



# PREDICTING RESILIENCE THROUGH THE LENS OF COMPETING ADJUSTMENTS TO VEGETATION FUNCTION

A case study in South-Eastern Australia

Manon Sabot | Martin De Kauwe | Andy Pitman | et al.

# PLANT OPTIMALITY THEORY IS ADVANCING THE REPRESENTATION OF ECOSYSTEM FLUXES IN LAND SURFACE MODELS (LSMs)



Research

## Whole-plant optimality predicts changes in leaf nitrogen under variable CO<sub>2</sub> and nutrient availability

Silvia Caldararu<sup>1</sup> , Tea Thum<sup>1</sup> , Lin Yu<sup>1</sup> and Sönke Zachle<sup>1,2</sup>



Research



## Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate

Cleiton B. Eller<sup>1,2</sup> , Lucy Rowland<sup>1</sup> , Maurizio Mencuccini<sup>3,4</sup> , Teresa Rosas<sup>3,4</sup> , Karina Williams<sup>5</sup> , Anna Harper<sup>6</sup> , Belinda E. Medlyn<sup>7</sup> , Yael Wagner<sup>8</sup> , Tamir Klein<sup>8</sup> , Grazielle S. Teodoro<sup>9</sup> , Rafael S. Oliveira<sup>2</sup> , Ilaine S. Matos<sup>10</sup> , Bruno H. P. Rosado<sup>10</sup> , Kathrin Fuchs<sup>11</sup> , Georg Wohlfahrt<sup>12</sup> , Leonardo Montagnani<sup>13</sup> , Patrick Meir<sup>14,15</sup> , Stephen Sitch<sup>1</sup> and Peter M. Cox<sup>6</sup>

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## A new version of the CABLE land surface model (Subversion revision r4601) incorporating land use and land cover change, woody vegetation demography, and a novel optimisation-based approach to plant coordination of photosynthesis

Vanessa Haverd<sup>1</sup>, Benjamin Smith<sup>1,2</sup>, Lars Nieradzik<sup>3</sup>, Peter R. Briggs<sup>1</sup>, William Woodgate<sup>4</sup>, Cathy M. Trudinger<sup>5</sup>, Josep G. Canadell<sup>1</sup>, and Matthias Cuntz<sup>6</sup>



Research

## Plant profit maximization improves predictions of European forest responses to drought

Manon E. B. Sabot<sup>1</sup> , Martin G. De Kauwe<sup>1,2</sup> , Andy J. Pitman<sup>1</sup> , Belinda E. Medlyn<sup>3</sup> , Anne Verhoef<sup>4</sup> , Anna M. Ukkola<sup>5</sup> and Gab Abramowitz<sup>1</sup>



# AND IT IS ALSO BEING USED TO FORECAST ECOSYSTEM RESILIENCE IN THE FACE OF CLIMATE CHANGE

## ECOLOGY LETTERS

Ecology Letters, (2018)

doi: 10.1111/ele.13136

### LETTER

### Tree carbon allocation explains forest drought-kill and recovery patterns

A. T. Trugman,<sup>1\*</sup> M. Detto,<sup>2</sup>  
M. K. Bartlett,<sup>2</sup> D. Medvigy,<sup>3</sup>  
W. R. L. Anderegg,<sup>1</sup> C. Schwalm,<sup>4,5</sup>  
B. Schaffer<sup>6</sup> and S. W. Pacala<sup>2</sup>



Stomatal optimization based on  
improves land surface model sim  
to climate

Cleiton B. Eller<sup>1,2</sup> , Lucy Rowland<sup>1</sup> , Maurizio Menc  
Anna Harper<sup>6</sup> , Belinda E. Medlyn<sup>7</sup> , Yael Wagner<sup>8</sup>   
Rafael S. Oliveira<sup>2</sup> , Ilaine S. Matos<sup>10</sup> , Bruno H. P. R  
Leonardo Montagnani<sup>13</sup> , Patrick Meir<sup>14,15</sup> , Stephen



### Towards species-level forecasts of drought-induced tree mortality risk

Martin G. De Kauwe<sup>1</sup> , Manon E. B. Sabot<sup>2,3</sup> , Belinda E. Medlyn<sup>4</sup> , Andrew J. Pitman<sup>2,3</sup> ,  
Patrick Meir<sup>5</sup> , Lucas A. Cernusak<sup>6</sup> , Rachael V. Gallagher<sup>4</sup> , Anna M. Ukkola<sup>2,3</sup> , Sami W. Rifai<sup>2,3</sup> and  
Brendan Choat<sup>4</sup>

Anna M. Ukkola<sup>5</sup> and Gab Abramowitz<sup>1</sup>

Geosci. Model Dev., 11, 2995–3026, 2018

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A new version of the CABLE land surface model (Subversion  
revision r4601) incorporating land use and land cover change

### The impact of rising CO<sub>2</sub> and acclimation on the response of US forests to global warming

John S. Sperry<sup>a,1</sup>, Martin D. Venturas<sup>a,1,2</sup>, Henry N. Todd<sup>a</sup>, Anna T. Trugman<sup>a,b</sup>, William R. L. Anderegg<sup>a</sup>, Yujie Wang<sup>a</sup>,  
and Xiaonan Tai<sup>c</sup>

Research

Research

improves predictions of European

, Andy J. Pitman<sup>1</sup> , Belinda E. Medlyn<sup>3</sup> , Anne Verhoef<sup>4</sup> ,

Geoscientific  
Model Development  
Open Access  
EGU

# SO, WHAT IS PLANT OPTIMALITY THEORY?

From the C perspective:

More photosynthesis  $\Rightarrow$  More growth

But what about limitations to growth? Need to account for:

H<sub>2</sub>O

Nutrients

Drought legacies



Optimisation theories typically trade off a photosynthetic or growth 'gain' function with a 'cost' function accounting for one or multiple limiting factors.





Optimisation theories typically trade off a photosynthetic or growth 'gain' function with a 'cost' function accounting for one or multiple limiting factors.

## BUT IN LSMs...



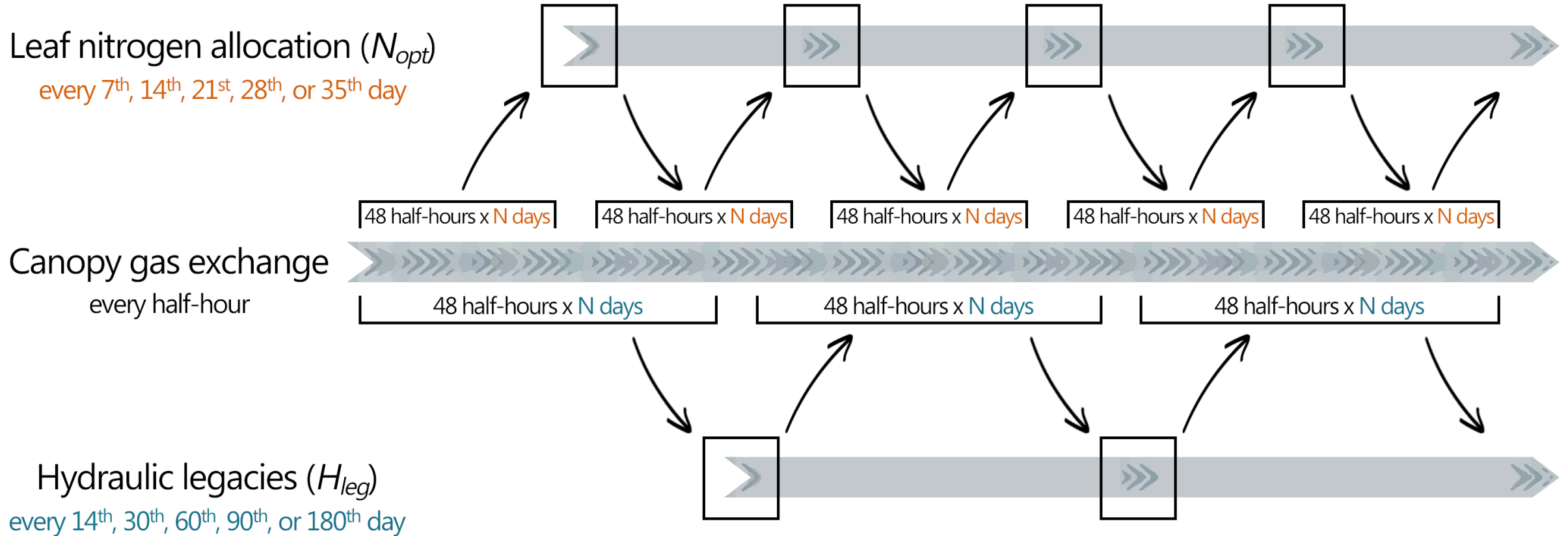
Structural limitations may prevent the effective combination of multiple limiting factors into a single 'cost' function and may also prevent reliance on a single overarching optimisation objective.

