

The authors thank the reviewers for thorough reading and comments to the manuscript. Please find responses to specific comments below.

Note: The authors added a full year of data (2017) to the updated manuscript.

**Reviewer 1 comment:**

The authors use additional vegetation/leaf level measurements of photosynthesis and conductance to strengthen their assertions of flux dynamics, although the discussion of these results feels rather like a tangential addition. These findings could be more strongly incorporated into the discussion of differences in fluxes from old and young leaves and into the discussion of the influence of diurnal cycles and hysteresis on seasonal trends.

[...] A more complete discussion of the old and young leaf-level data would likewise improve support for the conclusion that GPP was limited by leaf age in the summer. Following these additions, strong conclusions regarding the influence of global climate change on the future carbon exchange in these forests can be drawn.

**Response:**

Thank you for this suggestion. Although we lack site-specific data on leaf age effects on  $A_{\max}$ , we incorporated a relevant reference to the discussion: “In Australian woodlands, PC ( $A_{\max}$ ) of leaves was also found to decrease with leaf age,  $A_{\max}$  declined by 30% on average between young and old leaves, for 10 different species (Reich et al., 2009).”, L391-393. This suggests that both leaf age and LAI are important in limiting GPP at our site.

**Reviewer 1 comment:**

The work of A. Griebel on anisohydricity induced by mistletoes in these ecosystems could be drawn upon in greater detail during the discussion of leaf specific measurements and trends in seasonal response to moisture availability as it is likely as highly relevant to ecosystem carbon dynamics as it is to water dynamics.

**Response:**

Thank you for this suggestion. We would like to include discussion of the effects of biotic disturbance by mistletoe at our site, but these data are not yet publicly available. Moreover, detailed leaf-level responses are beyond the scope of this manuscript.

**Reviewer 1 comment:**

The authors conclude that diurnal patterns of NEE, GPP, and ER have central roles in determining the seasonal carbon source/sink dynamics, but a stronger analysis would significantly bolster this claim – a wavelet coherence analysis of the time series could be an informative addition that would support this conclusion more thoroughly.

**Response:**

Thank you for this suggestion. We conducted a wavelet coherence analysis to assess the coherence between GPP and D (figure S11). We did not add the figure to the main text, as the observed coherence between GPP and D is mostly due to daily cycle (GPP and D high during the day, low during night) and annual cycle (GPP and D high in summer, low in winter). Moreover, D covaries with other drivers such as PPFD and  $T_a$ , which makes it difficult to attribute coherence solely to D. Some interesting coherence appeared at weekly and monthly period. Furthermore, wavelet coherence is useful to quantify phase lags, but this is beyond the scope of the current manuscript.

**Reviewer 1 comment:**

Lastly, while this paper makes a significant contribution without it, an analysis of GPP in comparison to solar induced fluorescence (SIF) which has been recently shown as a better proxy for GPP than NDVI may prove very interesting.

**Response:**

Thank you for this suggestion. We note that EVI was better than NDVI for predicting PC and canopy conductance at our site. However, SIF analysis is beyond the scope of our work.

**Reviewer 1 comment:**

L243: Were leaves actually measured at 1.5km height as this sentence suggests? From what light environment were measured leaves collected?

**Response:**

Thank you for pointing out the typo. We also removed the detailed of leaf gas exchange measurement from section 2.13, L256-258, as we used previously published data.

**Reviewer 2 comment:**

Please eliminate the use of the diffusely defined term “atmospheric drought”. A term like “atmospheric demand” is more precise and appropriate.

**Response:**

Amended. L30, 33, 67, 307, 341, 372 and 462

**Reviewer 2 comment:**

Is it really true that the canopy height is ~25 m (L105) and the top of the profile and eddy covariance system is 29 m? This is rather close to a tall canopy for an eddy covariance application for observing ecosystem fluxes. A check of the site description is needed, and if indeed these numbers correct, a clearer presentation and discussion of the implications on representativeness of reported fluxes and analyses is in order.

**Response:**

We agree that our initial statement was misleading, so we used airborne LiDAR data to inspect the structural canopy properties within the footprint of the flux tower and have done an analysis of the cospectra of  $w$  and  $\text{CO}_2$  to assess any influence of the instrument height above the canopy on the turbulent transport characteristics (figure S3). We added a figure that summarizes the canopy structure as a height profile of the frequency of LiDAR returns to the supplements (figure S1) and amended the canopy description in section 2.1, L101-109, as follows:

“The flux tower is in a mature dry sclerophyll forest, with  $140 \text{ Mg C ha}^{-1}$  aboveground biomass and stand density of  $\sim 500 \text{ trees ha}^{-1}$ . The stand hosts a large population of mistletoe (*Amyema miquelii*), which is decreasing in abundance with increasing distance to the flux tower. The canopy structure comprises three strata, and the predominant canopy tree species are *Eucalyptus moluccana* and *E. fibrosa*. While individual trees can exceed 25 m height, an airborne LiDAR survey from November 2015 indicates an average canopy height of  $\sim 24 \text{ m}$  within a 300 m radius of the flux tower (supplement figure S1). The mid-canopy stratum (5-12 m) is dominated by *Melaleuca decora* and the understory is dominated by *Bursaria spinosa* with various shrubs, forbs, grasses and ferns present in lower abundance.”

Also, we added more details regarding the turbulent fluxes quality in the section 2.4, L163-165

“Although the tower height (29m) is rather close to the average canopy height (24m), cospectra analysis showed good quality turbulent fluxes (the high frequency followed the  $-4/3$  slope, thus we did not find any indications of systematic dampening in the cospectra, see figure S3).”

**Reviewer 2 comment:**

Was NDVI measured at the site or was a satellite product used? What was the rationale for using only NDVI versus EVI (or checking both)?

**Response:**

We used LANDSAT satellite products. We replaced NDVI with EVI in the main document, as it appeared to be more closely related to canopy dynamics at the site, and moved NDVI to the supplements (see figure 1, figure 6 and figure S9, EVI follows LAI time dynamic and is better correlated with PC and  $G_{s,max}$ ). We thank the reviewer for this useful observation.

**Reviewer 2 comment:**

A careful read and editing of the methods (and entire manuscript) is needed to ensure better consistency in the use of terminology and symbols be used. Furthermore, where possible, the use of more common symbols/abbreviations would be helpful. A non-exhaustive list of examples includes:

- $F_{CT}$  and  $F_{CS}$  are used to represent the eddy flux and storage flux, respectively (Eq. 1). Then  $F_c$  and  $S_c$  are used to represent the eddy flux and storage flux, respectively (L136).
- $F_N$  (e.g., L183-184) and  $R_n$  (L196) are used alternately to represent net radiation.
- The profile system measured  $CO_2$  “mixing ratios” (L115), then “concentration” is used later (L160-170) with a symbol similar to the “concentrations” referred to in relation to the high frequency density measurements made by the open path IRGA.
- Use  $\Delta$  or  $s$  for the slope of the saturation vapor pressure curve instead of  $\epsilon$
- Use LE or  $\lambda E$  for latent heat flux

**Response:**

We have revised the manuscript and improved the consistency of terminology throughout.

- $F_c$  and  $S_c \rightarrow F_{CT}$  and  $F_{CS}$ , L134
- $F_n \rightarrow R_n$ , L197, L210, L218
- More precision added:  $CO_2$  is measured in ppm and converted to  $\mu mol m^{-3}$  using ideal gas law equation. L171-172
- Equation (4), equation (6), L218,  $\epsilon \rightarrow \Delta$
- Equation (4), L217, latent heat flux  $L \rightarrow \lambda E$
- Equation (5), L221,  $U \rightarrow w_s$

**Reviewer 2 comment:**

The sign conventions regarding the directions of fluxes are mixed up in places. For example, in the abstract C sinks carry a positive sign for uptake (L18-19), but later in the text (L264-265) “C sinks” are reported with negative signs. Please carefully review the entire manuscript and ensure consistency throughout regarding sign conventions for fluxes, sinks, and sources.

**Response:**

We have consistently adopted the usual convention from micro-meteorology, that is C going out of the atmosphere is negative (uptake), and C going into the atmosphere is positive (source). L18

**Reviewer 2 comment:**

L111...The LI190SB quantum sensor is calibrated to report PPFD as  $\mu\text{mol}/\text{m}^2/\text{s}$ . Was this then converted to  $\text{W}/\text{m}^2$ ? Check the units throughout the manuscript because the reported values for incident PAR in  $\text{W}/\text{m}^2$  (e.g., L230-231 and 242, Figs. 1 and 3) are not physically possible. Also check to ensure that there was no effect on analyses and it is only an error in the manuscript text.

**Response:**

There was an error in the manuscript text; PPFD is measured in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . This has been corrected throughout the text, equations and figures. L83, 113, 235, 239, 245, 247, 252, 263, 309, 310, 320, 361, 362, 440, 442, 457, 464, 465, 472 and 479, figure 1, 3, 4 and 5, and equation (7)

**Reviewer 2 comment:**

L129-137: If the net ecosystem exchange reduces to the sum of the eddy flux and the storage flux, then don't worry about including advection in the equation. Just state the simplifying assumptions clearly in full in the text. Note that more than just well-developed turbulence (L133-134) is needed to simplify the mass balance on the control volume (e.g., horizontal homogeneity). Please be more complete in this description in the text. Were there any concerns regarding the validity of the simplifying assumptions because of proximity of the EC system to the canopy (as mentioned previously)?

**Response:**

We deleted the advection terms in equation (1), and added more precision regarding the assumption of negligible advection (quality flag of stationarity and turbulence development test, (Foken et al. 2004)). Relating to a comment above we also added a preliminary analysis of the turbulence characteristics to section 2.4, which will be finalized before submitting the revised manuscript (see response to second comment). Changes: L134-140

**Reviewer 2 comment:**

On the calculation of the eddy flux:

- It is more accurate to state that the IRGA measures the (number) densities of  $\text{CO}_2$  and water vapor (L142).
- Eq. 2 is not necessary with an adequate description in the text (but if you keep it define primes and the overbar). It's not the most elegant presentation in the current Eq 2...especially since the equation doesn't include the WPL terms, which are needed. Given the maturity of the EC method a text description is fine.
- L148-149. Rephrase: "Fluxes were rotated into the natural wind coordinate system using the double rotation method". Wilczak et al. isn't the best reference for the double rotation. The original is Tanner, C. B. and Thurtell, G. W.: 1969, Anemoclinometer Measurements of Reynolds Stress and Heat Transport in the Atmospheric Surface Layer, University of Wisconsin Tech. Rep., ECOM-66-G22-F, 82 pp. [Available from US Army Electronic Command, Atmospheric Sciences Laboratory, Ft. Huachuca, AZ 85613.] or referencing the chapter in the Handbook of Micrometeorology.
- L149...what time lags? Between the sonic and IRGA?
- L150-151. Block averaging is not a detrending operation.
- Check to make sure that the order of the steps in the description of the flux calculation matches what was actually done (e.g., one of the last items in the description concerns the removal of spikes in raw data, L153).

**Response:**

L144-166 (section 2.4)

- Concentration replaced with number density, L145
- Equation (2) deleted, the section 2.4, L144-165 describes the calculation details.
- Amended.
- Amended (yes, time lags between the sonic and IRGA, which are of course much smaller in open-path yet still recommended, due to the physical distance between the two instruments).
- Amended “We applied the block averaging method to calculate each half-hour average and fluctuation relative to the average, to calculate the covariance” L156-157
- Amended, 1. Raw data screening (spikes removal ...), 2. If 10% data is missing, flux will be flagged NA 3. Rotation 4. Time lags 5. Block average 6. WPL, flux calculation 7. Flags applied, L150-165

**Reviewer 2 comment:**

L168-182 (section 2.5)

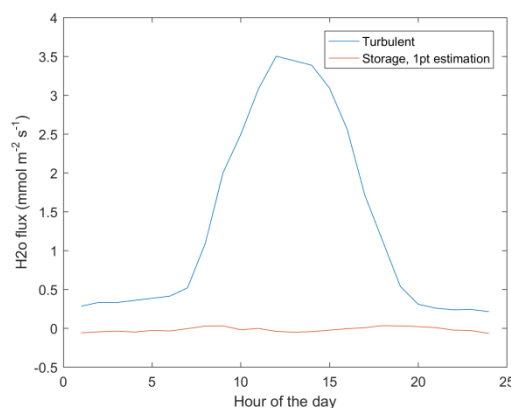
On the calculation of the storage flux:

- A complete description of Eq (4) is lacking (definition of all symbols etc.)
- Why were storage fluxes of water vapor not estimated? Is this a significant source of bias in LE measurements?

