



LEMONTREE

Land Ecosystem Models
based On New Theory,
obseRvations and
Experiments

Implementation of an eco-evolutionary approach to photosynthesis and acclimation in the JULES land surface model

Wenyao Gan · S.P. Harrison · I.C. Prentice · P.L. Vidale · M. Best



Imperial College
London



서울대학교
SEOUL NATIONAL UNIVERSITY



LPICEA | Lab of Plant Interactions:
Climate, Ecosystem & Atmosphere
Department of Earth System Science | Tsinghua University



COLUMBIA UNIVERSITY
IN THE CITY OF NEW YORK

Berkeley
UNIVERSITY OF CALIFORNIA



Utrecht University

u^b

UNIVERSITÄT
BERN



University of
Pittsburgh



ECMWF

Plant responses to environment happen at different timescales

Instantaneous response

Seconds to hours

Stomatal opening/closing, light reactions, enzyme kinetics respond immediately to changes in light, temperature, and CO₂



Acclimation

Days, weeks to months

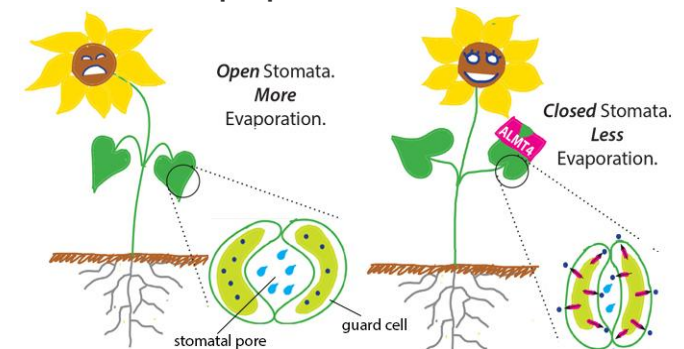
Physiological and structural adjustments: changes in V_cmax, J_{max}, stomatal sensitivity ξ , and leaf nitrogen allocation



Adaptation

Years and centuries

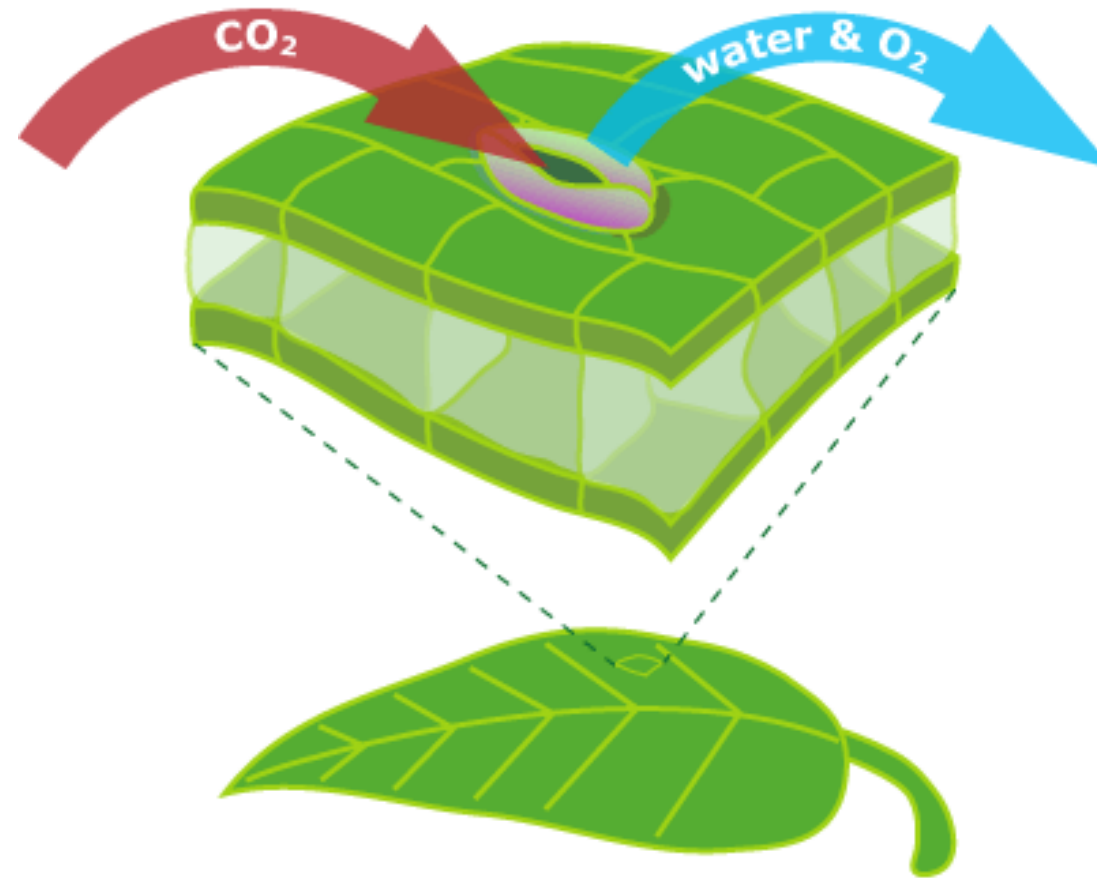
Evolutionary changes through competition, migration, and natural selection on trait distributions across populations