Testing has focused on optimality principles accounting for a given limiting resource in isolation, e.g., the cost of limited water supply OR that of limited nitrogen availability.

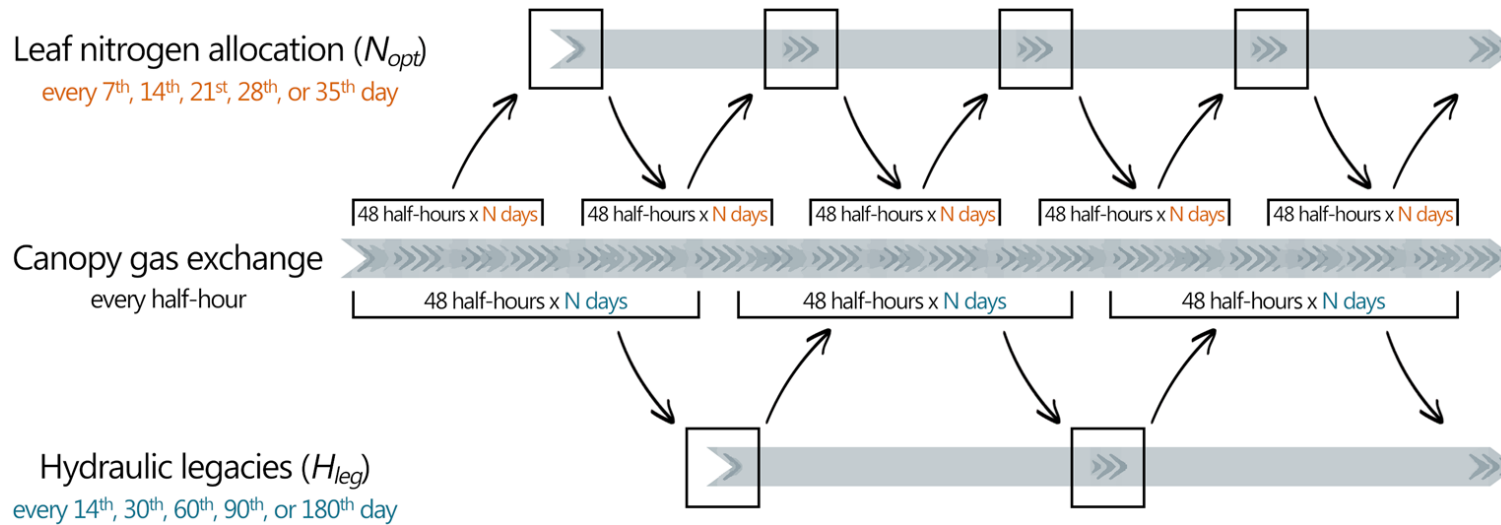
## WE WANTED TO:

- Know whether contrasting optimisation approaches could be applied together, including when hydraulic legacies from climate extremes affect optimisation outcomes.
- Know whether we could infer the timescales over which vegetation functions adjust to maximise resource investment and/or resilience.
- Explore the relationship between drought-driven foliage dynamics and plant hydraulic function.

# WE INCORPORATED COMPETING OPTIMISATION PRINCIPLES AND HYDRAULIC LEGACIES IN A LSM



# WE INCORPORATED COMPETING OPTIMISATION PRINCIPLES AND HYDRAULIC LEGACIES IN A LSM



optimisation of leaf nitrogen allocation  
(5 possible timeframes of application,  
optional routine)

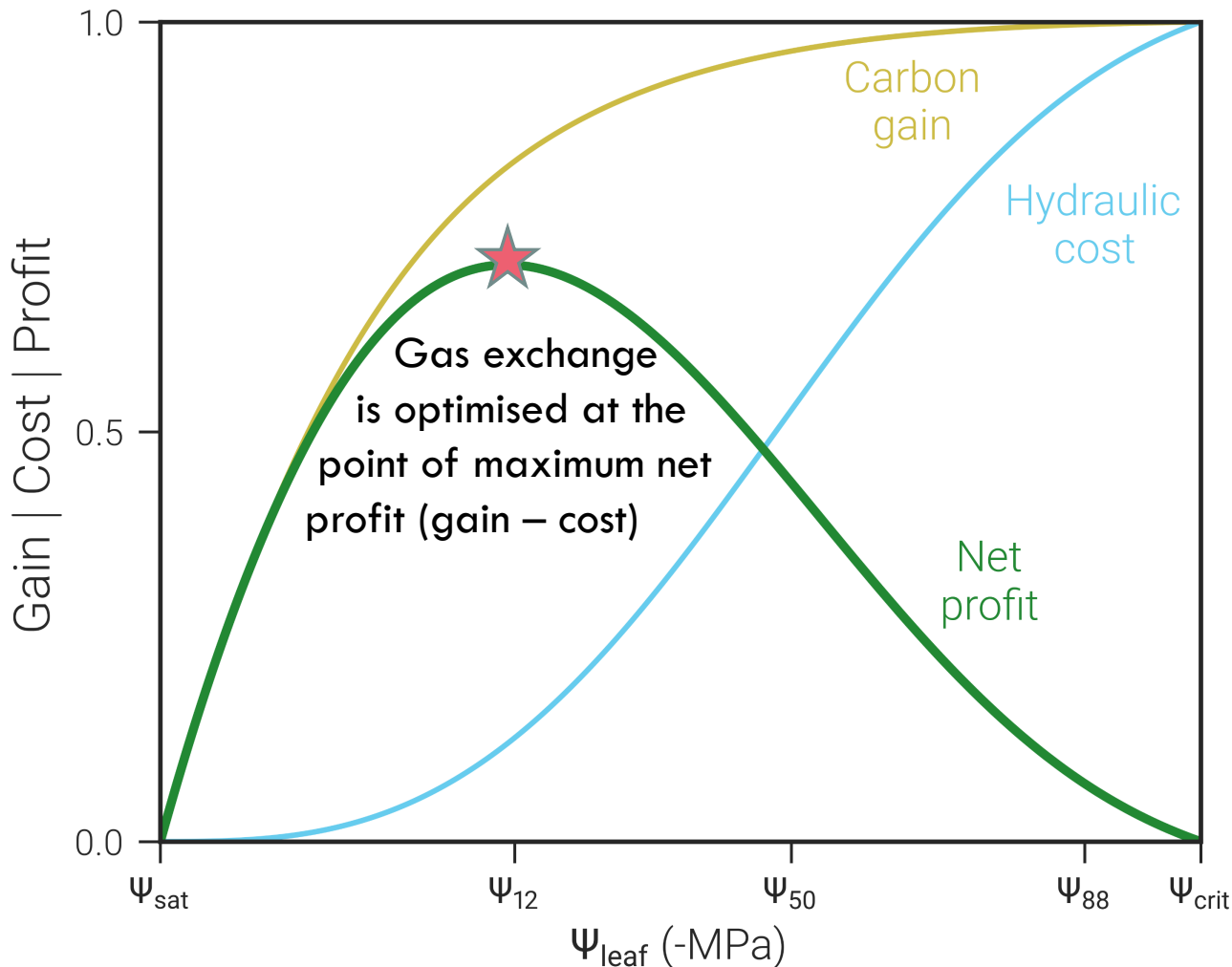
+ canopy gas exchange optimisation  
(every half hour, mandatory / default  
routine)

+ hydraulic legacies (5 possible  
timeframes of application, optional  
routine)

⇒ 36 simulation experiments were run to identify the timescales over which competing adjustments to vegetation function interact most consistently



# CANOPY GAS EXCHANGE



Canopy transpiration and photosynthesis are set by an instantaneous stomatal optimisation principle which trades off possible carbon gains with a hydraulic cost associated with maintaining leaf stomates open.

See Sperry et al., PC&E, 2017 and Sabot et al., New Phytol., 2020 for further information on this optimality principle.

