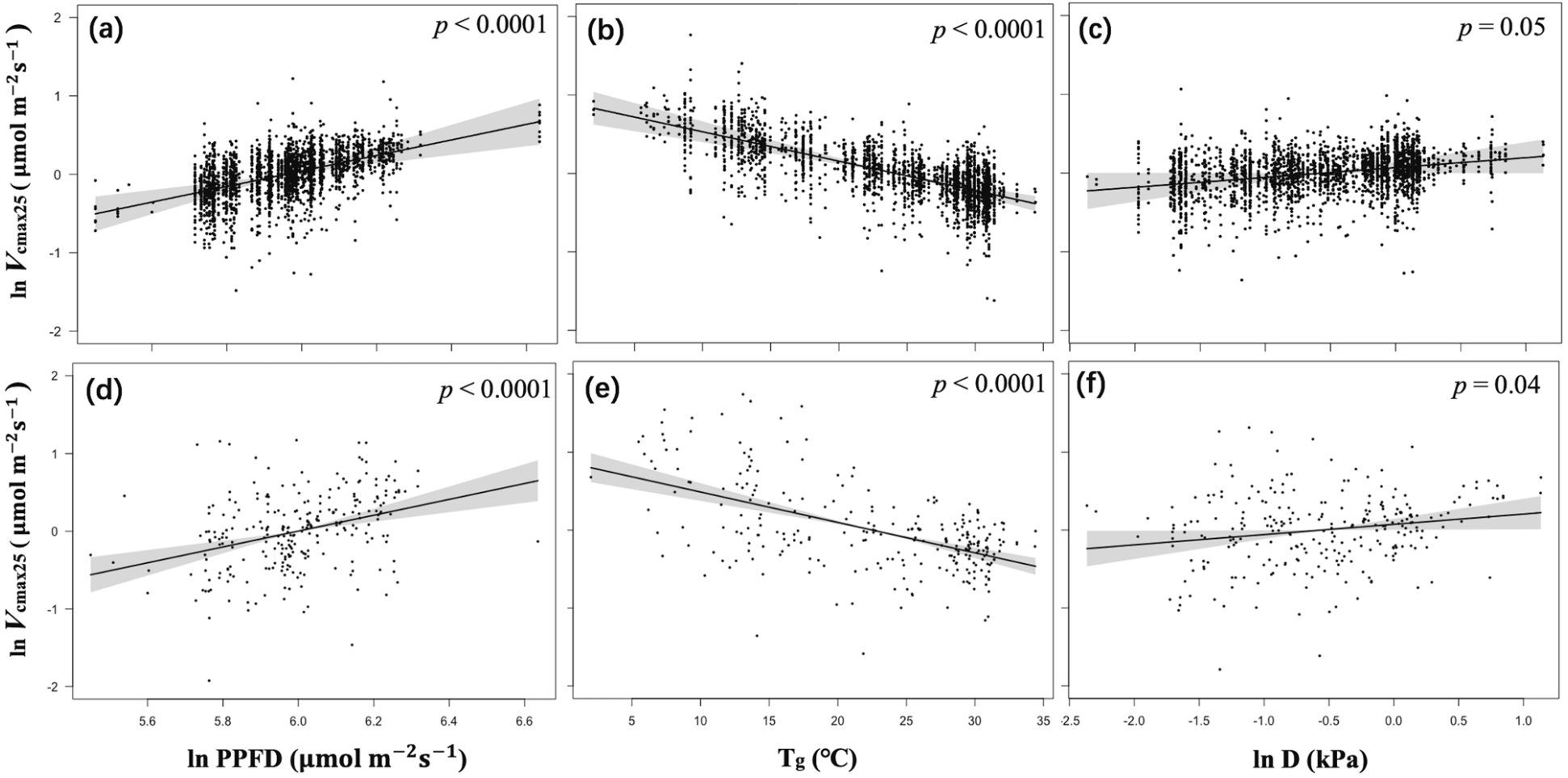
Environmental effects on V_{cmax25}

Predictor for V_{cmax25}	Theoretical value	Site-mean coefficient $R^2 = 0.31$
ln PPFD	1	1.02 ± 0.21
T_{growth}	–0.05 K^{-1}	–0.04 ± 0.01 K^{-1}
ln D	0.07	0.13 ± 0.06