**Response:**

- Amended: added: “Where C is CO<sub>2</sub> (μmol m<sup>-3</sup>) and t is time (s) (ΔC/Δt is the variation of C over 30 minutes), z is the height (m), k [1 to n = 8] represents each inlet. L175-176
- The main reason not to use the H<sub>2</sub>O signal from the LI840 is that we do not have heated lines and the tubes will have significant adsorption/desorption issues depending on conditions. So the signal would not be reliable.

We had a look at the 1-point estimation of H<sub>2</sub>O storage (from the Li-7500A at 29m), and it showed a low contribution of change in H<sub>2</sub>O storage to the total H<sub>2</sub>O flux (see figure below). Rather than using a low quality, noisy estimate of H<sub>2</sub>O from the 1-point estimation, we chose to assume that change in H<sub>2</sub>O storage was negligible.



**Figure 1** Diurnal course of H<sub>2</sub>O flux (mmol m<sup>-2</sup> s<sup>-1</sup>) turbulent exchange and change in storage (1 point estimation) in 2017.

**Reviewer 2 comment:**

L183. What exactly is specific heat density (SHD)?

**Response:**

This was a typo, SHD stands for specific humidity deficit. The section 2.6, L183-204, about gap-filling and partitioning, has been updated entirely with the most recent processing of the data, including 2017 for this revised manuscript.

**Reviewer 2 comment:**

L188-194. It would be worth presenting a footprint climatology in the supplementary information.

**Response:**

We added a footprint climatology to the supplementary information as suggested. (figure S5), referred to on L207 (section 2.7).

**Reviewer 2 comment:**

L195-199. Clarify whether closure was forced on the fluxes reported in the results.

**Response:**

We did not force closure on the fluxes reported, this was clarified in the text. L213-214.

**Reviewer 2 comment:**

L200-210. Why were the turbulent fluxes not substituted for available energy when calculating surface conductance? The spatial representativeness would be better.

**Response:**

Surface conductance was calculated using the turbulent flux of water vapor coming from evapotranspiration and the net radiation (equation (4)). We apologise that the notation was not clear in the previous version; this has been corrected. L217-221, section 2.9

**Reviewer 2 comment:**

Eq 7. Check the 2<sup>nd</sup> term in the denominator on the RHS...the exponent should be -0.67. Add a citation and be sure all terms are defined.

**Response:**

Amended. Equation (5)

**Reviewer 2 comment:**

L241-244. The description of leaf-level sampling needs more detail. Since there is a reference that describes these measurements in more detail, the description in this manuscript can be abbreviated, however, a more thorough description of the basics.

- The instrument used
- More details on leaf chamber conditions...were the temps, humidity etc matched to ambient?
- Were sunlit or shaded leaves (or both) measured?
- What species were targeted?

**Response:**

We removed the details of the methods because we used previously published data; we provide the citation to the paper L258.

**Reviewer 2 comment:**

L266-267. “Summer GPP was higher ( $-460 \pm 112 \text{ g C m}^{-2}$ ) compared to winter GPP ( $-291 \pm 28 \text{ g C m}^{-2}$ )”: -291 is higher (>) than -460. Check the manuscript for any other discrepancies when comparing magnitude and direction and ensure that the wording is correct.

**Response:**

Amended: Summer GPP was lower – i.e. more uptake ( $-400 \pm 97 \text{ g C m}^{-2}$ ) compared to winter GPP ( $-282 \pm 41 \text{ g C m}^{-2}$ ) (Table 1), that is a difference of  $\sim 118 \text{ g C m}^{-2}$ . L281

**Reviewer 2 comment:**

L272-278. It looks like there is still hysteresis during winter (albeit less severe than in summer, Figs. 2 and 3). It might be useful to add 2 panels to Fig. 3 and show surface conductance light responses to help with underscoring the importance of stomatal regulation of C fluxes.

**Response:**

We agree that there is still hysteresis during winter, and we adjusted the text, L291-292. Also, we added the panels to Fig. 3 indicating light response of surface conductance as suggested by the reviewer.

**Reviewer 2 comment:**

L336-337. Is soil respiration in the subsoil really that important to the integral over the whole profile?

**Response:**

This is a good point. We have measured soil respiration in a nearby site, showing that soil respiration can be limited in summer when surface soil is dry. This is also seen in the flux data, as shown in figure 1.

Text edit: low soil moisture in the shallow layers sometimes limited decomposition (January and February 2014, January and December 2015, January, February and December 2017 see Figure 1), but often regular rainfall maintained adequate soil moisture. L352-353

**Reviewer 2 comment:**

L345-356. The paragraph starts out by rather definitively stating that “strong stomatal regulation” was the driver of diurnal hysteresis in NEE during summer and then becomes less clear and murkier. Seems odd to take this approach if it is was found that there was strong stomatal regulation of GPP and NEE. Revise.

**Response:**

The authors agreed and revised the paragraph entirely (361-376):

“A strong morning-afternoon hysteresis of NEE response to PPFD occurred in summer, and less so in winter (Figure 3). In winter, low D and moderately warm daytime air temperatures and high PPFD were sufficient to maintain high photosynthesis rates throughout most of the day (Figure 1). In summer, two possible explanations of the diurnal hysteresis of NEE are (1) ER is greater in the afternoon compared to morning or (2) GPP is lower in the afternoon compared to morning.

Explanation (1) is plausible, as temperature drives autotrophic and heterotrophic respiration; however, it is unlikely to explain the hysteresis magnitude which is higher in summer compared to winter.

Explanation (2) could arise from lower afternoon stomatal conductance or lower photosynthetic capacity (e.g. the maximum rate of carboxylation ( $V_{cmax}$ ) decreases at high  $T_a$ ), or a combination of both or even circadian regulation (Jones et al. 1998; Resco de Dios et al. 2015). An analysis of surface conductance showed strong stomatal regulation (Figure 2, Figure 3, Figure 5), induced by high

atmospheric demand and high air temperature (Duursma et al. 2014), limiting photosynthesis during the afternoon of warm months (see Figure S10). These diurnal patterns of NEE, GPP and ER play a strong role in regulating the seasonal carbon cycling dynamics in this ecosystem. A wavelet coherence analysis between D and GPP showed strong coherence at seasonal time scale (periods of three months), see figure S11.”

**Reviewer 2 comment:**

L357-366. Hard to follow...especially the first sentence. Revise and clarify.

**Response:**

The authors agreed and revised the first sentence, L377-378:

“We observed comparable responses of leaf-level and ecosystem-level gas exchange to environmental drivers (Figure 5).”

**Reviewer 2 comment:**

L367. “Canopy dynamics”...be more specific about what you are referring to.

**Response:**

Right. We refer to leaf area index. Text amended.

Canopy dynamics → canopy dynamics (specifically, LAI in our analysis), L387

**Reviewer 2 comment:**

L390-393. Is the temperature/moisture regime at Cumberland Plain the only difference versus the other sites in eucalyptus forests? Are all the sites at similar ages and stages of succession?

**Response:**

The context of this statement is related to the climatic sensitivity of carbon fluxes and canopy conductance. While stand age or successional stage may affect the climatic sensitivity of the fluxes or conductance, all eucalyptus forests in the OzFlux network are mature and have been managed or disturbed to a similar degree (Hinko-Najera et al. 2017; Keith et al. 2012). The Cumberland Plain forest has somewhat lower LAI than the other forests, and has larger seasonal dynamics of LAI and carbon fluxes than Wombat Forest (Griebel et al. 2015). We have shown that GPP and conductance are strongly related to vapor pressure deficit (Fig 5) as well as LAI (Fig 6). Hence, a combination of stomatal conductance and leaf area are responsible for the climatic sensitivity of the site. We prefer not to expand the discussion on these points in order to maintain the focus of the paragraph, but we added a short phrase to link the statement to D, which we feel is the unique feature of our site (L409-412).

“Cumberland Plain has the highest mean annual temperature and the highest dryness index among the four Eucalyptus forest eddy-covariance sites in south-east Australia (Beringer et al. 2016), which could explain its strong sensitivity to D and hence its unique seasonality.”

**Reviewer 2 comment:**

Figs. 2 & 3. It still looks like there is hysteresis in winter...is it that it is not statistically significant?

**Response:**

There is a hysteresis in winter, but of lower magnitude. The text has been corrected accordingly.  
L291-292

**Reviewer 2 comment:**



Fig. 4. Check units for apparent quantum yields ( $\alpha$ ). These values seem high.

**Response:**

In the figure 4 y-label, the units specify that the y-axis is multiplied by  $10^{-2}$ , i.e. quantum yields value are around 0.02 ( $\mu\text{mol CO}_2 \mu\text{mol photon}^{-1}$ ), values comparable to (Aubinet et al. 2001, fig. 10). Note that Mitscherlich equation (7) fits the slope to NEE, not to GPP (as in Michaelis-Menten), so the slope accounts for ER and is bigger.

**References:**

Foken, T., M. Gockede, M. Mauder, L. Mahrt, B. Amiro, and W. Munger, 2004: Post-field data quality control. *Handbook of Micrometeorology: A Guide for Surface Flux Measurement and Analysis*, **29**, 181-208.

Hinko-Najera, N., and Coauthors, 2017: Net ecosystem carbon exchange of a dry temperate eucalypt forest. *Biogeosciences*, **14**, 3781-3800.

Keith, H., E. van Gorsel, K. L. Jacobsen, and H. A. Cleugh, 2012: Dynamics of carbon exchange in a Eucalyptus forest in response to interacting disturbance factors. *Agricultural and Forest Meteorology*, **153**, 67-81.

# Upside-down fluxes Down Under: CO<sub>2</sub> net sink in winter and net source in summer in a temperate evergreen broadleaf forest

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## Abstract

Predicting the seasonal dynamics of ecosystem carbon fluxes is challenging in broadleaved evergreen forests because of their moderate climates and subtle changes in canopy phenology. We assessed the climatic and biotic drivers of the seasonality of net ecosystem-atmosphere CO<sub>2</sub> exchange (NEE) of a eucalyptus-dominated forest near Sydney, Australia, using the eddy covariance method. The climate is characterized by a mean annual precipitation of 800 mm and a mean annual temperature of 18 °C, hot summers and mild winters, with highly variable precipitation. In the ~~three~~four-year study, the ecosystem was a ~~small sink in 2014 (54 each year (-225 g C m<sup>-2</sup> y<sup>-1</sup>), on average, with a stronger sink in 2015 (183 standard deviation of 108 g C m<sup>-2</sup> y<sup>-1</sup>) and even stronger sink in 2016 (337 g C m<sup>-2</sup> y<sup>-1</sup>), but these);~~ inter-annual variations were not related to ~~precipitation~~ meteorological conditions. Daily net C uptake was always detected during the cooler, drier winter months (June through August), while net C loss occurred during the warmer, wetter summer months (December through February). Gross primary productivity (GPP) seasonality was low, despite longer days with higher light intensity in summer, because vapour pressure deficit (D) and air temperature (T<sub>a</sub>) restricted surface conductance during summer while winter temperatures were still high enough to support photosynthesis. Maximum GPP during ideal environmental conditions was significantly correlated with remotely sensed enhanced vegetation index (EVI, r<sup>2</sup> = 0.46) and with canopy leaf area index (LAI) (r<sup>2</sup> = 0.24), which increased rapidly after mid-summer rainfall events. Ecosystem respiration (ER) was highest during summer in wet soils and lowest during winter months. ER had larger seasonal amplitude compared to GPP, and therefore drove the seasonal variation of NEE. Because summer carbon uptake may become increasingly limited by ~~Atmospheric~~atmospheric demand and high temperature, and ecosystem respiration could be enhanced by rising temperature, our results suggest the potential for large-scale seasonal shifts in NEE in sclerophyll vegetation under climate change.