# OPTIMAL LEAF N ALLOCATION



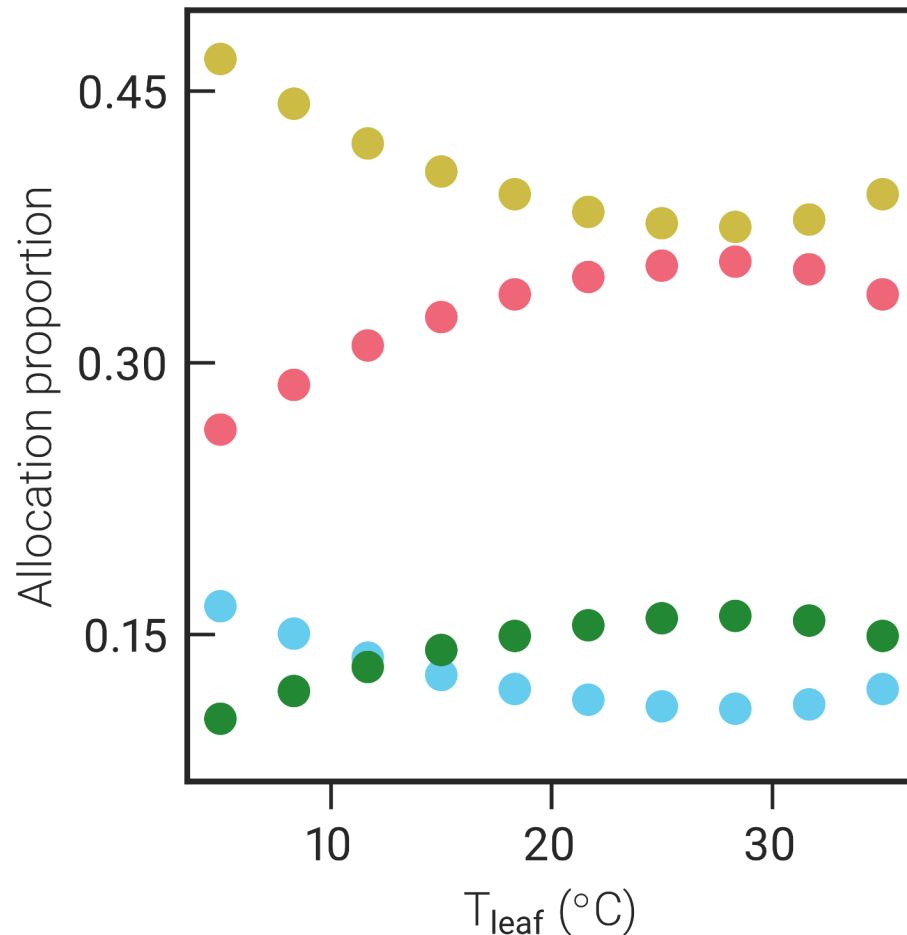
Photosynthetic N:

Chlorophyll ( $N_c$ )

Electron-transport ( $N_e$ )

Rubisco ( $N_r$ )

Other soluble proteins ( $N_s$ )



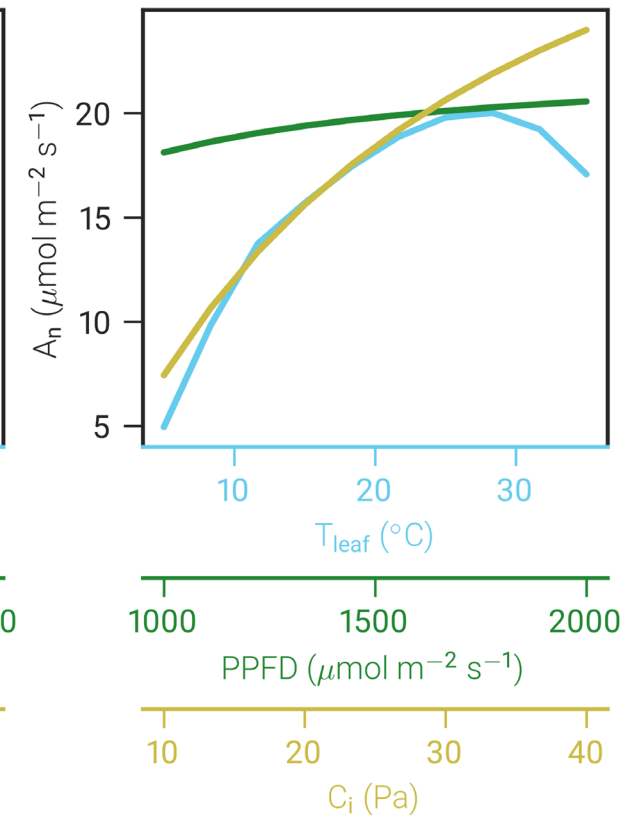
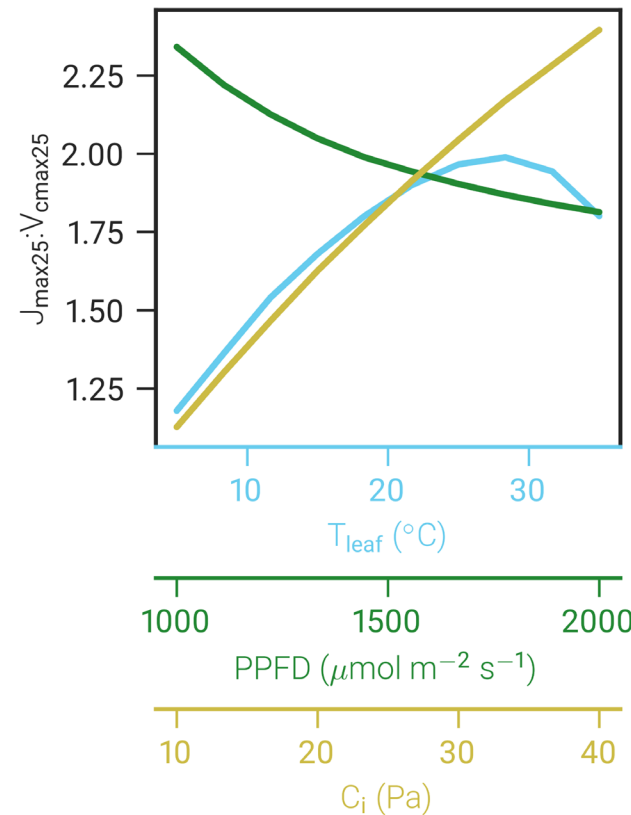
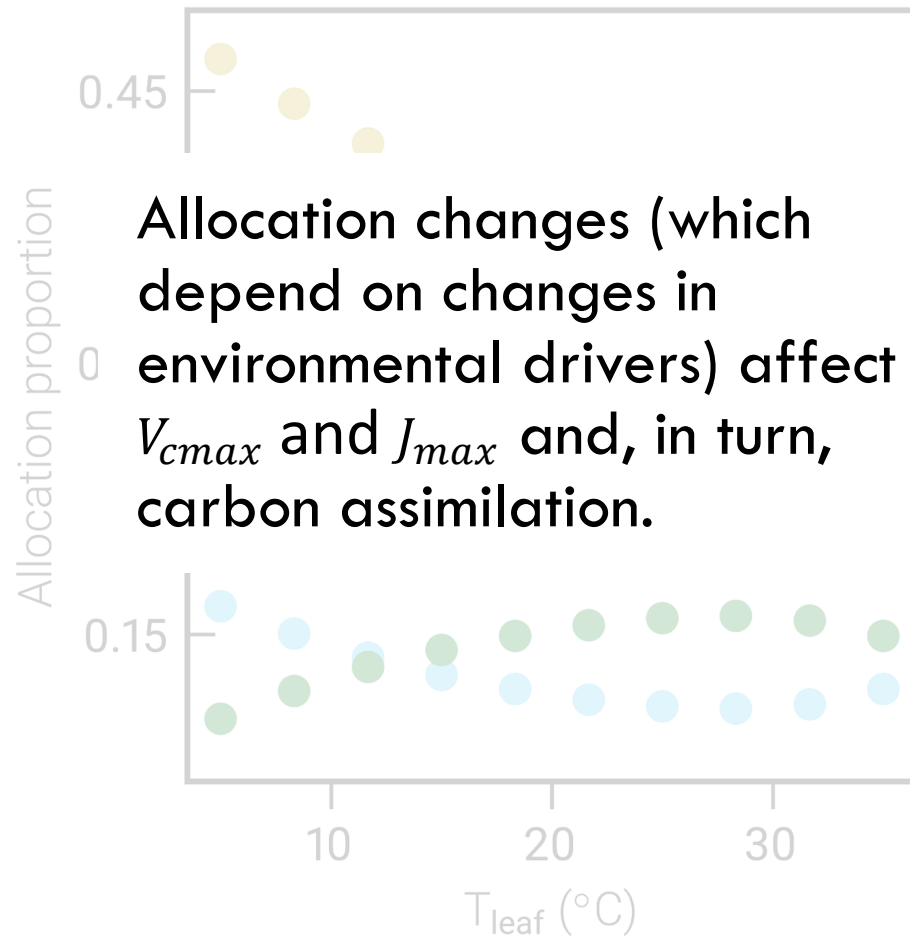
The amount of leaf nitrogen involved in photosynthesis and its allocation to photosynthetic compounds are optimised to account for antecedent environmental conditions (light, temperature, water availability) and leaf phenology (LAI) over a chosen period (N preceding days).