Peng *et al.* (2021) *Communications Biology*

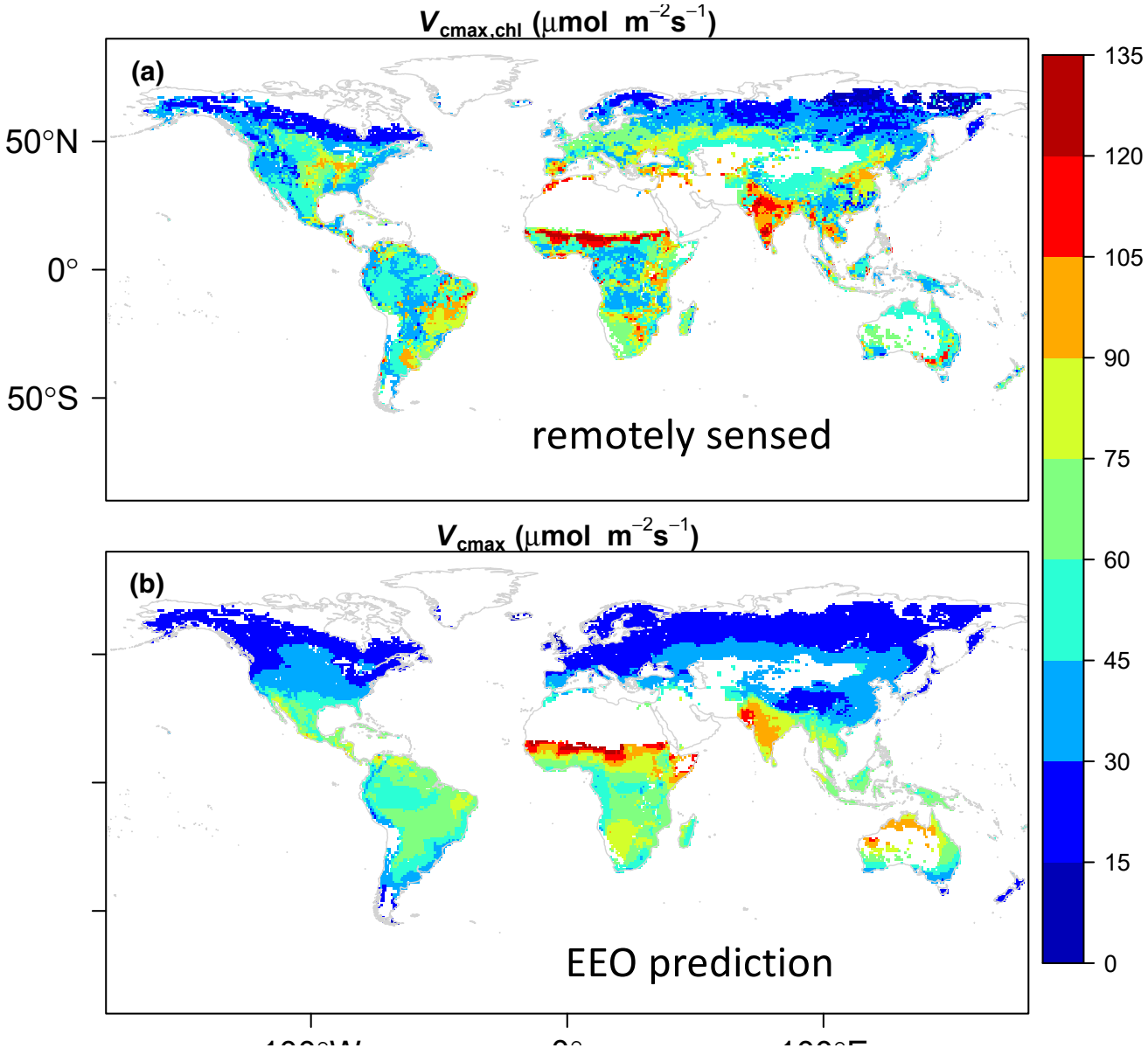
Environmental effects on V_{cmax25}