**Keywords:** net ecosystem exchange, seasonal variability, ~~Atmospheric~~atmospheric demand, canopy phenology

36

## 1. Introduction

37  
38 Forests and semi-arid biomes are responsible for the majority of global carbon storage by terrestrial  
39 ecosystems (Dixon et al., 1994; ~~Schimel et al., 2001~~; Pan et al., 2011; Poulter et al., 2014; ~~Schimel et~~  
40 ~~al. 2001~~). Photosynthesis and respiration by these biomes strongly influence the seasonal cycle of  
41 atmospheric CO<sub>2</sub> (~~Keeling et al., 2001; Baldocchi et al., 2016~~); (~~Baldocchi et al. 2016; Keeling et al.~~  
42 ~~2001~~). Continuous measurements of land-atmosphere exchanges of carbon, energy and water provide  
43 insights into the seasonality of forest ecosystem processes, which are driven by the interactions of  
44 climate, plant physiology and forest composition and structure (Xia et al., 2015). Net ecosystem  
45 exchange (NEE) seasonality is relatively well understood in cool-temperate ecosystems; deciduous  
46 trees can only photosynthesize when they have leaves and NEE dynamics are thus principally  
47 influenced by the phenology of canopy processes. NEE of deciduous forests thus has a more  
48 pronounced seasonality than that of evergreen conifer forests at similar latitudes (~~Novick et al.,~~  
49 ~~2015~~); (~~Novick et al. 2015~~). For high-latitude evergreen conifer forests, NEE seasonality is strongly  
50 limited by cold temperature limitation of photosynthesis (~~Kolari et al., 2007~~); (~~Kolari et al. 2007~~) and  
51 respiration. In contrast, seasonality of NEE in evergreen broadleaf forests, typically occurring in  
52 warm-temperate and tropical regions, is much less well understood (~~Wu et al., 2016~~; Restrepo-Coupe  
53 et al., 2017; ~~Wu et al. 2016~~).

54 The seasonality of gross primary productivity (GPP) in evergreen broadleaf forests may be driven by  
55 climate (e.g. dry/wet seasons) and/or by canopy dynamics (~~Wu et al., 2016~~); (~~Wu et al. 2016~~). In  
56 tropical evergreen forests, air temperature and day length are similar seasonally, but precipitation  
57 seasonality can be strong, with higher radiation and temperature (1 or 2 °C higher) in the dry season  
58 (~~Trenberth, 1983; Windsor, 1990~~); (~~Trenberth 1983; Windsor 1990~~). Counter-intuitively, GPP can be  
59 higher during the dry season, as cloud cover may limit productivity in the wet season (Graham et al.,  
60 2003; ~~Hutyra et al. 2007~~; Saleska et al., 2003; ~~Hutyra et al., 2007~~). Canopy dynamics can be an  
61 important determinant of GPP seasonality in evergreen broadleaf forests; although leaves are present  
62 in the canopy year-round in evergreen canopies, LAI may show considerable temporal variability  
63 seasonally as new leaves are produced and old leaves die, especially during leaf flush and senescence  
64 periods (Duursma et al., 2016; ~~Wu et al., 2016~~). The leaf light use efficiency and water use  
65 efficiency may both vary as leaves age: young leaves and old leaves are less efficient than mature  
66 leaves, reflecting changes in photosynthetic capacity (Wilson et al., 2001; ~~Wu et al., 2016~~). The  
67 timing of leaf flush and senescence can depend on the environment and on species; environmental  
68 stress, such as drought, can induce the process of senescence (~~Lim et al. 2007~~; Munné-Bosch and  
69 Alegre, 2004; ~~Lim et al., 2007~~).

70 In temperate evergreen broadleaved forests, such as eucalypt-dominated sclerophyll vegetation in  
71 Australia, precipitation can be seasonal or aseasonal; furthermore, day length and temperature vary  
72 significantly between winter and summer. GPP can be limited by frost during winter and by drought  
73 during summer. Atmospheric demand indicated by high vapor pressure deficit (D<sub>v</sub>) and soil drought  
74 have different impacts on GPP, but they can interact to impact surface conductance (G<sub>s</sub>) (Medlyn et  
75 al., 2011; ~~Novick et al., 2016~~). In Australia's temperate eucalypt forests, canopy rejuvenation takes  
76 place in summer and is linked to heavy rainfall events (~~Duursma et al., 2016~~); (~~Duursma et al. 2016~~).  
77 However, since leaf flushing and shedding occur simultaneously in eucalypt canopies (~~Pook,~~  
78 ~~1984; Duursma et al., 2016~~); (~~Duursma et al. 2016; Pook 1984~~), the overall canopy volume can remain  
79 stable while the distribution of canopy volume changes with height (~~Griebel et al., 2015~~); (~~Griebel et~~  
80 ~~al. 2015~~). Eucalypt forests in southeast Australia have been found to act as carbon sinks all year long,  
81 with greater uptake in summer (~~van Gorsel et al., 2013~~; Hinko-Najera et al., 2017; ~~van Gorsel et al.~~  
82 ~~2013~~). Although canopy characteristics are key to understanding ecosystem fluxes, their dynamics in

Field Code Changed

83 Australian ecosystems can be particularly challenging to detect using standard vegetation indices  
84 | ~~(Moore et al., 2016)~~.(Moore et al. 2016). Nevertheless, the normalized difference vegetation index  
85 (NDVI) has successfully explained variability in photosynthetic capacity in Mediterranean, mulga and  
86 savanna ecosystems (Restrepo-Coupe et al., 2016).

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87 The environmental and biotic controls on the seasonal dynamics of ecosystem fluxes in broadleaved  
88 evergreen forests are still poorly understood. Our objective was to determine the seasonality of  
89 ecosystem CO<sub>2</sub> and H<sub>2</sub>O fluxes in a dry sclerophyll Eucalyptus forest; we evaluated the role of  
90 environmental drivers (~~PAR~~PPFD, T<sub>a</sub>, SWC and D) and canopy dynamics (as measured with  
91 ~~NDVI~~EVI, LAI, litter fall and leaf age) in regulating the seasonal patterns of net ecosystem exchange  
92 (NEE), gross primary productivity (GPP), ecosystem respiration (ER), evapotranspiration (ET) and  
93 surface conductance (G<sub>s</sub>) in an evergreen forest near Sydney, Australia. We also compared leaf-level  
94 to ecosystem-level water and carbon exchange in response to drivers, in order to gain confidence in  
95 our results and gain insights about the emergent properties from leaf to ecosystem scale. We  
96 hypothesised that canopy phenology (LAI and leaf age) explains temporal variation in photosynthetic  
97 capacity (PC) and G<sub>s</sub>. We anticipated that the ecosystem would be a carbon sink all year long.



## 2. Material and methods

### 2.1 Site description

The field site is the Cumberland Plain (AU-Cum in Fluxnet) forest SuperSite (de Dios et al., 2015) of the Australian Terrestrial Ecosystem Research Network (<http://www.tern.org.au/>), (Resco de Dios et al. 2015) of the Australian Terrestrial Ecosystem Research Network (<http://www.ozflux.org.au/>), located 50 km west of Sydney, Australia, at 19 m elevation, on a nearly flat floodplain of the Nepean-Hawkesbury River (latitude -33.61320; longitude 150.72446). Mean mid-afternoon (3 pm) temperature is 18 °C (max. 28.5 °C in January and min. 16.5 °C in July) and average precipitation is 801 mm year<sup>-1</sup> (mean monthly max. is 96 mm in January, and min. is 42 mm in September). The soil is classified as a Kandosol and consists of a fine sandy loam A horizon (0-8 cm) over clay to clay loam subsoil (8-40 cm), with pH of 5 to 6 and up to 5% organic C in the top 10 cm (Karan et al., 2016). The flux tower is in a mature dry sclerophyll forest, with 140 Mg C ha<sup>-1</sup> aboveground biomass and stand density of ~500 trees ha<sup>-1</sup>. The stand hosts a large population of mistletoe (*Amyema miquelii*), which decreases in abundance with increasing distance to the flux tower. The canopy structure comprises three strata, and the predominant canopy tree species are *Eucalyptus moluccana* and *E. fibrosa*, which grow to ~25 m height, an airborne LiDAR survey from November 2015 indicates an average canopy height of ~24 m and host within a large population of mistletoe (*Amyema miquelii*). In addition, the flux tower (supplement figure S1). The mid-canopy stratum (5-12 m) is dominated by *Melaleuca decora*, and the understory is dominated by *Bursaria spinosa* with various shrubs, forbs, grasses and ferns present in lower abundance.

### 2.2 Environmental measurements

Air temperature ( $T_a$ ) and relative humidity (RH) were measured using HMP45C (Vaisala, Vantaa, Finland) sensors at 7 m and 29 m heights. Vapour pressure deficit (D) was estimated from  $T_a$  and RH. Photosynthetically active radiation (PAR,  $\mu\text{PPFD}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) above the canopy (PAR,  $\mu\text{PPFD}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured using an LI190SB (Licor Inc., Lincoln NE, USA), and incoming and outgoing short and longwave radiation were measured using a CNR1 radiometer (Kipp & Zonen, Delft, Netherlands). Ancillary data were logged on CR1000 or CR3000 dataloggers (Campbell Scientific, Logan UT, USA) at 30 min intervals. Mixing ratios of CO<sub>2</sub> in air were also measured at 0.5 m, 1 m, 2 m, 3.5 m, 7 m, 12 m, 20 m, and 29 m above the soil surface using a LI840A Gas Analyzer (Licor Inc., Lincoln NE, USA); data from each height were logged on a CR1000 datalogger once every 30 minutes (1 minute air sampling per height).

Ground heat flux and soil moisture were averaged between two locations to represent the variable shading in the tower footprint. One location had a HFP01 heat flux plate and the other had a self-calibrating heat flux plate (HFP01SC) (Hukseflux, XJ Delft, Netherlands) installed at 8 cm below the soil surface. The heat flux plates were paired with a CS616 water content reflectometer (Campbell Scientific, Logan UT) installed horizontally at 5 cm below the soil surface and a TCAV averaging thermocouple (Campbell Scientific, Logan UT) installed with thermocouples at 2 cm and 6 cm below the soil surface for each pair. A CS616 installed vertically measured average soil water content from 7 to 37 cm (CS616). Rainfall was measured at an open area with a tipping bucket 2 km away from the study site.

140 *2.3 Net ecosystem exchange*

141 Continuous land-atmosphere exchange of CO<sub>2</sub> mass (net ecosystem exchange, NEE) was quantified  
142 from direct measurements of the different components of the theoretical mass balance of CO<sub>2</sub> in a  
143 control volume:

$$NEE = F_{CT} + F_{CS} + (F_{CAH} + F_{CAV}) \quad (1)$$

144 ~~Where  $F_{CT}$  is the vertical turbulent exchange flux,  $F_{CS}$  is the change in storage flux, and  $F_{CAH}$  and  $F_{CAV}$   
145 are the horizontal and vertical advection fluxes—assumed negligible when atmospheric turbulence is  
146 sufficient (Baldocechi et al., 1988; Aubinet et al., 2012). We used change point detection of the friction  
147 velocity ( $u^*$ ) threshold (Barr et al., 2013) to determine the turbulence threshold above which NEE (the  
148 sum of  $F_C$  and  $S_C$ ) is independent of  $u^*$ . However, we found no clear dependence of NEE on  $u^*$  hence  
149 no clear threshold (Figure S1), so we used a threshold of  $0.2 \text{ m s}^{-1}$  to be conservative.~~

150 Where  $F_{CT}$  is the vertical turbulent exchange flux, and  $F_{CS}$  is the change in storage flux. Advection  
151 fluxes are assumed negligible when atmospheric turbulence is sufficient (Aubinet et al. 2012;  
152 Baldocchi et al. 1988), and when quality flags of stationarity and turbulence development test were  
153 good (Foken et al. 2004). We used change-point detection of the friction velocity ( $u^*$ ) threshold (Barr  
154 et al. 2013) to determine the turbulence threshold above which NEE (the sum of  $F_{CT}$  and  $F_{CS}$ ) is  
155 independent of  $u^*$ . However, we found no clear dependence of NEE on  $u^*$  hence no clear threshold  
156 (Figure S2), so we used a threshold of  $0.2 \text{ m s}^{-1}$  to be conservative.