This optimality principle is based on earlier work by Medlyn, Aust. J. Plant Physiol., 1996 (but it is not identical).

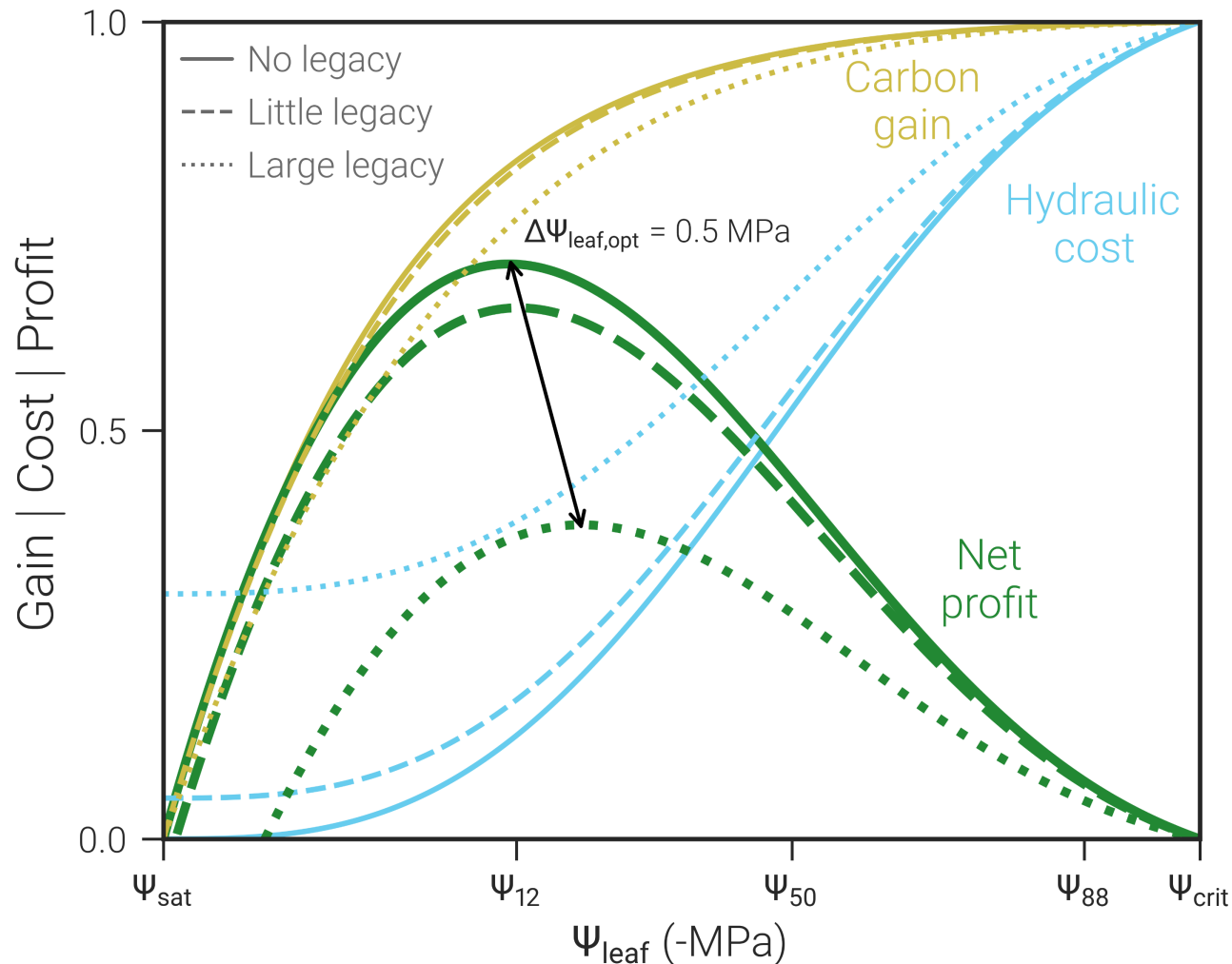
# OPTIMAL LEAF N ALLOCATION



Photosynthetic N:  
 Chlorophyll ( $N_c$ )  
 Electron-transport ( $N_e$ )  
 Rubisco ( $N_r$ )  
 Other soluble proteins ( $N_s$ )



# HYDRAULIC LEGACIES



Delayed and imperfect xylem recovery from past embolism are accounted for as ‘damage’ to the hydraulic pathway. Hydraulic legacies directly affect canopy gas exchange, and they indirectly affect the leaf nitrogen allocation routine via feedback through the canopy gas exchange routine.

See Lu et al., New Phytol., 2020 for the expression of a ‘damaged’ vulnerability curve.



# WE TESTED OUR MODEL AT EucFACE

**Water- & nutrient-limited site**

- + 3 ambient and 3 elevated [CO<sub>2</sub>] plots**
- + variable LAI and soil texture (moisture) across plots**
- + lots of observational data (2013 – 2020)**

# PREDICTABLE AND COHERENT ADJUSTMENTS TO FUNCTION

- Compared to our default model (canopy gas exchange alone), accounting for leaf N allocations ( $N_{opt}$ ) and/or hydraulic legacies ( $H_{leg}$ ) reduced the simulated WUE (ratio of carbon assimilation to transpiration) across site plots, to varying degrees depending on soil moisture, LAI, and  $[CO_2]$ .
- $N_{opt}$  drove change in the simulated WUE, contributions from  $H_{leg}$  were small.
- The higher the frequencies of simulated functional adjustments (e.g.,  $N_{opt}$  applied every 7<sup>th</sup> day rather than every 35<sup>th</sup> day), the less water-use efficient the model.



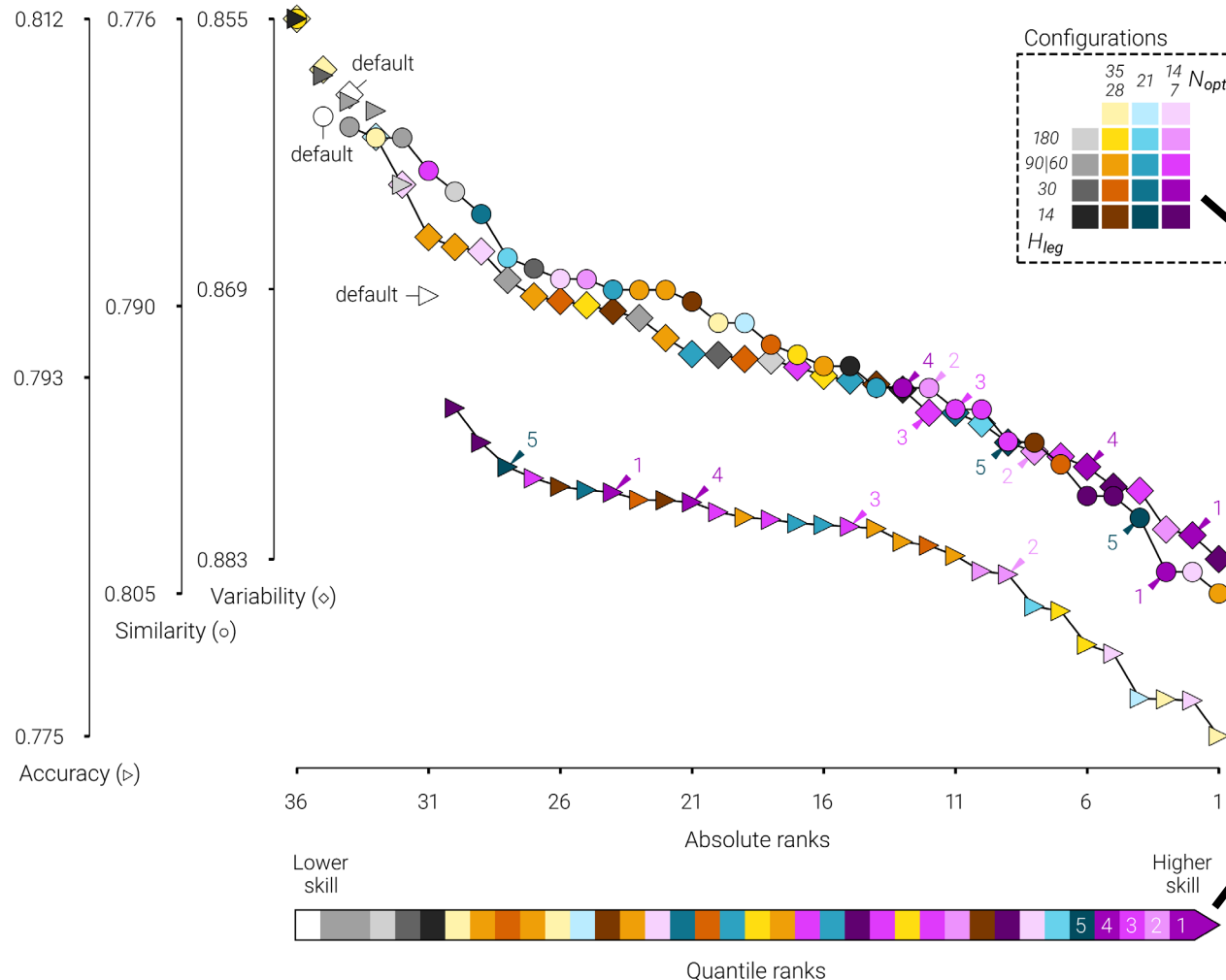
# MORE FREQUENT ADJUSTMENTS TO FUNCTION = INCREASED MODEL PERFORMANCE

Three statistical metrics were used to assess the model configurations' ability to capture daily observations of canopy transpiration:

- Accuracy: Mean Absolute Scaled Error, i.e., whether model predictions are more skilful than one-step forecasts of the observations
- Similarity: overlap between modelled and observed binned distributions
- Variability: ratio of modelled to observed sample deviation

Skill across these three metrics was summarised by quantile ranks, which consider a model configuration's performance relative to that of all other model configurations within each metric.

# MORE FREQUENT ADJUSTMENTS TO FUNCTION = INCREASED MODEL PERFORMANCE



The best overall model configuration combined  $H_{leg}$  applied every 30<sup>th</sup> day with  $N_{opt}$  applied every 7<sup>th</sup> day, in addition to accounting for canopy gas exchange every half-hour.



# WE WANTED TO KNOW:

- Whether contrasting optimisation approaches could be applied together, including when hydraulic legacies from climate extremes affect optimisation outcomes.

Different model configurations affected WUE simulations in a predictive and interpretable manner along axes of variation in soil moisture, LAI, and  $[\text{CO}_2]$ .

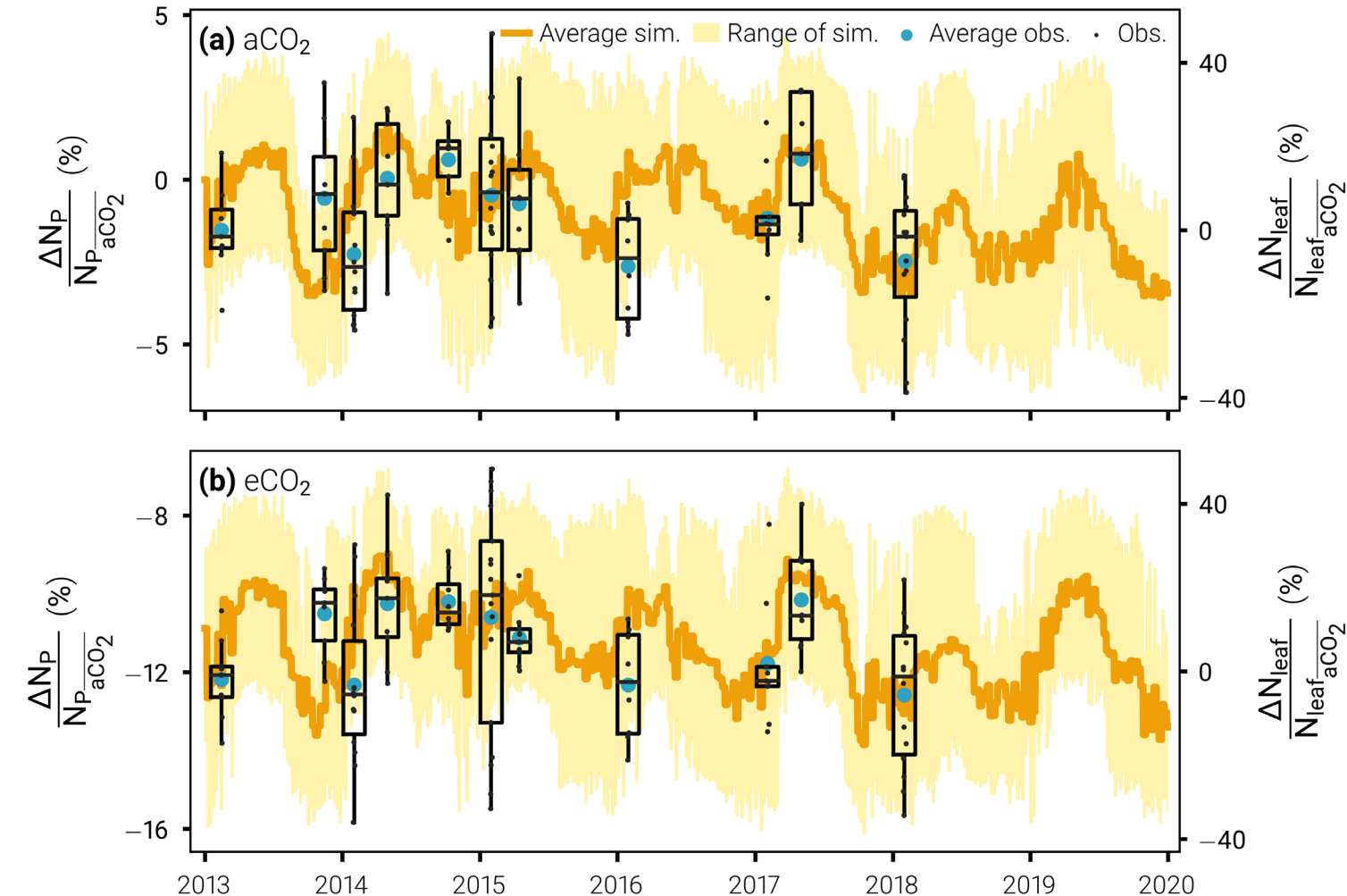
- Whether we could infer the timescales over which vegetation functions adjust to maximise resource investment and/or resilience.

Across model configurations, more frequent adjustments to function typically increased model performance.

**⇒ WHAT DID THE SIMULATED ADJUSTMENTS TO FUNCTION LOOK LIKE?**

# PREDICTED ADJUSTMENTS TO FUNCTION

(Best model configuration)



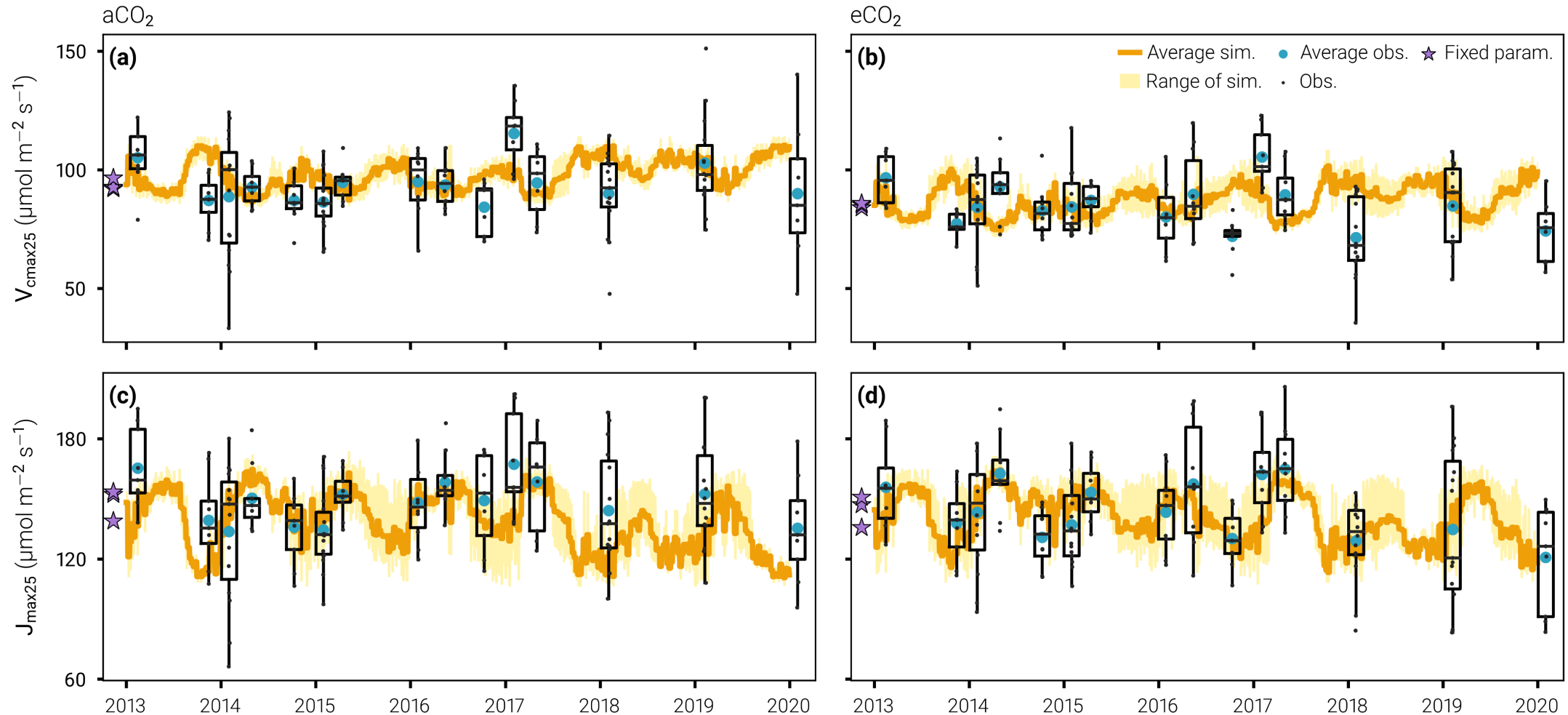
➤ Good agreement between the dynamics of the simulated leaf nitrogen directly involved in photosynthesis ( $N_p$ ) and those of the observed total leaf nitrogen ( $N_{leaf}$ ).