Unifying framework - Eco-evolutionary optimality

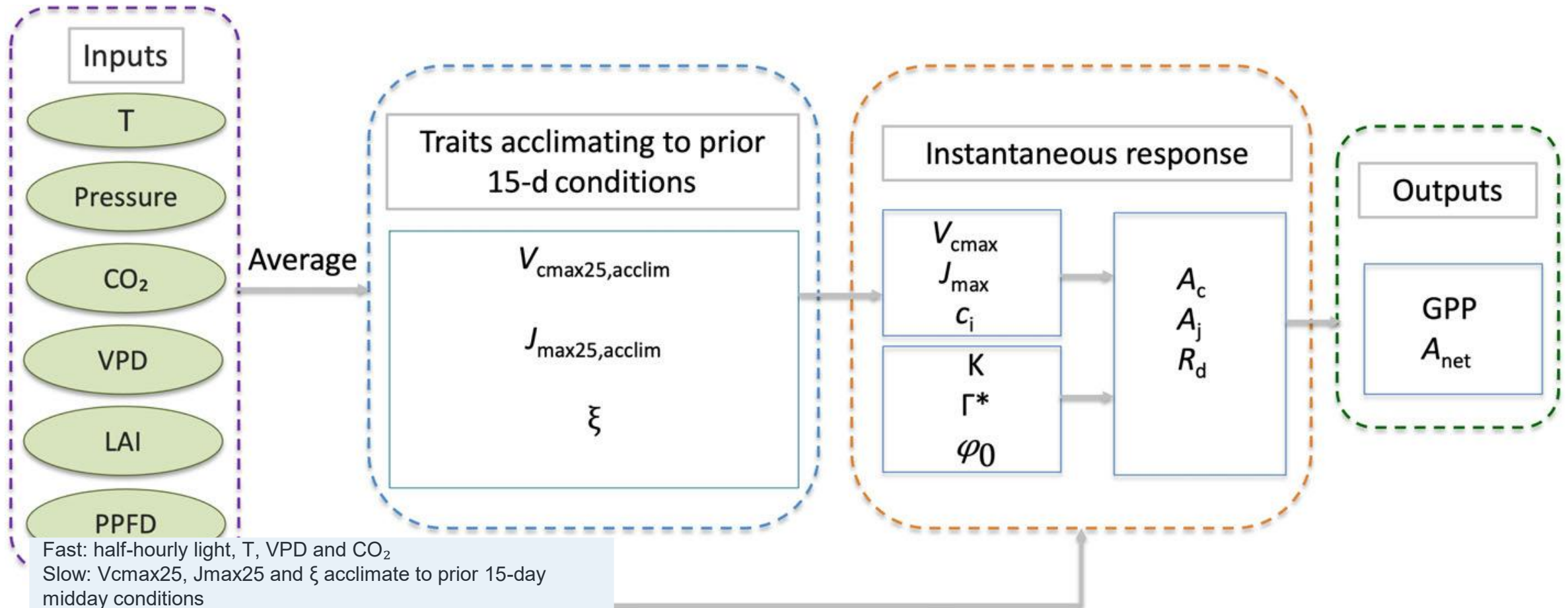
Key idea: carbon gain is optimized against two costs

- water loss through stomata $\rightarrow$ optimal χ and ξ
- maintenance of carboxylation capacity $\rightarrow$ optimal V_{cmax} and J_{max}



CO₂ enters while O₂
and water exits leaf
through leaf stomata

The sub-daily P model separates slow acclimation from fast instantaneous response



Three changes: $\Gamma^* \rightarrow 0$ · $\beta \rightarrow \beta_{C_4}$ · $m_j \rightarrow 1$

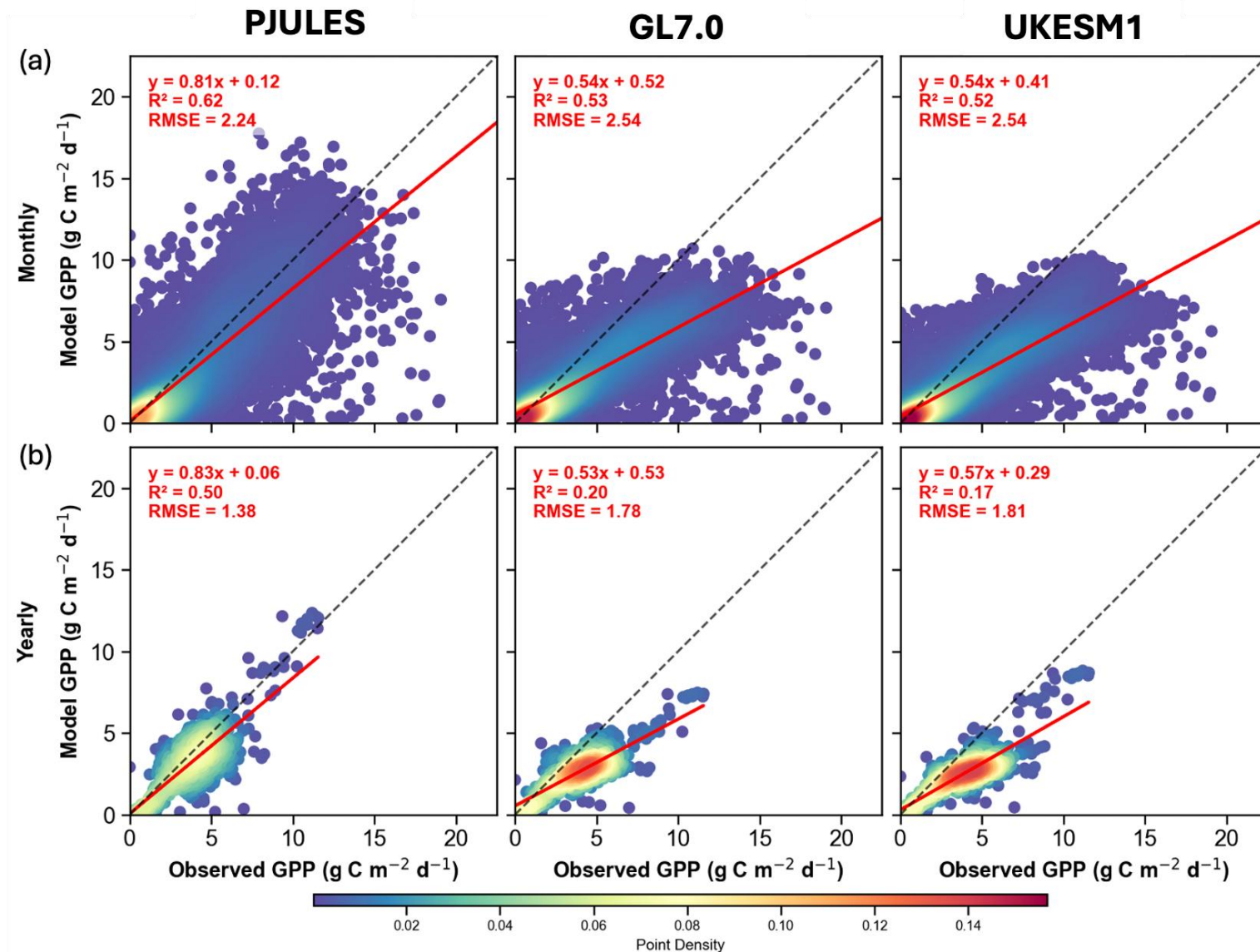
PJULES replaces PFT-dependent empirical parameters with environment-driven predictions