157 The calculation of each term, and the assumptions required for them to be representative of each half-  
158 hour flux are detailed below.

159 *2.4 Vertical turbulent flux ( $F_{CT}$ )*

160 The vertical turbulent fluxes of CO<sub>2</sub> ( $F_{CT}$ ,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and water ( $F_{WT}$ ,  $\text{mmol m}^{-2} \text{ s}^{-1}$ ) were measured  
161 using the eddy-covariance method (Baldocechi et al. 1988). Density ( $c$ ) of CO<sub>2</sub> or water vapor (open-  
162 path IRGA (LI-7500A, Licor Inc., Lincoln NE, USA)) and vertical wind speed ( $w$ ) (CSAT 3D sonic  
163 anemometer (Campbell Scientific, Logan UT, USA)) were measured at 10 Hz frequency at 29 m  
164 above the ground, and logged on a CR-3000 datalogger (Campbell Scientific, Logan UT, USA).  
165 Vertical turbulent fluxes were calculated from the 10 Hz data, using Eddy-Pro© software. Statistical  
166 tests for raw data screening followed (Vickers and Mahrt 1997), including spike count/removal,  
167 amplitude resolution, drop-outs, absolute limits and skewness and kurtosis tests. Low and high  
168 frequency spectral correction followed (Moncrieff et al. 2004), and (Moncrieff et al. 1997). The  
169 calculation allowed for up to 10% of missing 10 Hz data. (Baldocechi et al., 1988). Concentration ( $c$ )  
170 of CO<sub>2</sub> or water vapor (open path IRGA (LI 7500A, Licor Inc., Lincoln NE, USA)) and vertical wind  
171 speed ( $w$ ) (CSAT 3D sonic anemometer (Campbell Scientific, Logan UT, USA)) were measured at  
172 10Hz frequency at 29 m above the ground, and logged on a CR 3000 datalogger (Campbell Scientific,  
173 Logan UT, USA).  $F_{CT}$  and  $F_{WT}$  are calculated as the average 30 minute covariance of  $c$  and  $w$ . Fluxes  
174 were rotated into the natural wind coordinate system using the double rotation method (Wilczak et al.  
175 2001). Time lags between the sonic and IRGA were compensated using covariance maximization,  
176 within a window of plausible time lags (Fan et al. 1990). We applied the block averaging method to  
177 calculate each half-hour average and fluctuation relative to the average, to calculate the covariance  
178 (Gash and Culf 1996). Density fluctuations in the air volume were corrected using the WPL terms  
179 (Webb et al. 1980). Each half-hourly flux was associated with a quality flag (0: good quality, 1: keep  
180 for integrations, discard for empirical relationships, 2: remove from the data); these flags accounted  
181 for stationarity tests and turbulence development tests which are required for good turbulent flux  
182 measurements (Foken et al. 2004). In our 4-year record, 51% of  $F_{CT}$  fluxes had a flag of 0, 32% had a

183 flag of 1 and 17% had a flag of 2. Although the tower height (29m) is rather close to the average  
 184 canopy height (24m), cospectra analysis showed good quality turbulent fluxes (the high frequency  
 185 followed the -4/3 slope, thus we did not find any indications of systematic dampening in the  
 186 cospectra, see figure S3).

$$F_{CT} \text{ or } F_{WT} = \overline{w'e'} \quad (2)$$

187 ~~Vertical turbulent fluxes were calculated from the 10 Hz data, using Eddy Pro© software. The~~  
 188 ~~calculation allowed for up to 10% of missing 10 Hz data. Axis rotation for tilt correction used the~~  
 189 ~~double rotation method (Wilczak et al., 2001). Time lags were compensated using covariance~~  
 190 ~~maximization, within a window of plausible time lags (Fan et al., 1990). We applied the block~~  
 191 ~~averaging method for de-trending (Gash and Culf, 1996). Density fluctuations in the air volume were~~  
 192 ~~corrected using the WPL terms (Webb et al., 1980). Statistical tests for raw data screening followed~~  
 193 ~~(Vickers and Mahrt, 1997), including spike count/removal, amplitude resolution, drop-outs, absolute~~  
 194 ~~limits and skewness and kurtosis tests. Low and high frequency spectral correction followed~~  
 195 ~~(Monerieff et al., 2004), and (Monerieff et al., 1997). Each half hourly flux was associated with a~~  
 196 ~~quality flag (0: good quality, 1: keep for integrations, discard for empirical relationships, 2: remove~~  
 197 ~~from the data); these flags accounted for stationarity tests and turbulence development tests which are~~  
 198 ~~required for good turbulent flux measurements (Foken et al., 2004). In our 3-year record, 51% of  $F_{CT}$~~   
 199 ~~fluxes had a flag of 0, 32% had a flag of 1 and 17% had a flag of 2.~~

## 200 2.5 Storage flux ( $F_{CS}$ )

201 The change in storage flux ( $F_{CS}$ ,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was measured using a  $\text{CO}_2$  profiler system, such that  
 202 change of storage flux timestamp was the same as the turbulent flux timestamp. The change in storage  
 203 flux was calculated as (Aubinet et al., 2001):

$$F_{CS} = \frac{P_a}{R T_a} \int_0^h \frac{dC(z)}{dt} dz \quad (32)$$

204 Where  $P_a$  is the atmospheric pressure ( $P_a$ ),  $T_a$  is the temperature (K),  $R$  is the molar gas constant, and  
 205  $C(z)$  is  $\text{CO}_2$  (~~ppm) at the height  $z$ ,  $\mu\text{mol m}^{-3}$ ) at the height  $z$ .  $\text{CO}_2$  is measured in ppm and converted to~~  
 206  ~~$\mu\text{mol m}^{-3}$  using ideal gas law equation, where the air temperature and air pressure at each inlet is~~  
 207 ~~estimated from a linear interpolation between sensors at the top of the tower (29m) and sensors at the~~  
 208 ~~bottom of the tower (7m). As we only measure a limited number of heights, this equation becomes, in~~  
 209 practice:

$$F_{CS} = \left(\frac{\Delta C}{\Delta t}\right)_{k=1} \times z_{k=1} + \sum_{k=2}^n \left\{ \left[\left(\frac{\Delta C}{\Delta t}\right)_k + \left(\frac{\Delta C}{\Delta t}\right)_{k-1}\right] \times \frac{z_k - z_{k-1}}{2} \right\} \quad (43)$$

210 Where  $C$  is  $\text{CO}_2$  ( $\mu\text{mol m}^{-3}$ ) and  $t$  is time (s) ( $\Delta C/\Delta t$  is the variation of  $C$  over 30 minutes),  $z$  is the  
 211 height (m),  $k$  [1 to  $n=8$ ] represents each inlet height.  $T_a$  was linearly interpolated from HMP at 29 m  
 212 and 7 m. We flagged and replaced the storage flux with a one-point approximation during profiler  
 213 outages (25% of the 34-year record), using the change in  $\text{CO}_2$  at 29 m height over 30 minutes as  
 214 derived in EddyPro (Aubinet et al., 2001)(Aubinet et al. 2001). These data were not used for empirical  
 215 relationships, but kept for annual sum calculations. Storage flux of water vapour was assumed to be  
 216 negligible. For visualisation of the diurnal course of storage flux and turbulent flux, see Figure S2S4.

## 217 2.6 Gap-filling of environmental variables and NEE separation into gross fluxes

218 ~~The OzFluxQC processing We used the PyFluxPro software, based on SOLO neural network, was~~  
 219 ~~used for gap-filling climatic variables and fluxes, and for partitioning the NEE into gross primary~~

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220 productivity (GPP) and ecosystem respiration (ER) (~~Hsu et al., 2002; Isaac et al., 2017~~), using data  
 221 ~~with~~ (~~Isaac et al. 2017~~). ~~We only used observational data that passed the steady state and developed~~  
 222 ~~turbulence tests for gap-filling and for partitioning~~ (QC flags of 0 and 1 (~~Foken et al., 2004~~). In brief,  
 223 ~~gaps~~; (~~Foken et al. 2004~~)). In brief, ~~gaps in climate variables~~ were filled following the hierarchy of  
 224 using variables provided from 1) automatic weather stations from the closest weather station, 2)  
 225 numerical weather prediction model outputs (ACCESS regional, 12.5 km grid size provided by the  
 226 Bureau of Meteorology) and lastly 3) monthly mean values from the site-specific climatology. In a  
 227 next step the continuous climate variables were used to fill all fluxes by utilizing the ~~embedded~~ SOLO  
 228 neural network with 25 nodes and 500 iterations on monthly windows. ~~We~~ ~~We used~~ 'Random Forest'  
 229 (~~Breiman 2001~~) to determine and rank potential explanatory variables for explaining latent heat flux  
 230 ( $\lambda E$ ), sensible heat flux (H) and NEE. We then selected the ~~five variables with the highest feature~~  
 231 ~~importance for each flux and compared the gap-filling performance of the neural network for each~~  
 232 ~~flux with the performance based on an educated guess of potential relevant drivers based on the~~  
 233 ~~highest  $r^2$~~ . We selected the variable array with the highest Pearson correlation coefficient (r) and  
 234 lowest root mean square error (RMSE) for gap-filling in PyFluxPro, which identified net radiation  
 235 ( $F_{ns}$ ), specific heat density ( $SHDR_n$ ), soil water content (SWC), soil temperature ( $T_s$ ), wind speed ( $w_s$ )  
 236 and vapor pressure deficit (D) for  $\lambda E$  ( $r = 0.93$ , RMSE = 32.0); down-welling shortwave radiation  
 237 ( $F_{sd}$ ), air temperature ( $T_a$ ),  $T_s$ ,  $w_s$ , SWC and wind speed ( $w_s$ )D for latent heat flux;  $F_nH$  ( $r = 0.97$ ,  
 238 RMSE = 23.1) and  $F_{sd}$ , D,  $T_a$  and  $w_s$  for sensible heat flux and D,  $T_a$ , shortwave incoming radiation  
 239 ( $F_{sd}$ ) for NEE. In addition,  $T_s$  and SWC for NEE ( $r = 0.87$ , RMSE = 4.04). To gap-fill ER, all  
 240 nocturnal observational data (at night, we assume GPP = 0 so NEE = ER) that passed all quality  
 241 control checks and the  $u^*$ -filter were modelled using  $T_s$ ,  $T_a$  and SWC as drivers ~~in SOLO on the full~~  
 242 ~~dataset with 10 nodes and 500 iterations~~. Lastly, this ~~gapfilled data~~ (gap-filled ER ~~from nighttime~~  
 243 ~~NEE~~) was used to infer GPP as the result of NEE - ER.