$\Delta N_p$ : difference between the time-varying  $N_p$  and the average  $N_p$  from across the aCO<sub>2</sub> plots at the onset of the simulations ( $N_{p_{aCO_2}}$ ).

$\Delta N_{leaf}$ : difference between the time-varying  $N_{leaf}$  and the average  $N_{leaf}$  at the aCO<sub>2</sub> rings during the first measurement campaign in 2013 ( $N_{leaf_{aCO_2}}$ ).

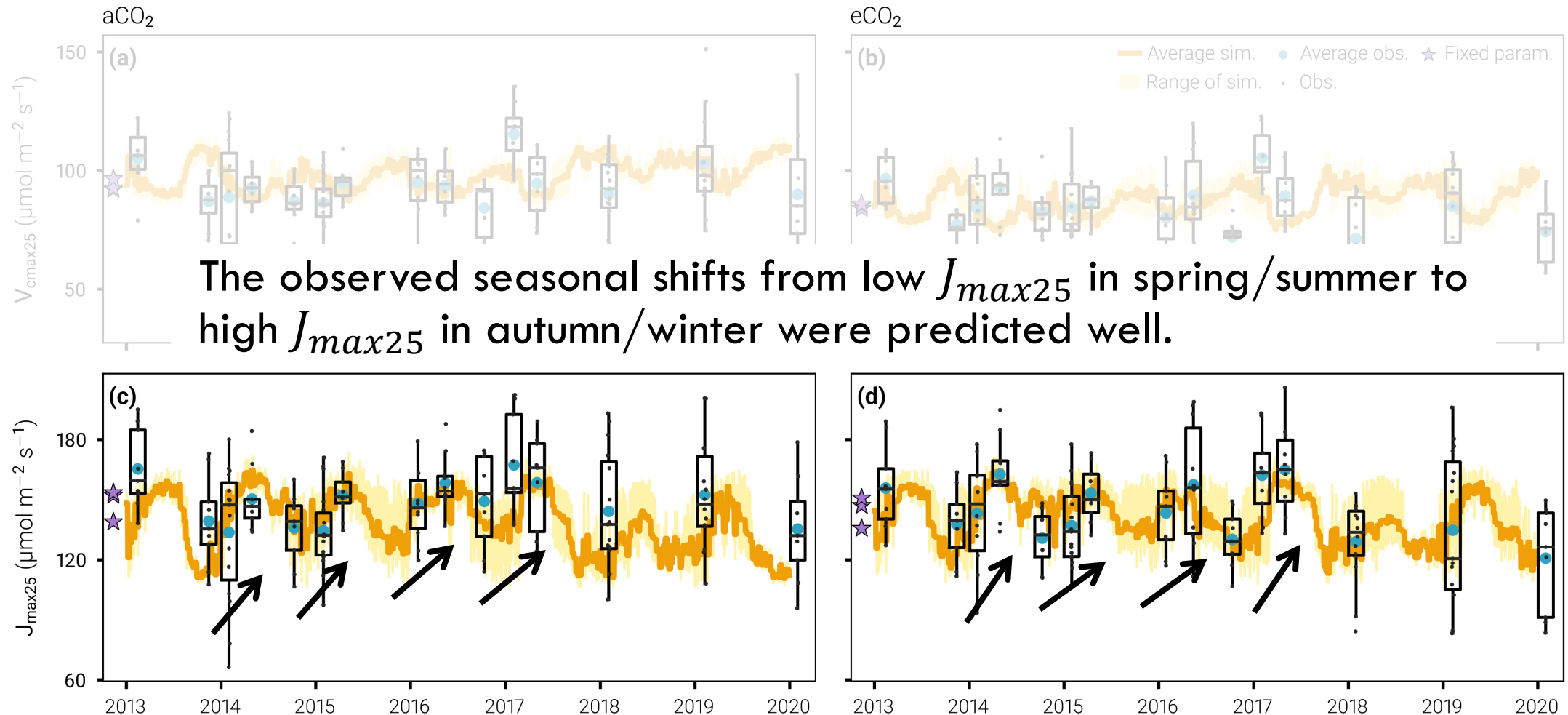
# PREDICTED ADJUSTMENTS TO FUNCTION

(Best model configuration)



# PREDICTED ADJUSTMENTS TO FUNCTION

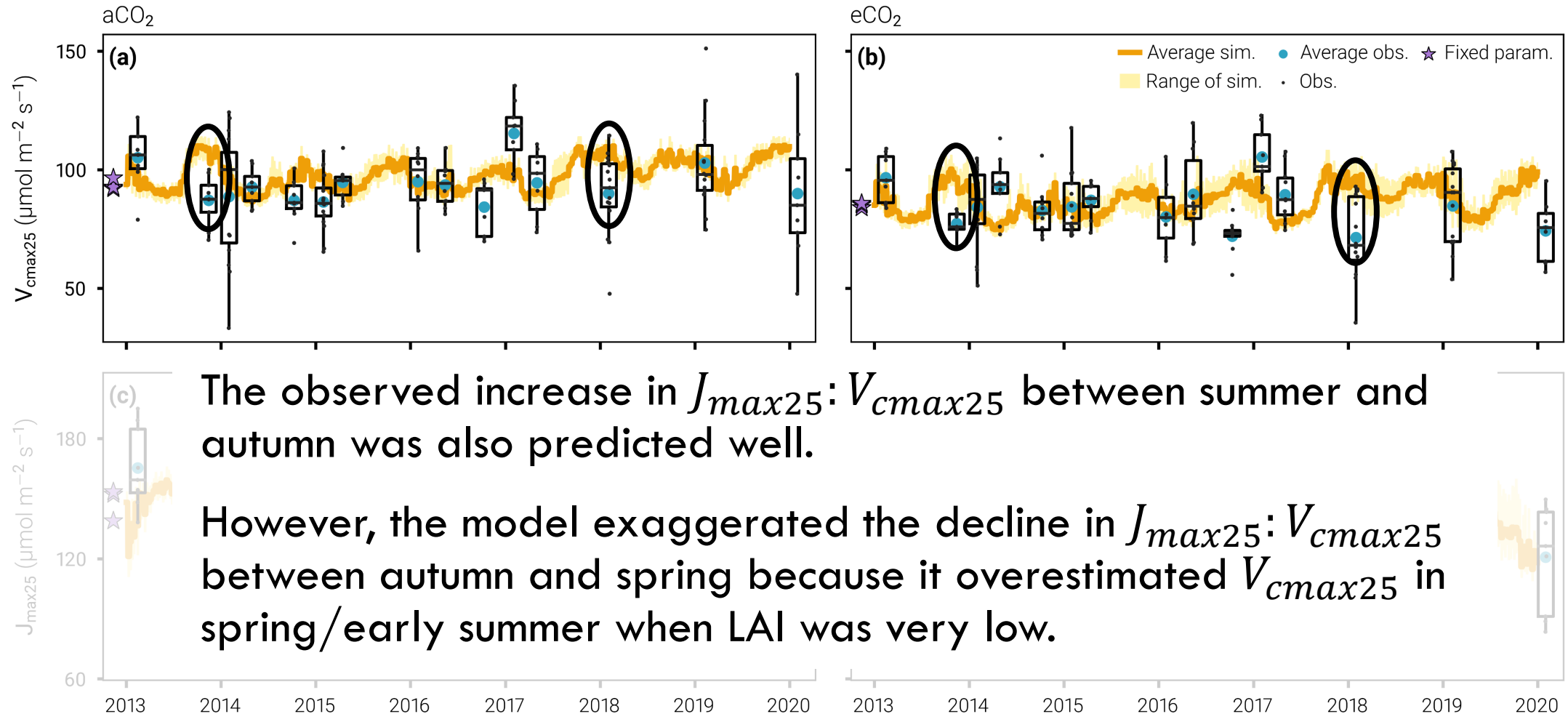
(Best model configuration)