Feature	JULES-GL7.0	JULES-UKESM1	PJULES
Plant types	5 PFTs	13 PFTs	C ₃ / C ₄ only
Photosynthesis	Collatz et al. (1991)	Collatz et al. (1991)	P-model
Stomatal cond.	Jacobs scheme	Jacobs scheme	Least-cost (ξ)
Vcmax / Jmax	PFT-specific fixed	PFT-specific fixed	Env.-predicted
Acclimation	None	None	15-day memory
Canopy scheme	Multi-layer (10)	Multi-layer (10)	Big-leaf

LEAF SCHEME • 6 Collatz biochemical parameters; +2 Jacobs stomatal parameters; +fd respiration; +glmin conductance

CANOPY & STRESS • PAR/optics (kpar, kext, omega, alpar, orient, can_struct_a) • N profile (kn or knl) • soil-moisture pathway (fsmc / ψ thresholds) → exact set is configuration-dependent

PJULES outperforms standard JULES at monthly and yearly timescales



Monthly GPP

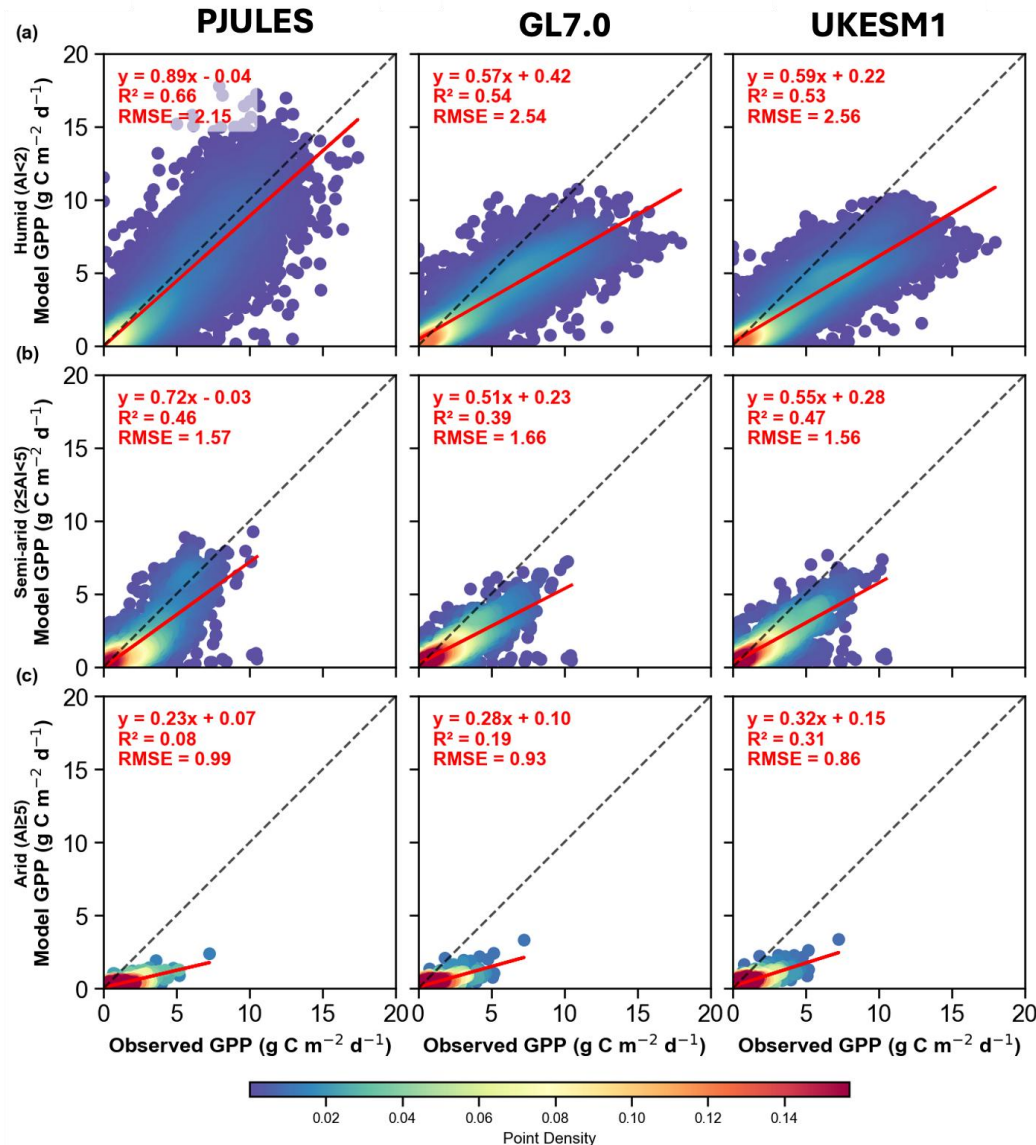
PJULES: $R^2 = 0.62$, RMSE = 2.24
GL7.0: $R^2 = 0.53$, RMSE = 2.54
UKESM1: $R^2 = 0.53$, RMSE = 2.49