### 244 2.7 Flux footprint

245 ~~We analysed which turbulent flux was out of the footprint according to (Kljun et al., 2004), using a~~  
 246 ~~criterion that at least 75% of the turbulent flux ( $F_{CF}$ ) should come from within the forest area. We~~  
 247 ~~used Nearmap high resolution aerial imagery to determine the extent of the forest ecosystem~~  
 248 ~~surrounding the tower. We found that, after  $u^*$  filtering,  $CO_2$  turbulent fluxes ( $F_{CF}$ ) originated from~~  
 249 ~~the footprint of interest. We assumed that the ecosystem within the footprint was homogeneous for the~~  
 250 ~~purpose of this study.~~

251 ~~We analysed the footprint climatology of AU-Cum site according to (Kormann and Meixner 2001),~~  
 252 ~~using the R-Package "FREddyPro" (Figure S5). We assumed that the ecosystem within the footprint~~  
 253 ~~was homogeneous for the purpose of this study.~~

### 254 2.8 Energy balance

255 We evaluated the energy balance closure with the ratio of available energy (~~net radiation ( $R_n$ ) - soil~~  
 256 ~~heat flux (G)) to the sum of turbulent heat fluxes (latent heat flux (L) + sensible heat flux ( $\lambda E + H$ )).~~  
 257 On a daily basis, the energy balance closure was 70% (Figure ~~S3S6~~), consistent with the well-known  
 258 and common issue of a lack of closure (~~Foken 2008; Foken et al. 2006; Wilson et al., 2002; Foken et~~  
 259 ~~al., 2006; Foken, 2008~~). ~~We did not use the criteria that closure had to be met for the reported fluxes.~~

### 260 2.9 Surface conductance

261 ~~Surface conductance ( $G_s$ ) was derived by inverting the Penman-Monteith equation (Monteith, 1965):~~

262 ~~Surface conductance ( $G_s$ ) was derived by inverting the Penman-Monteith equation (Monteith 1965):~~

$$G_s = \frac{\gamma L g_a}{\epsilon R_n + \rho C_p D g_a - L(\epsilon + \gamma)} G_s = \frac{\gamma \lambda E g_a}{\Delta R_n + \rho C_p D g_a - \lambda E (\Delta + \gamma)} \quad (64)$$

263 Where  $\gamma$  is the temperature dependent psychrometric constant ( $\text{kPa K}^{-1}$ ),  $L\lambda E$  is the latent heat flux  
 264 ( $\text{W m}^{-2}$ ),  $\epsilon\Delta$  is the temperature dependent slope of the saturation-vapor pressure curve ( $\text{kPa K}^{-1}$ ),  $R_n$  is  
 265 net radiation ( $\text{W m}^{-2}$ ),  $\rho$  is the dry air density ( $\text{kg m}^{-3}$ ),  $D$  is vapor pressure deficit ( $\text{kPa}$ ),  $C_p$  is the  
 266 specific heat of air ( $\text{J kg}^{-1} \text{K}^{-1}$ ), and  $g_a$  is the bulk aerodynamic conductance, formulated as an  
 267 empirical relation of wind speed ( $w_s$ ,  $\text{m s}^{-1}$ ) and friction velocity ( $u^*$ ,  $\text{m s}^{-1}$ ) (Thom, 1972):

$$g_a = \frac{1}{\frac{u}{u^*} + 6.2 \frac{u^{+0.67}}{u^{*2}} + 6.2 \frac{w_s}{u^{*2}} + 6.2 u^{*-0.67}} \quad (75)$$

268 In the analysis for  $G_s$ , we were interested in transpiration (T) rather than evaporation (E), so we  
 269 excluded data if precipitation exceeded 1 mm in the past 2 days, 0.5 mm in the past 24 hours, and 0.2  
 270 mm in the past 12 hours (Knauer et al., 2015)(Knauer et al. 2015). We assumed that evaporation (E) is  
 271 negligible using these criteria (Knauer et al., 2017)(Knauer et al. 2017), which excluded 40% of the  
 272 data.

## 273 2.10 Potential evapotranspiration

274 ~~Potential evapotranspiration rate (PET) was derived using Penman-Monteith equation (Monteith,~~  
 275 ~~1965):~~

276 Potential evapotranspiration rate (PET) was derived using Penman-Monteith equation (Monteith  
 277 1965):

$$PET = \frac{\epsilon R_n + C_p \rho G_a D}{\gamma [\epsilon + \gamma (1 + \frac{G_a}{G_{s,max}})]} PET = \frac{\Delta R_n + C_p \rho G_a D}{\gamma [\Delta + \gamma (1 + \frac{G_a}{G_{s,max}})]} \quad (86)$$

278 where  $G_{s,max}$  is the well-watered reference surface conductance, calculated as the average of  $G_s$  at the  
 279 study site when soil moisture exceeds the 75% quantile and  $D$  is above 0.9 and below 1.1 kPa (Novick  
 280 et al. 2016).

## 281 2.11 Dynamics of canopy phenology (leaf area index, litter and leaf production) and

### 282 photosynthetic capacity

283 We evaluated the dynamics of canopy leaf area index (LAI) by measuring canopy light transmittance  
 284 with three under-canopy PARPPFD sensors and one above canopy PARPPFD sensor LI190SB (Licor  
 285 Inc., Lincoln NE, USA) following the methods presented in (Duursma et al., 2016)(Duursma et al.  
 286 2016). Although we use the term LAI, this estimate does include non-leaf surface area (stems,  
 287 branches). We collected litterfall ( $L_f$ ,  $\text{g m}^2 \text{month}^{-1}$ ) in the tower footprint approximately once per  
 288 month, from nine litter traps ( $0.14 \text{ m}^2$  ground area) located near the understory PARPPFD sensors.  
 289 We estimated specific leaf area (SLA) of Eucalyptus and mistletoe leaves by sampling approximately  
 290 50 fresh leaves of each, in June 2017 (SLA =  $56.4 \text{ cm}^2 \text{g}^{-1}$  for eucalyptus,  $40.3 \text{ cm}^2 \text{g}^{-1}$  for mistletoe).  
 291 For each month, we partitioned the litter into Eucalyptus leaves, mistletoe leaves, and other (mostly  
 292 woody) components. We used this SLA to estimate leaf litter production ( $L_p$ ) in  $\text{m}^2 \text{m}^{-2} \text{month}^{-1}$  of  
 293 eucalyptus, mistletoe, and total as the sum of both. Then, we estimated leaf growth ( $L_g$ ,  $\text{m}^2 \text{month}^{-2}$ ) as  
 294 the sum of the net change in LAI ( $\Delta L$ ) and  $L_p$ . Photosynthetic capacity (PC) is defined as median  
 295 GPP when PARPPFD is  $800\text{-}1200 \text{ W}\mu\text{mol m}^{-2} \text{s}^{-1}$  and  $D$  is 1.0 to 1.5 kPa.

296 2.12 Analysis of light-response of NEE

297 We evaluated the light response of NEE using a saturating exponential function (Eq. 5) to test whether  
298 parameters varied between seasons (Mitscherlich, 1909; Aubinet et al., 2001; Lindroth et al., 2008;  
299 Mitscherlich 1909).

$$NEE = -(NEE_{sat} + R_d) \left( 1 - \exp \left[ \frac{-\alpha PAR}{NEE_{sat} + R_d} \right] \right) + R_d \quad (5)$$

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300 where the parameter  $R_d$  is the intercept, or NEE in the absence of light, often called dark respiration;  
301  $NEE_{sat}$  is NEE at light saturation and  $\alpha$  is the initial slope of the curve, expressed in  $\mu\text{mol CO}_2 \mu\text{mol}$   
302  $\text{photon}^{-1}$  and representing light use efficiency when ~~photosynthetically active radiation~~  
303 ~~(PAR)~~ photosynthetic photon flux density (PPFD) is close to 0. We only used daytime quality checked  
304 NEE data to fit the model ( $q_c = 0$ ; (Foken et al., 2004)(Foken et al. 2004), LI-7500 signal strength =  
305 max, all inlets of profiler system data available and  $u^* > 0.2 \text{ m s}^{-1}$ ), see Figure S4S7.

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306 2.13 Leaf gas exchange spot measurements

307 Spot measurement of leaf level net photosynthesis at light saturation  $A_{max}$  (~~PAR~~  $1800 \text{ W m}^{-2}$ ),  
308 transpiration  $T$ , stomatal conductance  $g_s$ , and  $D$  were measured at 1.5 km for the flux tower site, see  
309 (Gimeno et al., 2016).

310

311 | [We used previously published data of spot leaf gas exchange measurements in a nearby site for](#)  
312 | [comparison with ecosystem fluxes \(Gimeno et al. 2016\).](#)

### 313 3. Results

#### 314 3.1 Seasonality of environmental drivers and leaf area index

315 Climatic conditions were favorable for growth at the site year-round. The monthly average of daily  
316 maximum ~~of~~ air temperature was 16.3 °C during the coldest month (July 2015), and the lowest  
317 monthly average of daily maximum ~~PARPPFD~~ was 878  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the winter (June 2015; Figure  
318 1c). Although less rainfall occurred during winter months compared to summer months, precipitation  
319 occurred throughout the year (Figure 1b). Soil volumetric water content in the shallow (0-8 cm) layer  
320 was about 10% except immediately following rain events (Figure 1b). In contrast, soil water content  
321 in the clay layer (8 -38cm) remained above 30% for the duration of the study (data not shown).  
322 AverageMonthly average of daily maximum ~~of~~ air temperature ranged from 16.3 °C in July 2015 to  
323 ~~3432.7~~ °C in ~~December 2016~~; AverageJanuary 2017; monthly average of daily maximum D ranged  
324 from 0.9 kPa in June 2015 to 3.4 kPa in ~~December 2016~~January 2017 (Figure 1c). For visualisation of  
325 seasonal and diurnal ~~trend~~trends of radiation, air temperature, D and SWC, see supplement Figure  
326 ~~SSS8~~.

327 Canopy leaf area index varied between 0.7 (in December 2014) and 1.1  $\text{m}^2 \text{m}^{-2}$  (in February 2015)  
328 (Figure 1d). LAI followed a distinct pattern: it peaked in late summer (around January), and then  
329 continuously decreased until the new leaves emerged the following year. A late leaf flush was  
330 observed in 2017 (April). Litter production was concurrent with leaf growth and also peaked in  
331 summer, before and during the leaf flush, and was lower in winter (Figure 1d).

#### 332 3.2 Seasonality of carbon and water fluxes

333 Contrary to expectations, the ecosystem was always a sink for carbon in winter (~~-127146~~  $\text{g C m}^{-2}$  ~~in~~  
334 ~~2014~~, ~~-135~~ on average, with a standard deviation of 22  $\text{g C m}^{-2}$  ~~in 2015 and -99~~  $\text{g C m}^{-2}$  ~~in 2016~~), and  
335 usually a carbon source or close to neutral in summer (~~+97.44~~  $\text{g C m}^{-2}$  ~~in 2014~~, ~~+31~~ on average, with a  
336 standard deviation of 43  $\text{g C m}^{-2}$  ~~in 2015 and -15~~  $\text{g C m}^{-2}$  ~~in 2016~~) (Table 1). On average, summer  
337 Summer GPP was higher (~~460 ± 112~~ lower - i.e. more uptake (~~-400 ± 97~~  $\text{g C m}^{-2}$ ) compared to winter  
338 GPP (~~-291 ± 282~~ ~~82 ± 41~~  $\text{g C m}^{-2}$ ) (Table 1), that is a difference of ~~~ 169118~~  $\text{g C m}^{-2}$ . However,  
339 average summer ER was much higher (~~497 ± 574~~ ~~44 ± 56~~  $\text{g C m}^{-2}$ ) compared to winter ER (~~171 ±~~  
340 ~~26159 ± 35~~  $\text{g C m}^{-2}$ ) (Table 1), a difference of ~~~ 326285~~  $\text{g C m}^{-2}$ . The summer vs. winter ER  
341 difference was close to more than double the GPP difference; thus, ER had a relatively larger effect  
342 over the seasonality of NEE.

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#### 343 3.3 Diurnal trend of CO<sub>2</sub> flux and drivers in winter and summer

344 The diurnal pattern of NEE in clear-sky conditions differed between summer and winter (Figure 2).  
345 Relatively speaking, diurnal NEE was more symmetric in the winter than in summer. That is, morning  
346 and afternoon NEE pattern resembled a mirror image and total integrated morning NEE was similar to  
347 integrated afternoon NEE during the winter, but strong hysteresis occurred in the summer (Figure 2).  
348 This pattern also translated into hysteresis in the NEE light response curve in summer, but ~~not to a~~  
349 lesser degree in winter (Figure 3).