…all species (above), site means (below)…



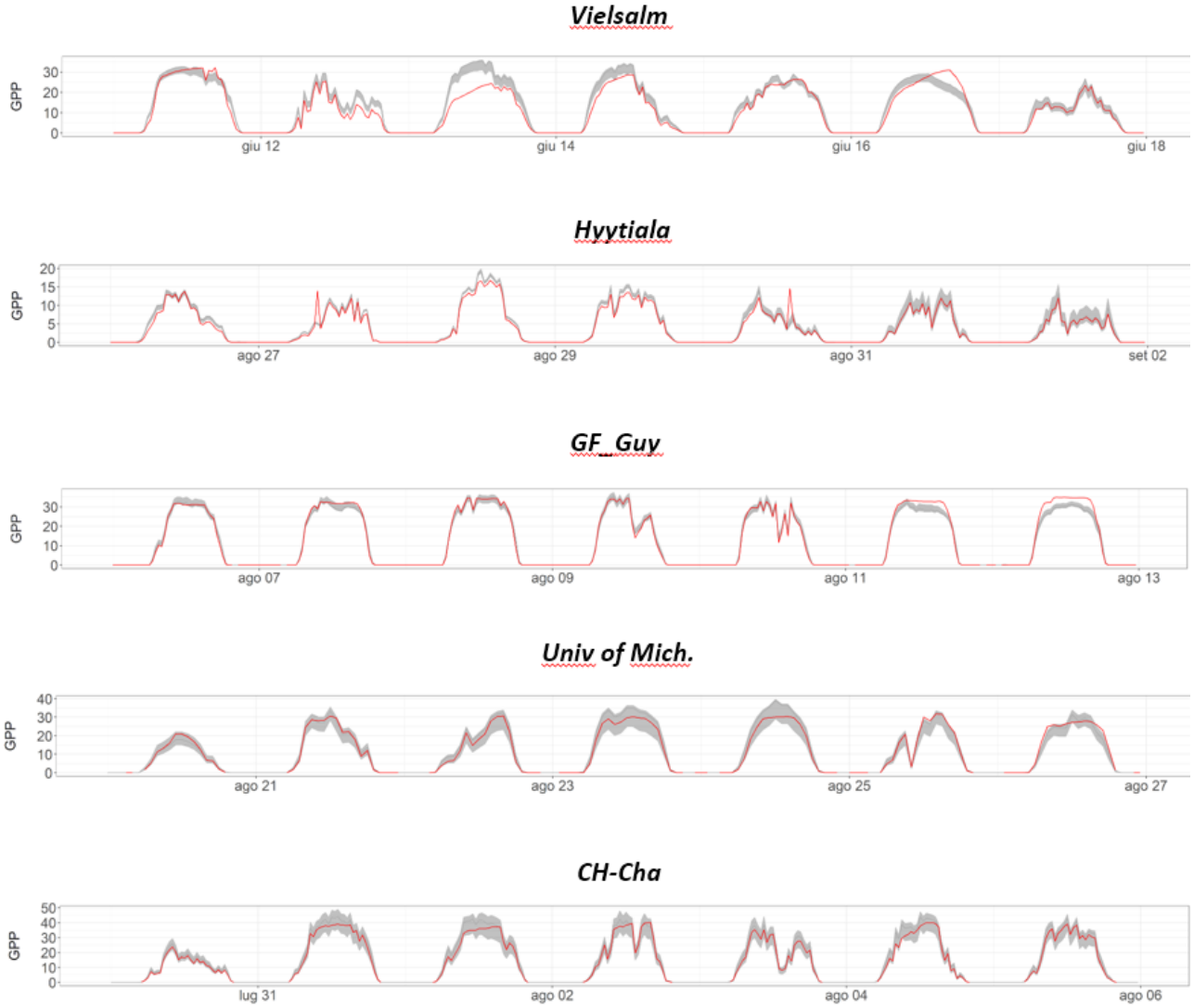
Peng *et al.* (2021) *Communications Biology*