Yearly GPP

PJULES: $R^2 = 0.46$, RMSE = 1.69
GL7.0: $R^2 = 0.32$, RMSE = 2.00
UKESM1: $R^2 = 0.26$, RMSE = 1.95

Panel labels: P-model = PJULES, Multi-layer = GL7.0, Multi-layer 13 = UKESM1.

Performance advantage is strongest at humid sites all models degrade with aridity



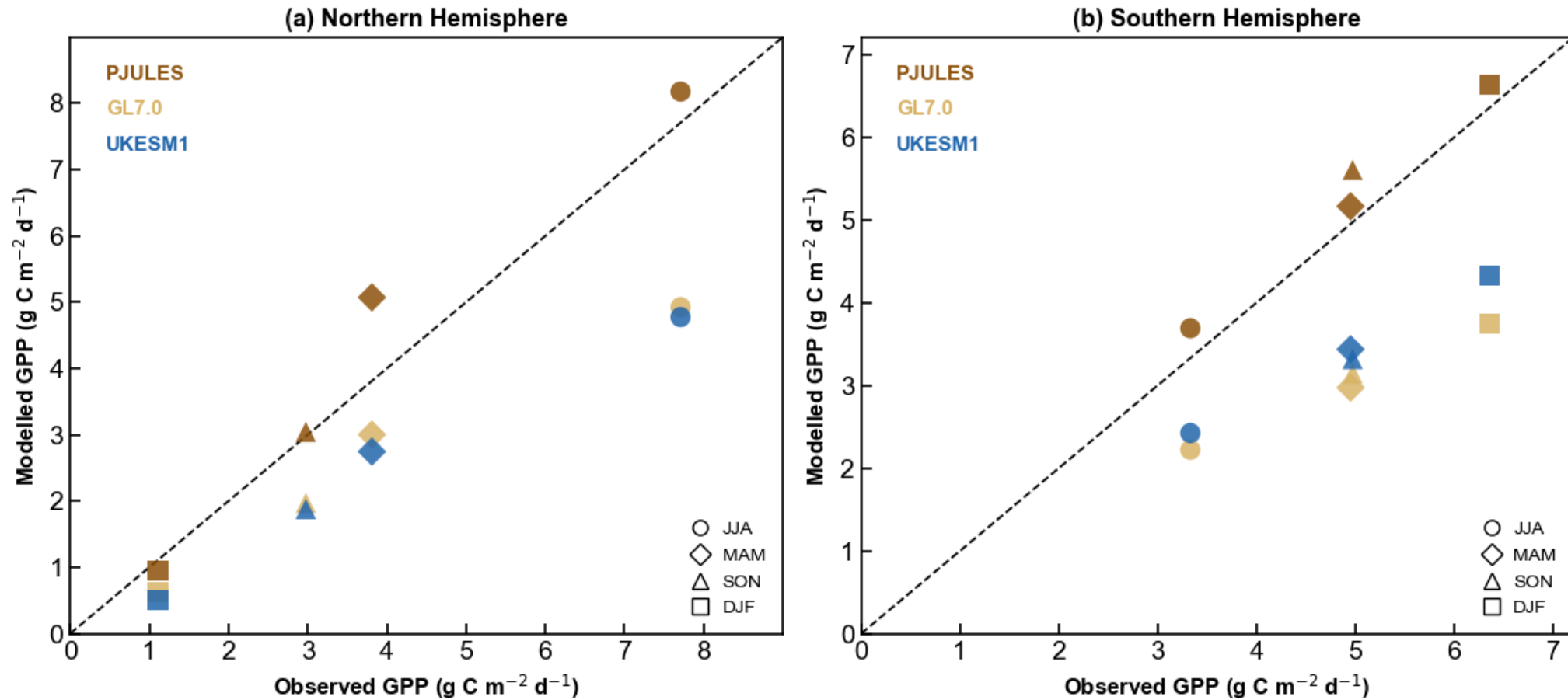
- PJULES performs best at humid sites ($R^2 = 0.66$, RMSE = 2.15)