#### 350 3.4 Analysis of NEE light response curve

351 The parameters of the NEE light response in summer and winter are shown in Figure 4 (see methods,  
352 Eq. 5). The initial slope of NEE with light ( $\alpha$ ) showed no clear dependence on  $T_{\text{soil}}$  in winter but  
353 exhibited sensitivity during summer, dropping precipitously at soil temperature above 23 °C (Figure  
354 4a).  $\alpha$  increased with SWC in winter and summer by a factor of 21.5 (Figure 4b). In both winter and  
355 summer  $\alpha$  decreased with D ( $D > 1$  kPa) and in a similar fashion, approaching ~~to~~ a saturating value of  
356 0.01 ( $\mu\text{mol } \mu\text{mol}^{-1}$ ) at a D of about 2 kPa (Figure 4c). The fitted NEE at saturating light ( $\text{NEE}_{\text{sat}}$ ) was

357 not related to  $T_{\text{soil}}$  in winter but decreased with increasing  $T_{\text{soil}}$  in summer (Figure 4d).  $NEE_{\text{sat}}$  was  
 358 higher in winter than in summer for a given SWC. The relationship with D was more complicated,  
 359 tending to increase with D in winter, but decreasing with increased D in summer, dropping from 9 to  
 360  $3 \mu\text{mol m}^{-2} \text{s}^{-1}$  as D increased from 1 to 4 kPa.  $R_d$  was significantly higher in summer than winter  
 361 across all conditions of  $T_{\text{soil}}$ , SWC and D (Figure 4g, h, i).  $R_d$  increased with  $T_{\text{soil}}$  in winter and less so  
 362 in summer. In winter,  $R_d$  increased with SWC in dry condition in winter and plateaued at up to SWC  
 363 of 11%; in summer,  $R_d$  was more sensitive to SWC in summer, doubling from a rate of  $\sim 4$  in dry soils  
 364 to  $\sim 8 \mu\text{mol m}^{-2} \text{s}^{-1}$  in wet soils as SWC increased from about 8 to 20%.

### 365 3.5 Atmospheric demand and soil drought control on GPP, ET, $G_s$ and WUE

366 We evaluated the effect of soil water content (SWC at 0-8 cm depth) and vapour pressure deficit (D)  
 367 on GPP, ET, water use efficiency (WUE) and canopy conductance ( $G_s$ ) under high radiation ("PAR-  
 368 saturated"; PARlight-saturated"; PPFD > 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), after filtering periods following rain  
 369 events in order to minimise the contribution of evaporation to ET (see Methods) (Figure 5). In  
 370 summer, PARlight-saturated GPP decreased above D  $\sim 1.3$  kPa, but in winter, GPP did not vary with  
 371 D. In summer and in winter, GPP increased with SWC (Figure 5a). This is consistent with Figure 4,  
 372 where  $R_d$  and  $NEE_{\text{sat}}$  both increased with SWC. In summer, PARlight-saturated ET increased with D  
 373 up to  $\sim 1.3$  kPa, above which it reached a plateau. In winter, ET kept increasing with D, as D rarely  
 374 exceeded 2 kPa. In both seasons, ET increased with SWC (Figure 5b). Surface conductance decreased  
 375 with D and SWC especially in summer, indicating strong stomatal regulation (Figure 5bd). Water use  
 376 efficiency (WUE) decreased with increasing D in summer and in winter, because ET increased but -  
 377 GPP declined (Figure 5c).

378 We compared these ecosystem-scale results to the equivalent at the leaf-scale, which are net  
 379 photosynthesis at light saturation  $A_{\text{max}}$  (PARPPFD  $\sim 1800$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), leaf transpiration T, leaf  
 380 water use efficiency, and stomatal conductance  $g_s$  (Figure 5, black lines). These leaf level  
 381 measurements are expressed on a leaf-area basis, as oppositecompared to ground area for ecosystem  
 382 scale. We observed that  $A_{\text{max}}$ , T and  $g_s$  were more sensitive to D than corresponding ecosystem-scale  
 383 responses.  $A_{\text{max}}$  was much higher than  $GPP_{\text{max}}$  at D  $\sim 1$  kPa, while  $g_s$  was comparable in magnitude to  
 384  $G_s$  in the same condition. Leaf transpiration peaked around D = 1.2 kPa, while ET plateaued. Leaf  
 385 water use efficiency was overall higher than ecosystem WUE.

### 386 3.6 Canopy phenology control ~~of~~ GPP

387 Monthly average ~~of~~ photosynthetic capacity (PC) varied by a factor of  $\sim 2.7$  across the study period,  
 388 ranging from 68.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  before the leaf flush in November 20152014 to 49.415  $\mu\text{mol m}^{-2} \text{s}^{-1}$   
 389 after the leaf flush occurred in March 2016. We expected that PC could be predicted by LAI and/or  
 390 NDVI, EVI and  $G_s$ . Leaf area index (LAI) and photosynthetic capacity (PC) were significantly  
 391 correlated; the slope was significantly different from zero ( $r^2 = 0.24$ ,  $p \leq 0.02005$ ,  $PC = 10.98.8$  LAI  
 392  $+ 1.83.7$ , Figure 6). By contrast, NDVI-EVI was not even more significantly correlated with PC ( $r^2 =$   
 393 0.46,  $p < 0.005$ ,  $PC = 52$  EVI  $- 5.3$ , Figure 6).  $G_{s,\text{max}}$  was significantly correlated with PC ( $p = 0.05$ ,  $r^2 =$   
 394 0.142,  $p < 0.005$ ,  $PC = 5209$   $G_{s,\text{max}} + 8.69$ ) and LAI ( $p = 0.006$ ,  $r^2 = 0.2527$ ,  $p < 0.005$ ,  $G_{s,\text{max}} =$   
 395 0.0151 LAI  $- 1.8e-3 - 0.17$ ) and with NDVI ( $p = 0.003$ , EVI ( $r^2 = 0.2429$ ,  $p < 0.005$ ,  $G_{s,\text{max}} = 2.3$  EVI  $-$   
 396 0.015 NDVI  $- 4.4e-3 - 0.45$ ). The correlations with NDVI were less significant than with EVI (see figure  
 397 S9).



399 **4. Discussion**

400 We measured ~~three~~four consecutive years of carbon, water and energy fluxes in a native evergreen  
401 broadleaf Eucalyptus forest, including canopy dynamics and environmental drivers  
402 (photosynthetically active radiation, air and soil temperature, precipitation, soil water content, and  
403 atmospheric demand). We hypothesised that the Cumberland Plain forest would be a carbon sink all  
404 year-round, similar to other eucalypt forests (Keith et al., 2012; Beringer et al., 2016; Hinko-Najera et  
405 al., 2017; Keith et al. 2012). We also hypothesised higher net carbon uptake during summer, due to  
406 warmer temperatures, higher light and longer day length contributing to higher photosynthesis,  
407 compared to winter. However, the Cumberland Plain forest site was a net source of carbon during  
408 summer, and a net sink of carbon during winter.

409 The seasonal pattern of NEE was driven mostly by ER, as the seasonal amplitude of ER was larger  
410 than the seasonal amplitude of GPP. The seasonality of ER may be explained by the positive effects  
411 of higher temperatures on the rates of autotrophic respiration (Tjoelker et al., 2001)(Tjoelker et al.  
412 2001), and on the activity of microbes to increase soil organic matter decomposition (Lloyd and  
413 Taylor, 1994)(Lloyd and Taylor 1994); low soil moisture remained high enough to rarely limit in the  
414 shallow layers sometimes limited decomposition, especially in the subsoil (January and February  
415 2014, January and December 2015, February and December 2017, see Figure 1), but often regular  
416 rainfall maintained adequate soil moisture. The relatively low seasonality of GPP may be partly  
417 explained by lower photosynthetic capacity in early summer (before January) when LAI is/was at its  
418 lowest, and the leaves have reached maximum age because new leaves have not yet emerged. The  
419 ER-driven seasonality of NEE is in sharp contrast with cold temperate forests where GPP drives the  
420 seasonality of NEE. ER-driven NEE seasonality was also observed in an Asian tropical rain forest, as  
421 ER was higher than GPP in the rainy season leading to net ecosystem carbon loss, while in the dry  
422 season, ecosystem carbon uptake was positive (Zhang et al., 2010)(Zhang et al. 2010). This pattern  
423 was also observed in an Amazon tropical forest (Saleska et al., 2003).

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424 ~~Diurnal~~ A strong morning-afternoon hysteresis of NEE response to PPFD occurred in summer ~~was~~  
425 associated with strong stomatal regulation, induced by high atmospheric demand and high air  
426 temperature (Duursma et al., 2014), limiting photosynthesis during the afternoon of warm months (see  
427 Figure S6), and less so in winter (Figure 3). In winter, low D and moderately warm daytime air  
428 temperatures and high PAR/PPFD were sufficient to maintain high photosynthesis rates throughout  
429 most of the day. ~~Two~~ (Figure 1). In summer, two possible explanations of the diurnal hysteresis of  
430 NEE ~~in summer~~ are (1) ER is greater in the afternoon compared to morning or (2) GPP is lower in the  
431 afternoon compared to morning. Explanation (1) is plausible, as temperature drives autotrophic and  
432 heterotrophic respiration; however, it is unlikely asto explain the hysteresis ~~only happened~~ magnitude  
433 which is higher in summer, ~~and not in~~ compared to winter. Explanation (2) could arise from lower  
434 afternoon stomatal conductance or lower photosynthetic capacity; (e.g. the maximum rate of  
435 carboxylation (Vcmax) decreases at high T<sub>a</sub>), or a combination of both or even circadian regulation  
436 (de Dios et al., 2015; Jones et al., 1998)(Jones et al. 1998; Resco de Dios et al. 2015). An analysis of  
437 surface conductance showed strong stomatal regulation (Figure 2, Figure 3, Figure 5), induced by  
438 high atmospheric demand and high air temperature (Duursma et al. 2014), limiting photosynthesis  
439 during the afternoon of warm months (see Figure S10). These diurnal patterns of NEE, GPP and ER  
440 play a strong role in regulating the seasonal carbon cycling dynamics in this ecosystem. A wavelet  
441 coherence analysis between D and GPP showed strong coherence at seasonal time scale (periods of  
442 three months), see figure S11.



443 We observed comparable ~~light saturated leaf~~ecosystem  $A_{\max}$ , GPP, T, ET, WUE and  $g_s$ / $G_s$  responses to  
444 ~~D (of leaf-level and ecosystem-level gas exchange to environmental drivers~~ (Figure 5). The ~~difference~~  
445 ~~in larger~~ magnitude of GPP and  $A_{\max}$  ~~than GPP~~ at high D may be explained by the proportion of  
446 shaded leaves: ~~LAI is around  $1 \text{ m}^2$  [leaf area]  $\text{m}^{-2}$  [ground area], a proportion of these leaves are in the~~  
447 ~~shadow, it is thus expected that  $A_{\max}$  (expressed per  $\text{m}^2$  of leaves) will be higher in the ecosystem.~~ The  
448 similar magnitude for  $G_s$  and  $g_s$  was also expected, as LAI is close to 1 and  $R_n$  is not a driver for  
449 stomatal conductance. The peaked pattern of T versus D, as opposite to ~~plateaued/saturating~~ pattern of  
450 ET, may be explained by (1) the contribution of soil evaporation to ET or (2) the presence of  
451 mistletoe, known for not regulating their stomata (~~Griebel et al., 2017~~)(Griebel et al. 2017). The  
452 higher magnitude of leaf water use efficiency results from the combination of higher  $A_{\max}$  and similar  
453 or lower leaf transpiration compared to ET. ~~Furthermore, we compared leaf level  $g_l$  and ecosystem~~  
454 ~~level  $G_l$ , using the optimal stomatal conductance model (Medlyn et al. 2011):  $G_l$  was lower than  $g_l$~~   
455 ~~( $1.6 \pm 0.06$  for  $G_l$ ,  $4.4 \pm 0.2$  for  $g_l$ , see figure S12).~~