V_{cmax} – leaf chlorophyll content vs EEO prediction



Dong *et al.* (2022)
New Phytologist

Separation of time scales => diurnal cycles of GPP



temperate mixed forest

boreal forest

tropical forest

temperate deciduous forest

grassland

Mengoli *et al.* (2021) *JAMES*

Stomatal behaviour: current models

Ball-Berry $\chi = 1 - 1/mh$

Leuning $\chi = f_0 (1 - D/D_{00})$ where $D_{00} = D_0 (\alpha - 1)$,
and $f_0 = 1 - 1/\alpha$

Medlyn* $\chi = g_1/(g_1 + \sqrt{D})$

*g_1 for PFTs: Lin *et al.* (2012) *Nature Climate Change*

green quantities are PFT-specific parameters

An EEO model

Plants must **transport** water in order to **take up** CO_2

Least-cost hypothesis: minimize $a\,(E/A) + b\,(V_{cmax}/A)$

$$\chi = \gamma + (1-\gamma)\,\xi/(\xi + \sqrt{D}) \qquad \approx \quad \xi/(\xi + \sqrt{D})$$

where

$\gamma = \Gamma^*/c_a$ and $\xi = \sqrt{(bK/1.6a)}$

b is constant

a declines with temperature (due to viscosity)

1 Both can be estimated from independent data

2 Strong (acclimated) effects of temperature and elevation on ξ

Prentice *et al.* (2014) *Ecology Letters*

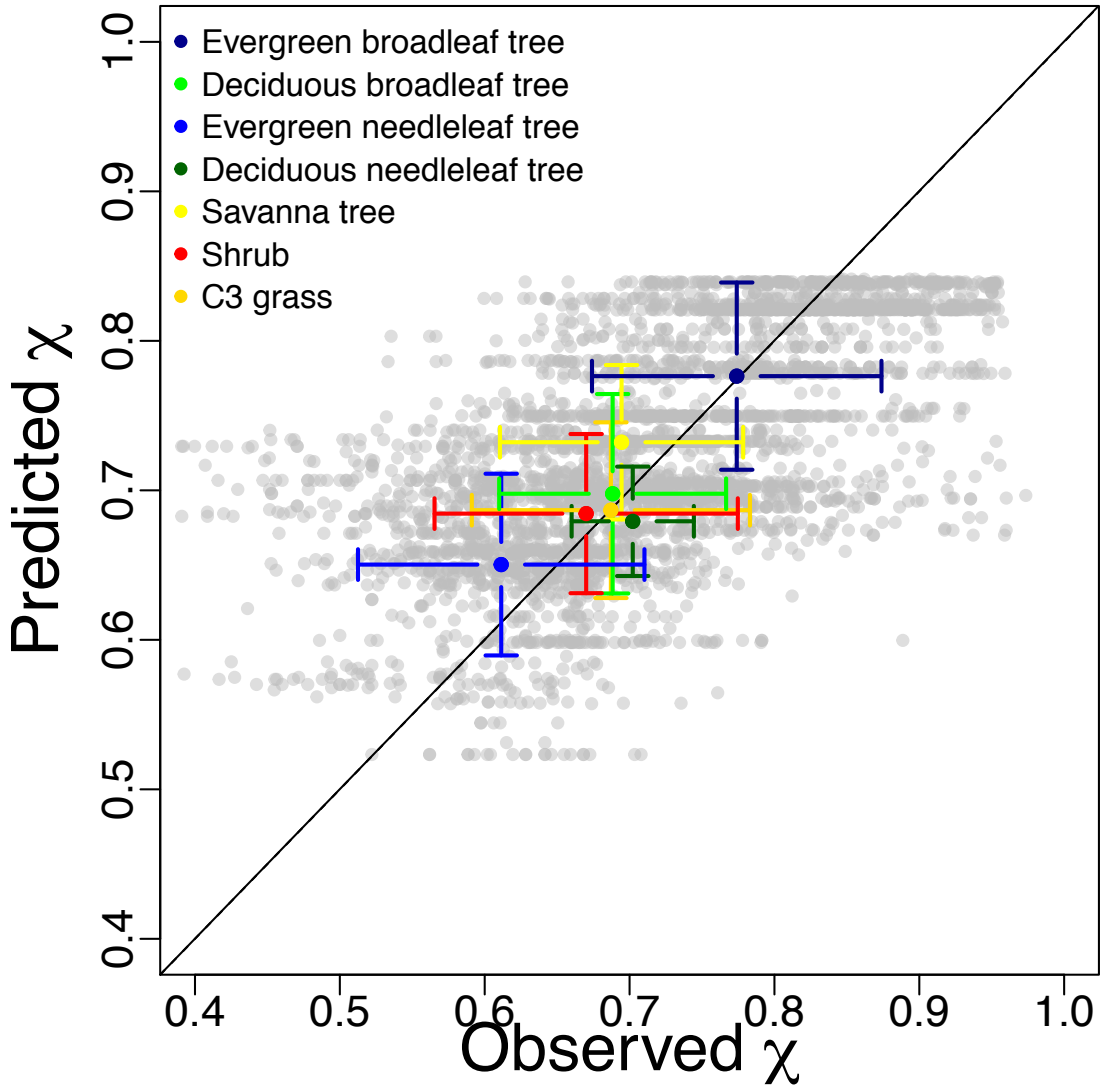
Quantitative effects on χ: predictions *versus* data (leaf $\delta^{13}C$)