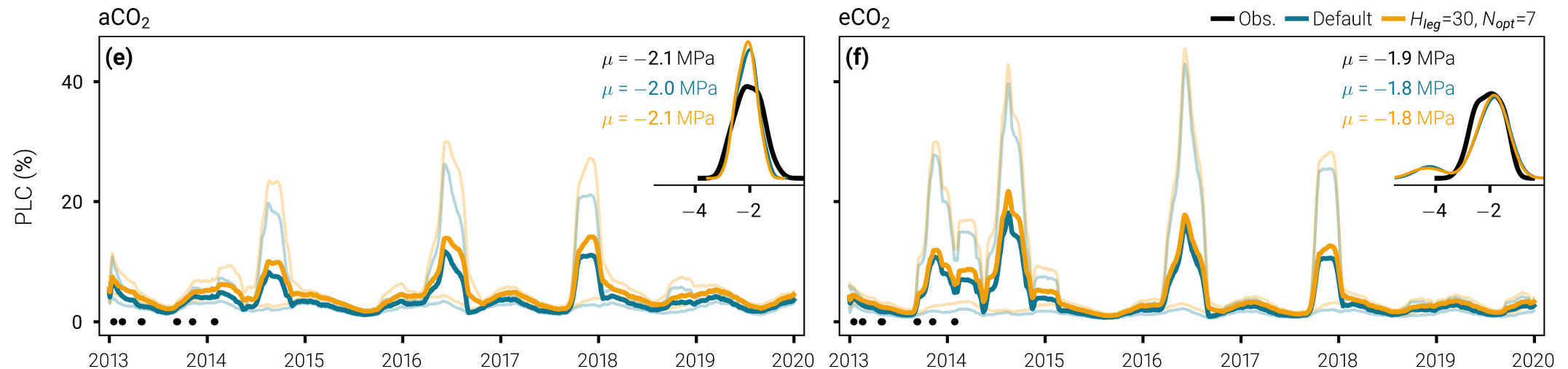
# PREDICTED ADJUSTMENTS TO FUNCTION

(Best model configuration)



# PREDICTED ADJUSTMENTS TO FUNCTION

(Best model configuration)

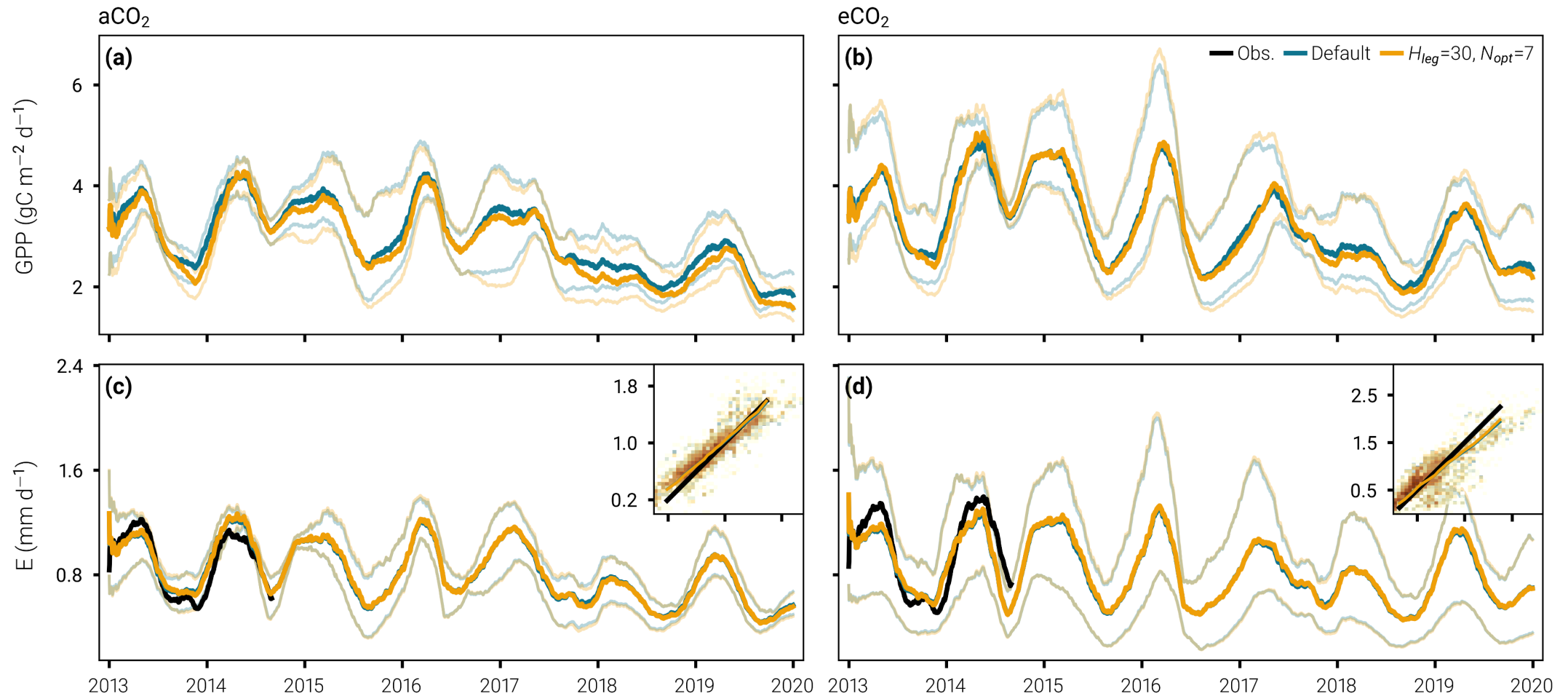


Leaf water potential was fairly well captured (inset density plots), for the dates at which observations were collected in 2013/2014 (marking dots along the x- axis).

Significant percentage losses of hydraulic conductivity (PLC) but small hydraulic legacy effect (<15% extra PLC in the best model configuration compared to the default, lasting no more than 2 months).

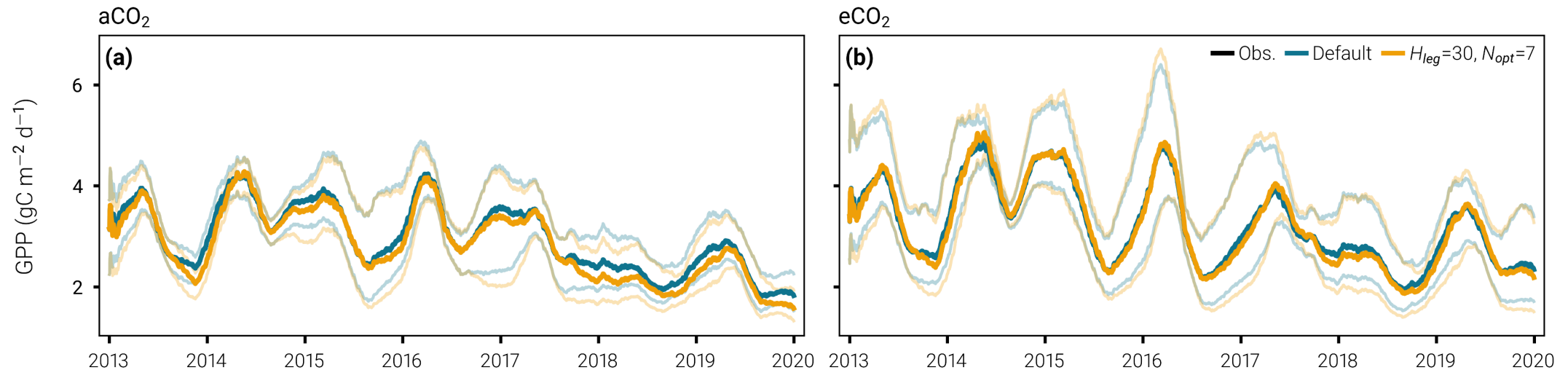
# PREDICTED ADJUSTMENTS TO FUNCTION

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# PREDICTED ADJUSTMENTS TO FUNCTION

(Best model configuration)