456 Our study demonstrated that canopy dynamics (~~specifically, LAI in our study~~) play an important role  
457 in regulating seasonal variations in GPP even in evergreen forests. Similar observations emerged from  
458 a tropical forest, where leaf area index and leaf age explained the seasonal variability of GPP (Wilson  
459 et al., 2001; Wu et al., 2016), as the photosynthetic capacity (PC, the maximum rate of GPP in  
460 optimal environmental condition) varied with leaf age. ~~In Australian woodlands, PC ( $A_{\max}$ ) of leaves~~  
461 ~~was also found to decrease with leaf age.  $A_{\max}$  declined by 30% on average between young and old~~  
462 ~~leaves, for 10 different species (Reich et al. 2009).~~ In the Cumberland Plain forest, periods with high  
463 LAI co-occur with mature, efficient leaves, and periods with low LAI co-occur with old, less efficient  
464 leaves. LAI was correlated with PC, which was probably the result of both a greater number of leaves  
465 and more efficient leaves. Remotely sensed vegetation indices such as ~~enhanced vegetation index~~  
466 ~~(EVI) or normalized difference vegetation index (EVI) or (NDVI)~~ assess whether the target being  
467 observed contains live green vegetation. In Australia, NDVI and EVI were good predictors of  
468 photosynthetic capacity in savanna, mulga and Mediterranean-mallee ecosystems (~~Restrepo-Coupe et~~  
469 ~~al., 2016).~~ However, for Cumberland Plain forest NDVI was a poor predictor of PC, which could be  
470 explained because (1) greenness did not drive photosynthetic potential, which could be because the  
471 understory greening has only subtle influence on PC or (2) there is a bias or a scale mismatch in the  
472 NDVI measurements. Unfortunately, satellite derived LAI values are (~~Restrepo-Coupe et al. 2016~~).  
473 ~~For our site, EVI was a good predictor of PC, which was surprising as satellite-derived LAI values~~  
474 ~~have been found to be~~ typically inaccurate in open forests and forests in southeast Australia (~~Hill et~~  
475 ~~al., 2006), which might also indicate limitations of satellite products to establish successful relations~~  
476 ~~between NDVI and GPP in sclerophyll ecosystems.~~(Hill et al. 2006). NDVI was a poor predictor of  
477 PC (see figure S9).

478 In a global study, it was shown that mean annual NEE decreased with increasing dryness index  
479 (PET/P) in sites located below  $45^\circ$  N latitude (~~Yi et al., 2010~~)(Yi et al. 2010). It has also been shown  
480 that *Eucalyptus* grow more slowly in warm environments (~~Prior and Bowman, 2014~~). At Cumberland  
481 Plain, and in a previous study (Prior and Bowman 2014). At our site, and in a previous study in  
482 *Eucalyptus* forest (~~van Gorsel et al., 2013~~)(van Gorsel et al. 2013), GPP decreased with D above a  
483 threshold of  $\sim 1.3$  kPa. Our results indicate that surface conductance ( $G_s$ ) decreased above that  
484 threshold, suggesting that the decrease in GPP is caused by stomatal regulation. As D correlates with  
485 air temperature, it is difficult to distinguish the relative contribution of D and  $T_a$  to the decrease of  $G_s$ ,  
486 but they are thought to both impact  $G_s$  (~~Duursma et al., 2014~~). The (Duursma et al. 2014). Cumberland  
487 Plain has the highest mean annual temperature and the highest dryness index among the four

488 Eucalyptus forest eddy-covariance sites in south-east Australia (Beringer et al. 2016), which could  
489 explain its [strong sensitivity to D and hence its](#) unique seasonality.  
490

## 491 **5. Conclusions**

492 The Cumberland Plain forest was a net C source in summer and a net C sink in winter, in contrast to  
493 other Australian eucalypt forests which were net C sinks year-round. ER drove NEE seasonality, as  
494 the seasonal amplitude of ER was greater than GPP. ER was high in the warmer, wetter months of  
495 summer, when environmental conditions supported high autotrophic respiration and heterotrophic  
496 decomposition. Meanwhile, GPP was limited by lower LAI and probably older leaves in early  
497 summer, and by high D which limited  $G_s$  throughout the summer. Despite being evergreen, there was  
498 significant temporal variation in LAI, which was correlated with monthly photosynthetic capacity  
499 and monthly surface conductance. Understanding LAI dynamics and its response to precipitation  
500 regimes will play a key-role in climate change feedback.

## 501 **Code and data availability**

502 All the datasets and scripts used in this manuscript can be downloaded at:  
503 <https://doi.org/10.5281/zenodo.10698621219977>

## 504 **Author contribution**

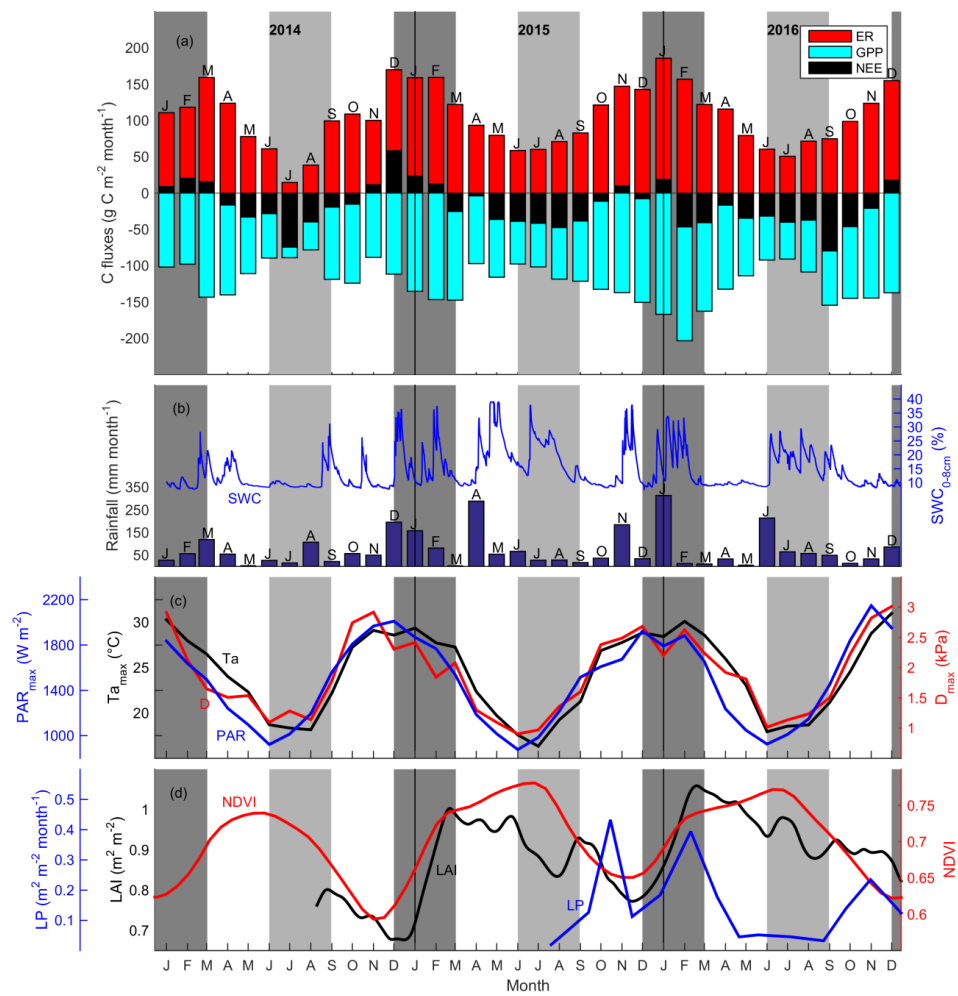
505 DT, VRD, EP, AAR conceived the project; CVMB, CM, EP, AAR, AG, MMB, DM collected the  
506 data and assured the maintenance of the experiment; AAR, AG, DM, CAW, EP, PI, VRD, analysed  
507 the data; AAR, EP, ~~VDR~~VRD wrote the manuscript with input from all other authors.

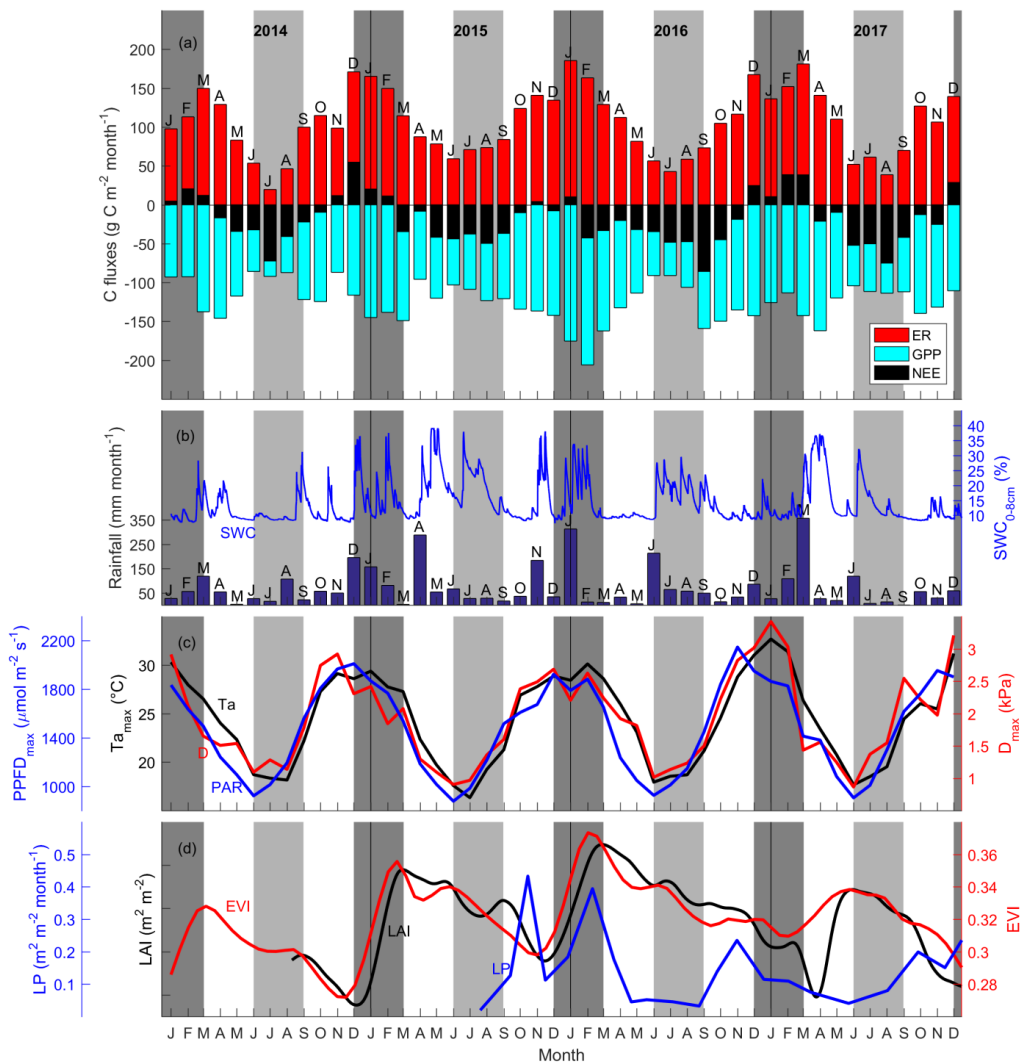
508 The authors declare that they have no conflict of interest.

## 509 **Acknowledgements**

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512 thank Jason Beringer, Helen Cleugh, Ray Leuning, ~~Dan Metzen~~ and Eva van Gorsel for advice and  
513 support. Senani Karunaratne provided soil classification details.