All three models underestimate GPP with increasing aridity

Current soil moisture stress function (β) is likely too aggressive

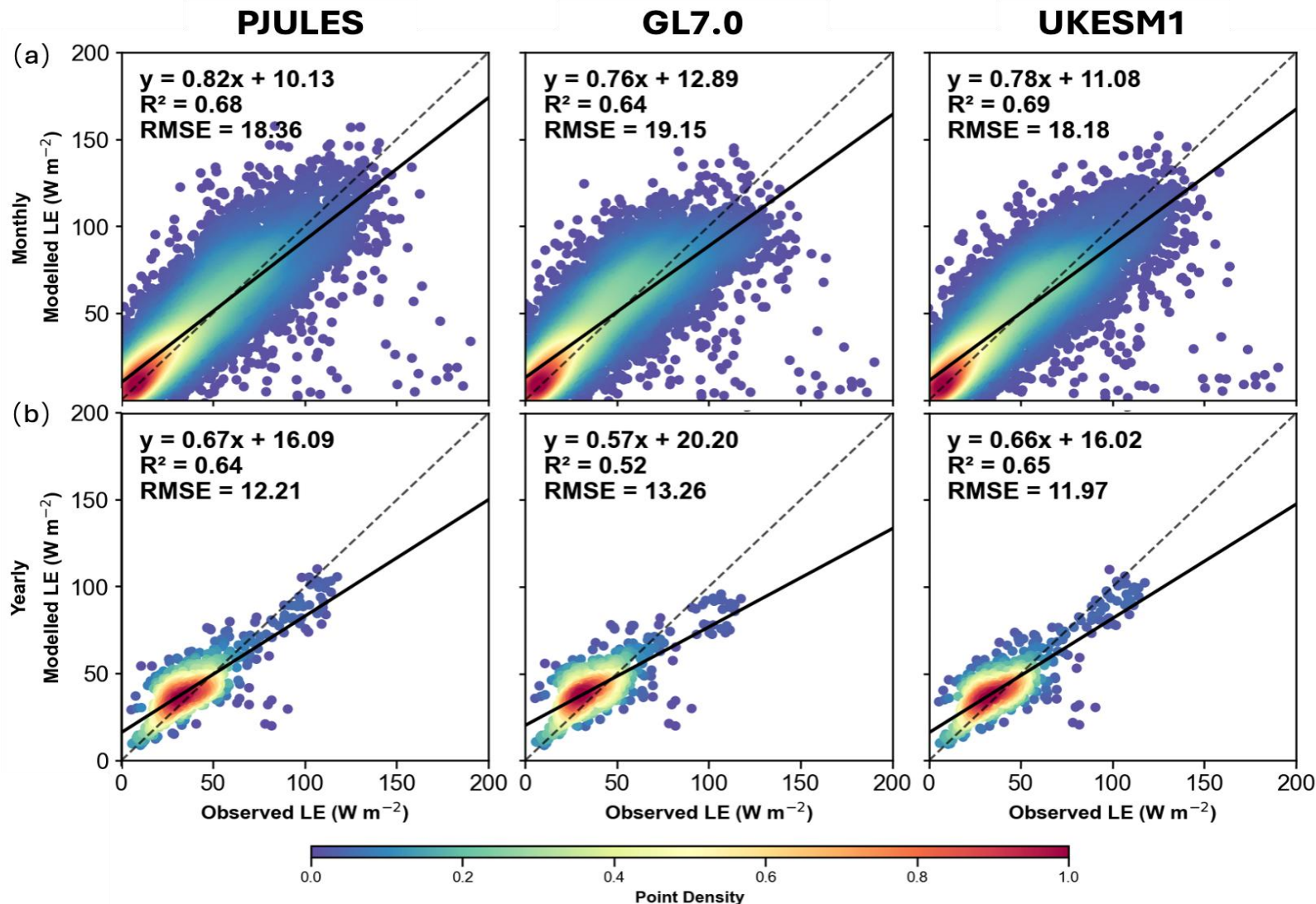
An aridity-adapted β scheme (Mengoli et al., 2025) is a clear next step

PJULES captures seasonal GPP cycles better than multi-layer configurations



- **Summer (JJA):** PJULES overestimates by only 6% vs 26–34% underestimation in GL7.0 and UKESM1
- **Spring (MAM):** PJULES overestimates by 33% — early green-up bias linked to phenology