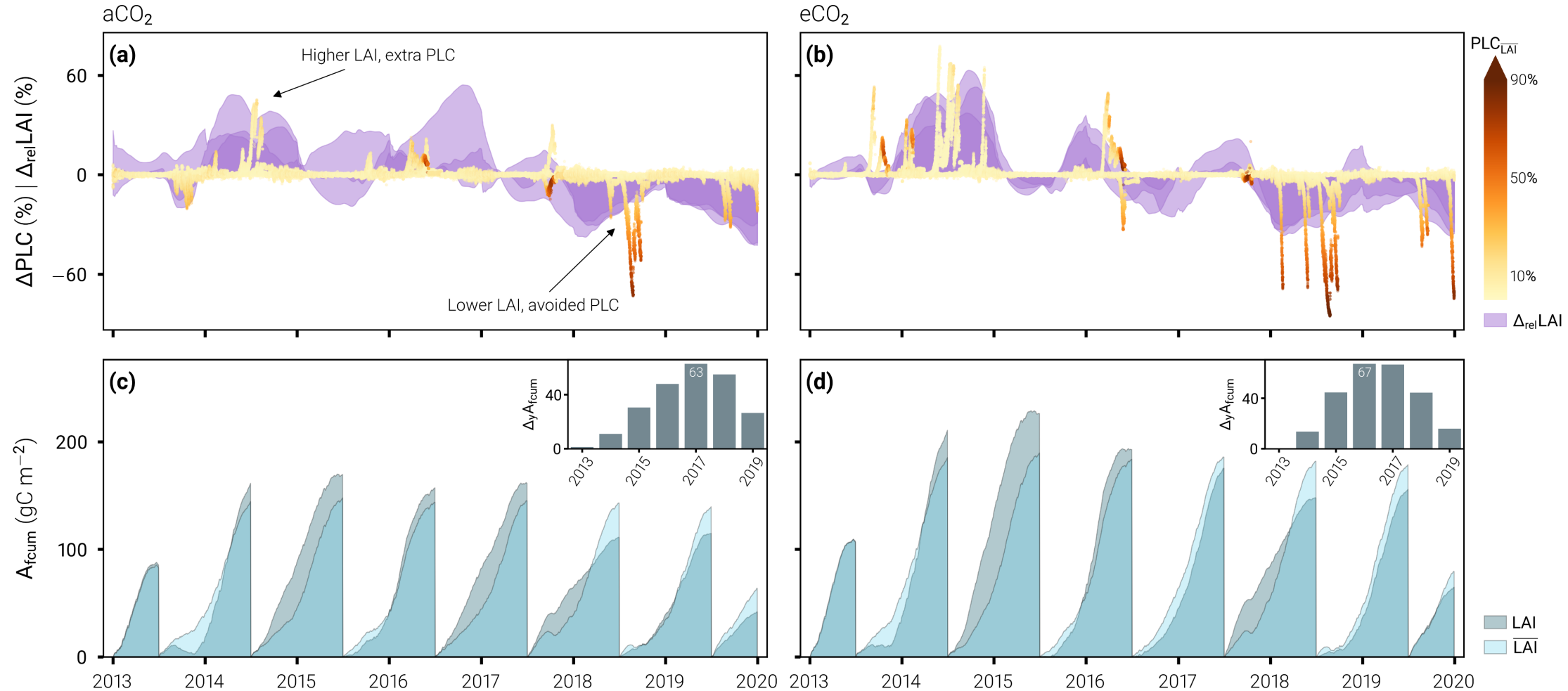
Limited impacts on the canopy fluxes, although the GPP simulated by the best model configuration could be >10% lower than the default's in spring/summer/dry years.

Departure from the default model configuration more pronounced at the aCO<sub>2</sub> than at the eCO<sub>2</sub> plots: greater CO<sub>2</sub> fertilisation effect simulated by accounting for N<sub>opt</sub> and H<sub>leg</sub> (+13.1% GPP between aCO<sub>2</sub> and eCO<sub>2</sub> in the best model vs. +9.6% in the default).

# UNDERSTANDING THE LACK OF SIMULATED HYDRAULIC LEGACY: FOLIAGE RESPONSE TO DROUGHT

(Best model  
configuration)

Simulations  
driven by  
the actual  
LAI minus  
simulations  
driven by  
an average  
phenology  
of the  
observed  
LAI ( $\overline{\text{LAI}}$ ).

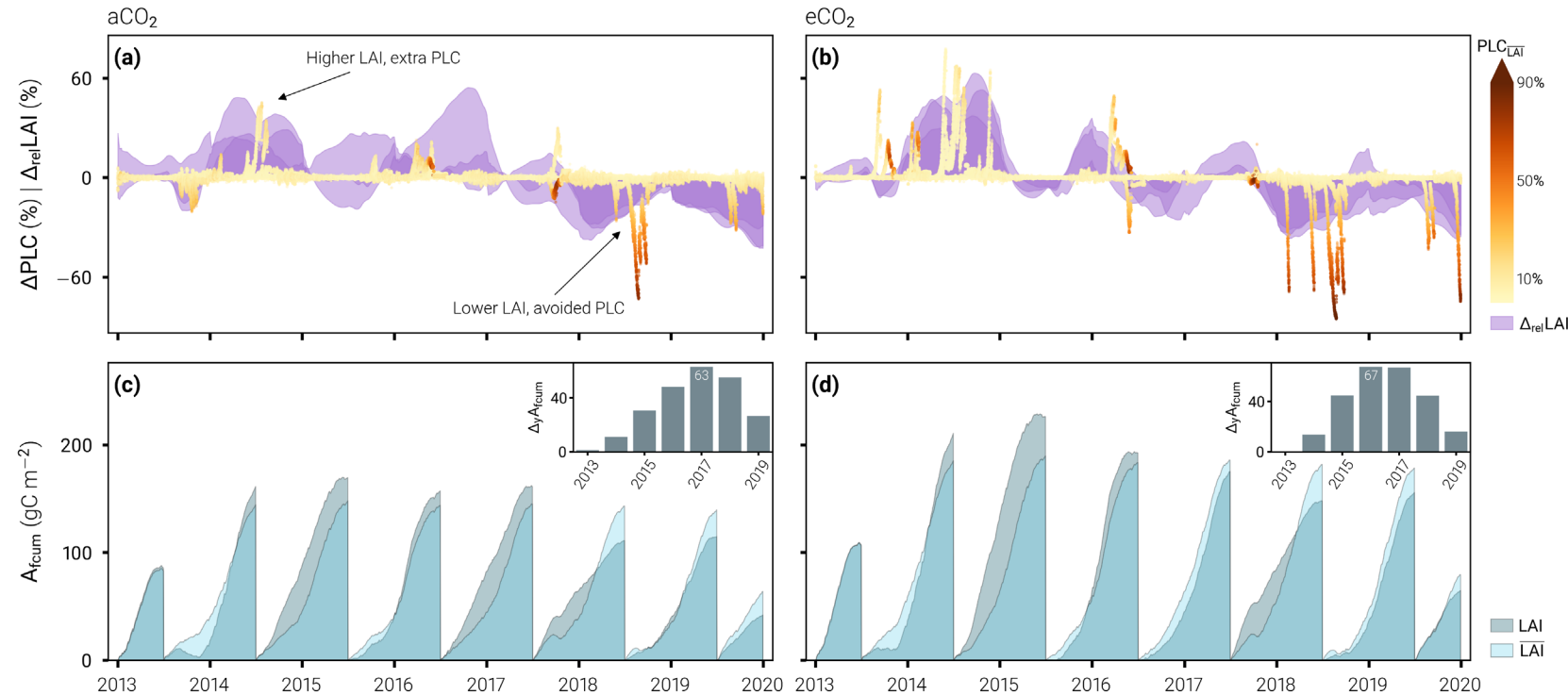


# UNDERSTANDING THE LACK OF SIMULATED HYDRAULIC LEGACY: FOLIAGE RESPONSE TO DROUGHT

(Best model  
configuration)

Higher than average LAI  
(wet years) led to extra  
PLC, and to increasing  
carbon storage ( $A_{fcum}$ ) until  
c. 2016 ( $eCO_2$ ) or c. 2017  
( $aCO_2$ ).

After those years (dry  
years), the trend was  
reversed.



⇒ Drought legacy effects were accounted for through LAI dynamics that prevented hydraulic damage.



# TAKEAWAY

Competing optimisation approaches affected model simulations in a predictive manner, via interactive physiological adjustments that could also be interpreted theoretically.

Significant canopy PLC, but no sustained hydraulic damage thanks to LAI dynamics that averted hydraulic conductivity loss.

**How to capture LAI dynamics during drought is a key research frontier for predictions of canopy dieback and/or plant mortality.**

Don't hesitate to get in touch :)  
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