	predicted* (by theory)	fitted (by regression)
temperature (K)	0.054	0.052 ± 0.006
ln vpd	–0.5	–0.55 ± 0.06
elevation (km)	–0.08	–0.11 ± 0.03

*calculated as per previous slide, and logit-transformed

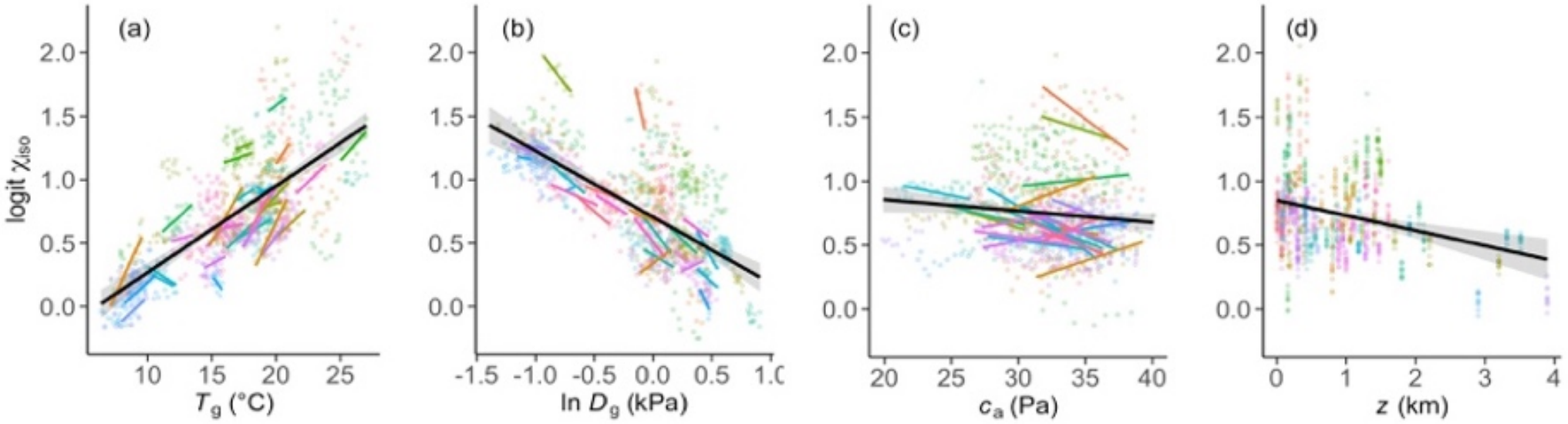
Wang *et al.* (2017) *Nature Plants*

One equation fits all PFTs



Wang *et al.* (2017) *Nature Plants*

Environmental effects on χ (tree-ring $\delta^{13}C$)



Lavergne *et al.* (2020) *New Phytologist*

Why does it matter?

Interpretation of observations:

- Example: declining leaf N content (Dong *et al.* 2022 *New Phytologist*) is **not** caused by limited N supply, but by rising CO_2 and warming.

Projections of the carbon cycle:

- Example: if acclimation is ignored, modelled future GPP and land CO_2 uptake are **too small**.

LEMONTREE

Land Ecosystem Models based On New Theory, obseRvations and ExperimEnts

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