Improved GPP simulation is not accompanied by degradation in latent heat flux



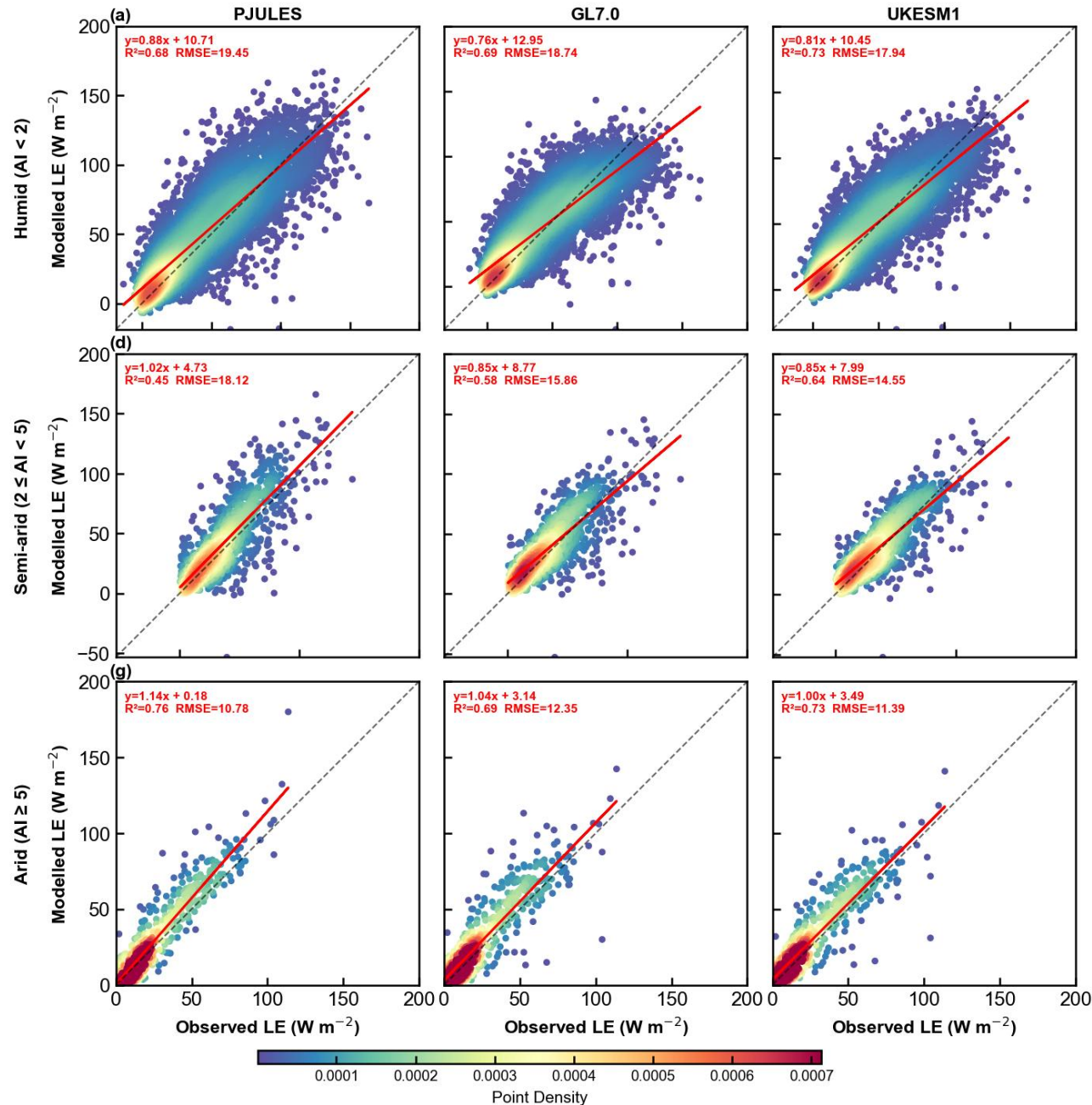
Implication

- PJULES produces a more physically consistent representation of carbon and water fluxes

GPP and LE improvements are not in tension — unlike empirical tuning approaches

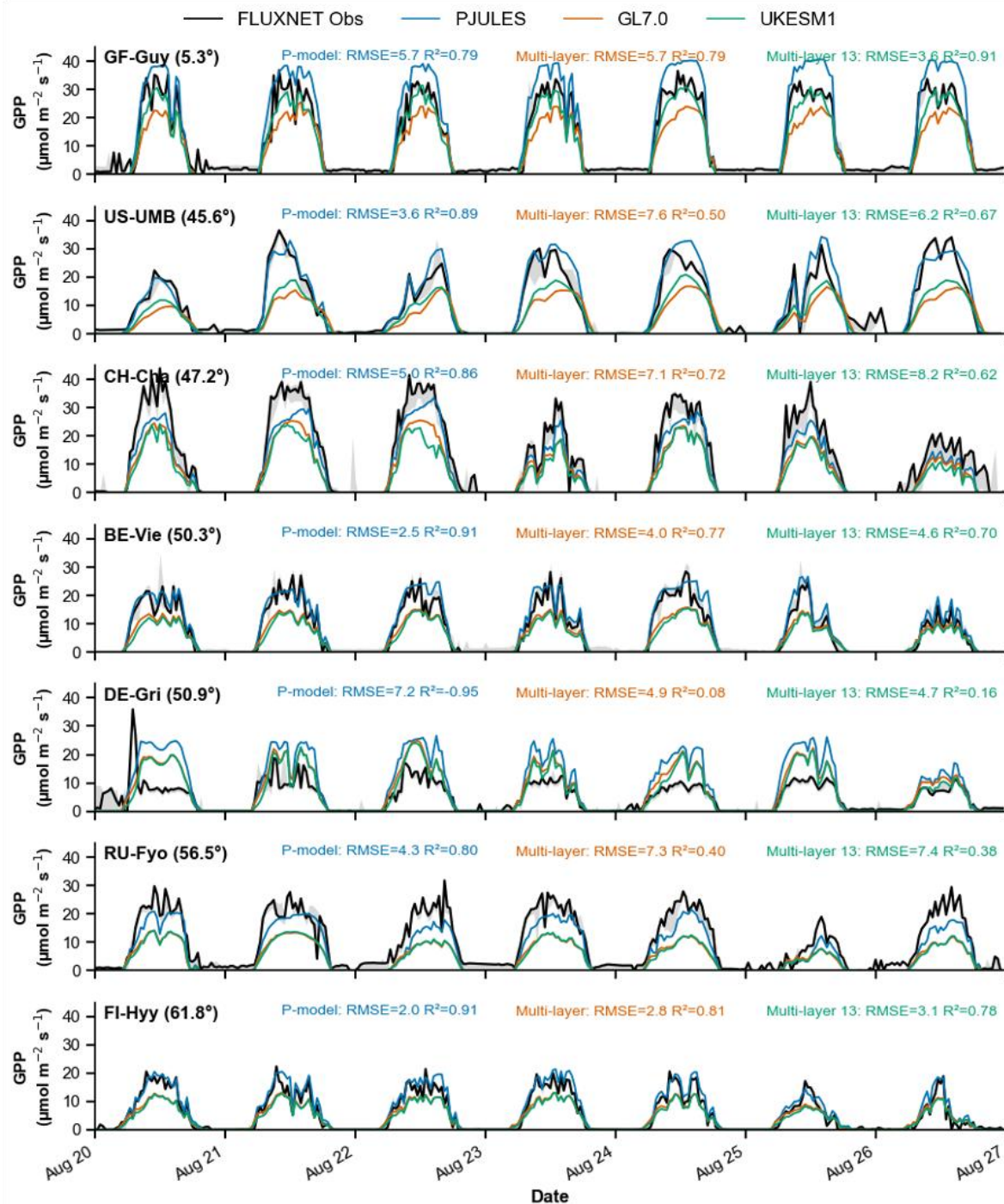
The optimality-based approach couples carbon and water at the mechanistic level through ξ

Latent heat flux is well simulated across aridity gradients; Better than carbon flux



- PJULES slope closest to 1:1 at humid (0.88) and semi-arid (1.02) sites
- R^2 values are comparable across models: differences in LE skill are much smaller than the GPP improvements seen with PJULES.

At arid sites, all three configurations perform similarly ($R^2 = 0.69$ – 0.76) — LE is less sensitive to photosynthesis scheme choice where soil evaporation dominates.

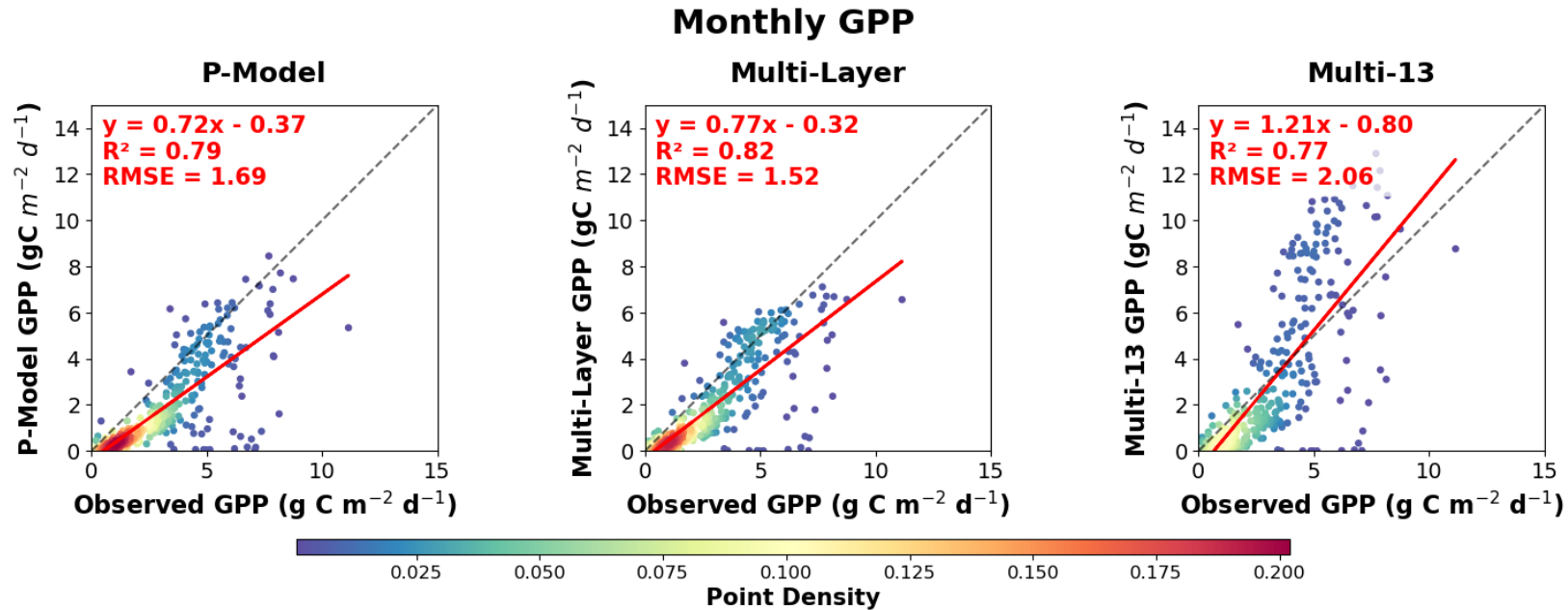


PJULES tracks the diurnal cycle better than multi-layer schemes

Half-hourly GPP over one week (20–27 Aug), seven sites ordered by latitude (5°N to 62°N).

- **Temperate & boreal forests:** PJULES best captures the timing and amplitude of the midday peak, with the highest R^2 and lowest RMSE at five of seven sites (FI-Hyy $R^2=0.91$, RMSE=2.0; BE-Vie $R^2=0.91$; US-UMB $R^2=0.89$).
- **Multi-layer schemes:** GL7.0 and UKESM1 underestimate midday GPP at most forest sites, flattening the daytime peak.
- **Tropical evergreen (GF-Guy):** PJULES overshoots the midday peak; the 13-PFT UKESM1 fits best here ($R^2=0.91$ vs 0.79)

C₄ performance is competitive without PFT-specific photosynthetic tuning

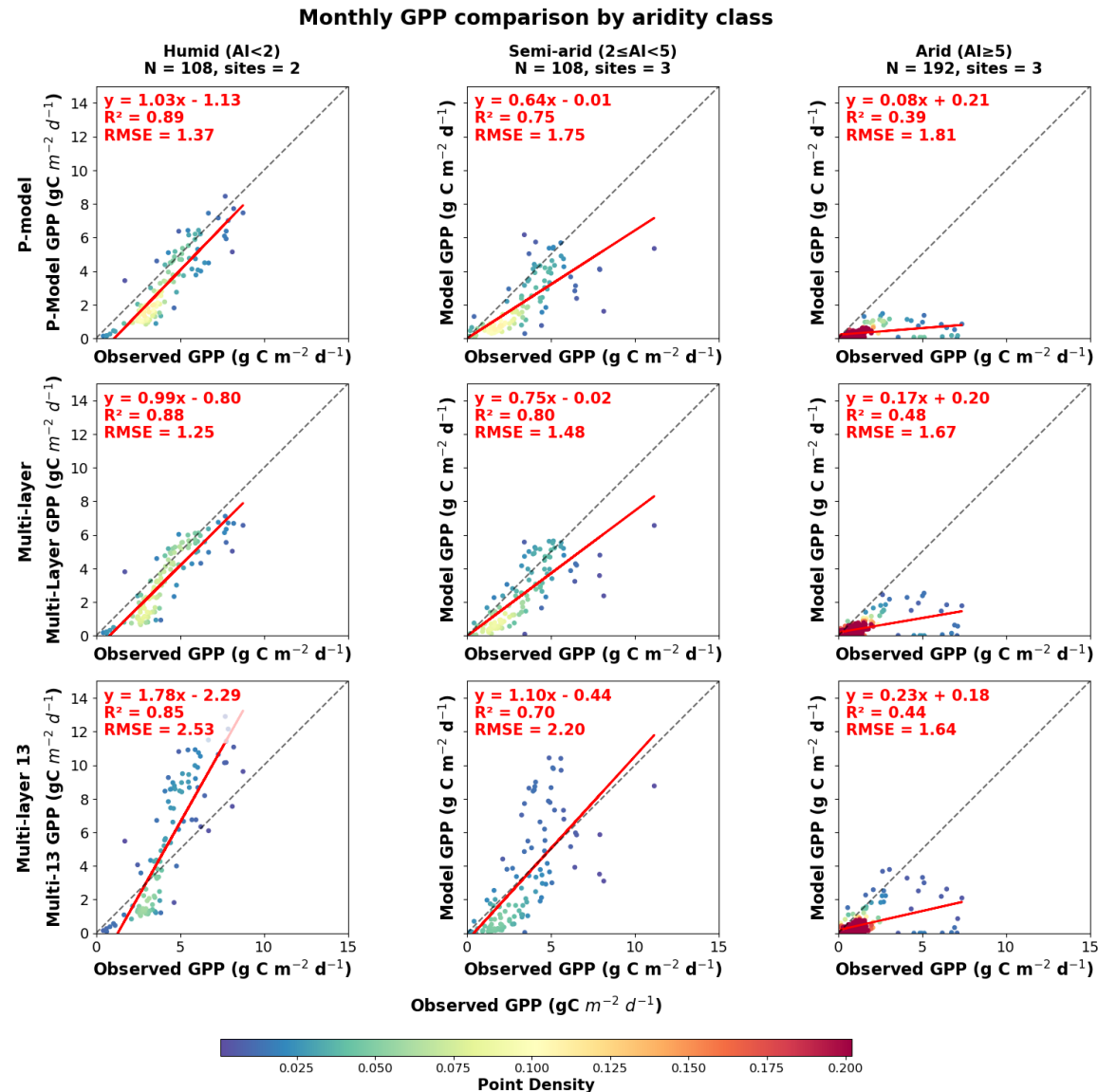


Monthly C₄ GPP

PJULES: $R^2 = 0.79$, $RMSE = 1.69$
GL7.0: $R^2 = 0.82$, $RMSE = 1.52$
UKESM1: $R^2 = 0.77$, $RMSE = 2.06$

- PJULES slope = 0.72: comparable to the 5-PFT multi-layer scheme (0.77)
- UKESM1 (13 PFTs) overestimates by ~20% (slope = 1.21) at high C₄ GPP

C4 humid-site performance similar to all schemes collapse at arid C4 sites



- PJULES sits closest to 1:1 at humid C4 sites (slope = 1.03, $R^2 = 0.89$)
- UKESM1 (13 PFTs) inflates humid C4 GPP by ~80% (slope = 1.78)
- All three schemes lose skill at semi-arid and collapse at arid ($R^2 < 0.5$, slope < 0.25)
- Same aridity bottleneck as C3: soil-moisture stress function (β) is the shared next step

What this means for JULES



Parameter-sparse

Replaces Collatz–Jacobs photosynthesis while keeping the wider JULES land-surface framework.



Carbon gains, water intact

Improves GPP with no degradation of water fluxes.



A clear next priority

Dry-site failure points to soil-moisture stress (β) as the process to fix next.

Looking Ahead: a JULES development pathway

- 1** Global configuration
Align interfaces, namelists and diagnostics; add documentation and regression tests
Site to global offline benchmarking
- 2** Coupled run
coupled sensitivity, with GPP, ET and energy diagnostics with GCMs
- 3** Strengthen JULES drought responses
Test aridity-adapted β and carbon–water coupling across dry sites and extremes
- 4** Dynamic LAI; phenology
Prognostic LAI from the P-model optimality framework, coupled to the sub-daily scheme



Scan for the paper

C₃ and C₄ share the optimality framework but differ in biochemical constraints

C3

$$\xi = \sqrt{\frac{\beta(K + \Gamma^*)}{1.6\eta^*}}$$
$$\chi = \frac{\Gamma^*}{c_a} + \left(1 - \frac{\Gamma^*}{c_a}\right) \frac{\xi}{\xi + \sqrt{D}}$$
$$m_j = \frac{c_a - \Gamma^*}{c_a + 2\Gamma^*}$$
$$m_c = \frac{c_i - \Gamma^*}{c_i + K}$$
$$\beta \approx 146 \text{ (C}_3 \text{ constant)}$$

C4

$$\xi = \sqrt{\frac{\beta K}{1.6\eta^*}}$$
$$\chi = \frac{\xi}{\xi + \sqrt{D}}$$
$$m_j = 1$$
$$m_c = \frac{\chi}{\chi + K/c_a}$$
$$\beta \approx 146/9 \approx 16.2 \text{ } (\beta_{C_3} : \beta_{C_4} = 9 : 1)$$

MECHANISTIC INTERPRETATION • C₃ retains photorespiration (Γ*) and Rubisco limitation; C₄ represents CO₂ concentration by setting Γ* ≈ 0 and modifying β. • Both pathways retain environment-driven χ/ξ and acclimation. • This is a parsimonious pathway distinction—not a claim that C₃ and C₄ are physiologically identical.