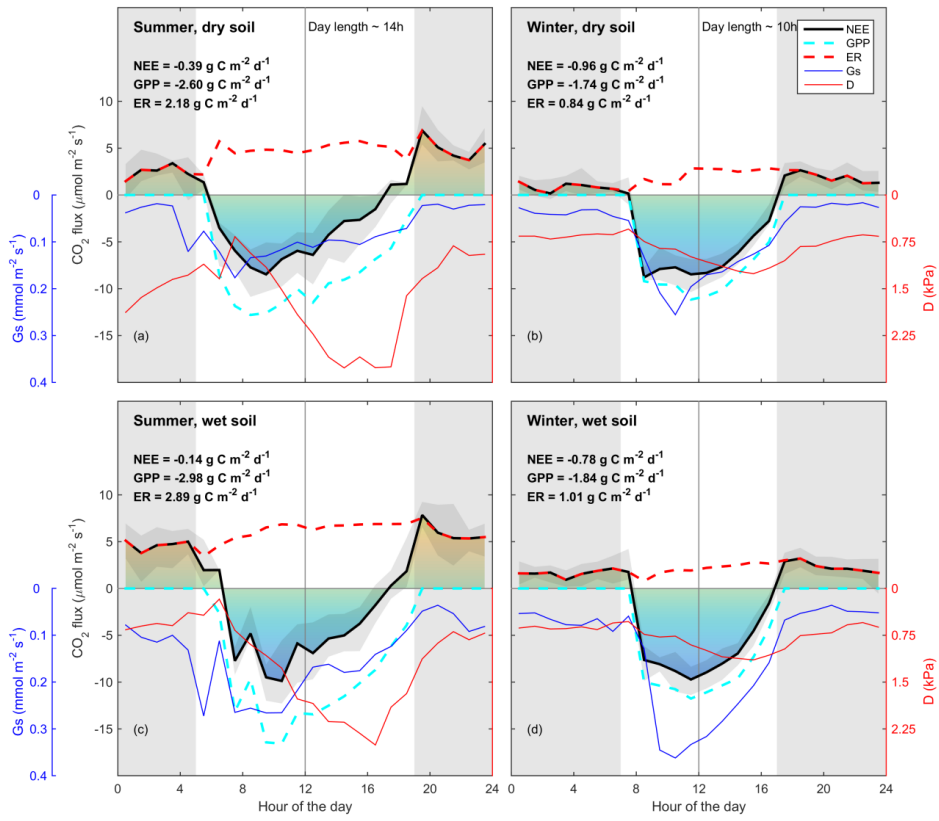
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517 **Figure 1** a) Time series of monthly carbon flux (net ecosystem exchange (NEE), ecosystem respiration (ER) and gross  
 518 primary productivity (GPP),  $\text{g C m}^{-2} \text{ month}^{-1}$  (negative indicates ecosystem uptake); b) rainfall,  $\text{mm month}^{-1}$ ; soil water  
 519 content from 0 to 8 cm ( $\text{SWC}_{0-8\text{cm}}$ , %); c) average of daily maximum for each month photosynthetically active  
 520 radiation (PAR<sub>max</sub>,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ), air temperature (Ta<sub>max</sub>, °C) and vapour pressure deficit (D<sub>max</sub>, kPa); d)  
 521 Canopy dynamics trends (normalized difference enhanced vegetation index (NDEVI), unitless); leaf area index (LAI,  
 522  $\text{m}^2 \text{ m}^{-2}$ ) from November 2013 to April 2016 and litter production (LP,  $\text{m}^2 \text{ m}^{-2} \text{ month}^{-1}$ ). Shaded areas shows summer (dark  
 523 grey) and winter (light grey). Note Ta<sub>max</sub> and PAR<sub>max</sub>, PPFD<sub>max</sub> remained above 15 °C and 800  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ .

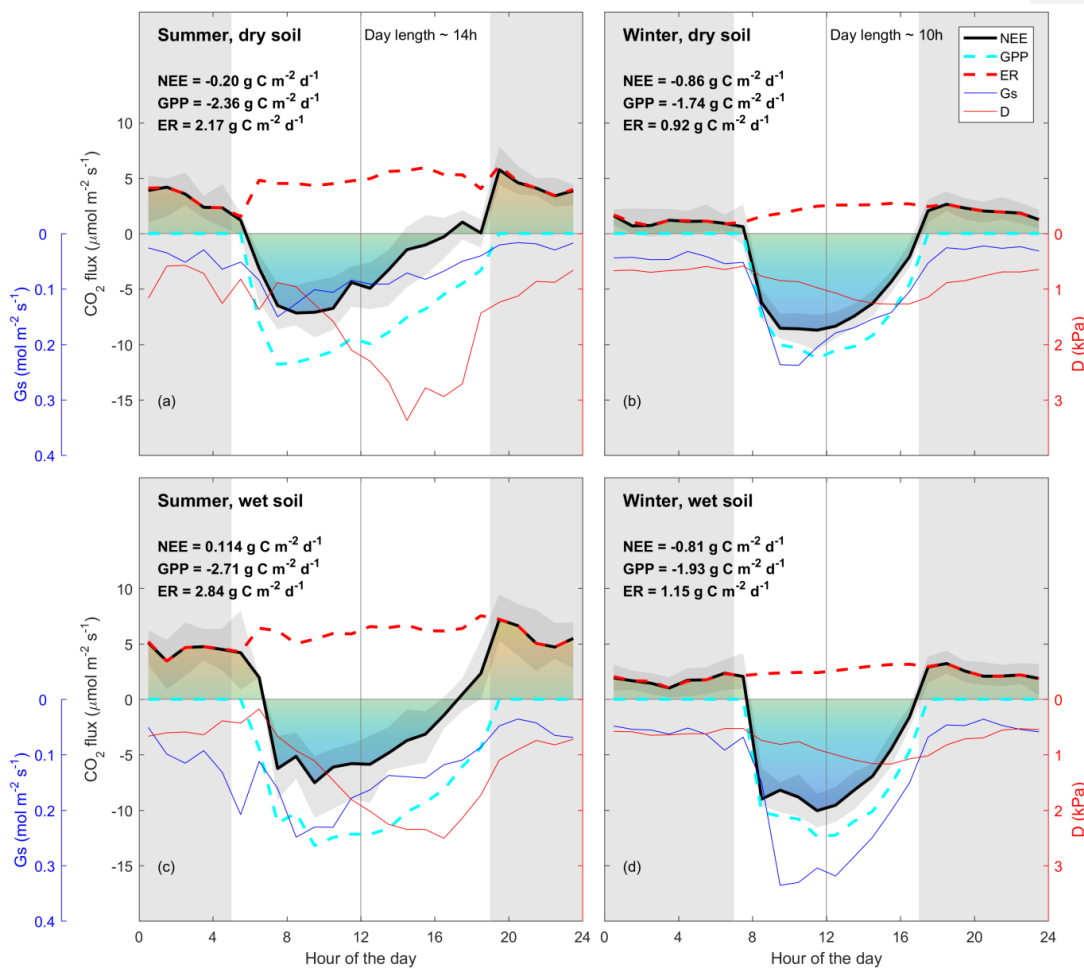
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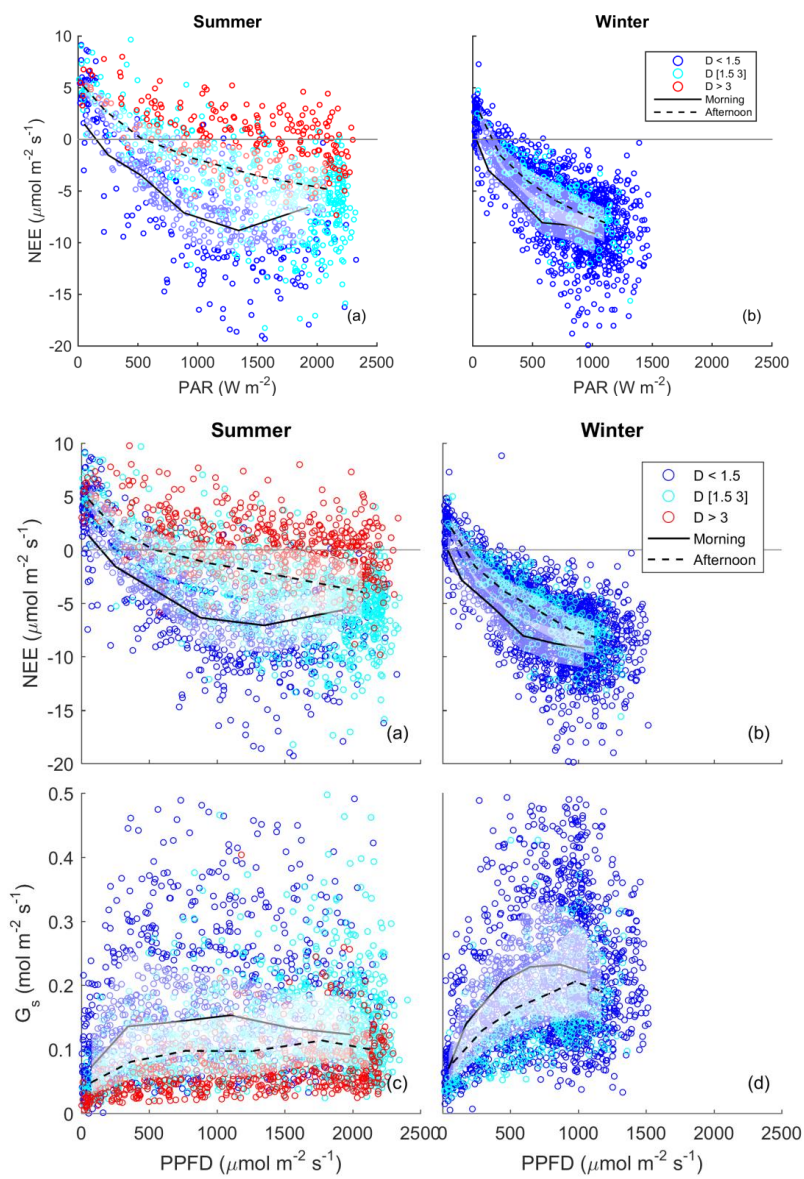
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**Figure 2** Diurnal trend (line: median and shade: quartile) of clear-sky measured net ecosystem exchange (NEE, thick black line,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); estimated daytime ecosystem respiration (ER, inferred from a neural network fitted on nighttime NEE, thick dotted red line,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); estimated gross primary productivity (GPP, inferred as NEE – estimated daytime ER, thick dotted cyan line,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); measured vapour pressure deficit (D, thin red line, kPa); and estimated surface conductance ( $G_s$ , inferred from Penman-Monteith, blue line,  $\text{mmol m}^{-2} \text{s}^{-1}$ ). Grey shade shows night-time (sunset to sunrise). NEE, GPP and ER number are calculated by integrating the diurnal fluxes as shown in the figure. “Wet” and “dry” soil is defined as below or above the median of soil water content during summer or winter. Summer is December through February. Winter is June through August, as defined by the Sydney bureau of meteorology. Colours under NEE rate are shown for visualisation. Note that there is an asymmetry between morning and afternoon NEE in summer, but not less so in winter. Note that ecosystem respiration (nighttime NEE) is enhanced by SWC in summer, but not less so in winter. Data used in this figure correspond to clear-sky half-hour values, where high quality measured data for NEE were available.



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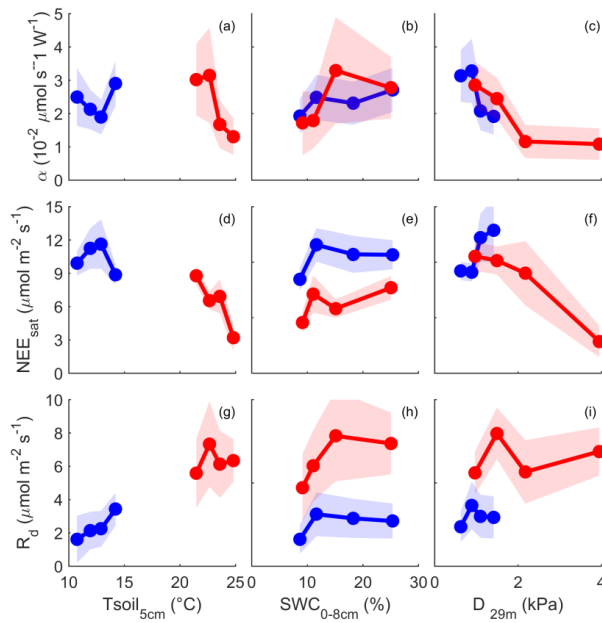


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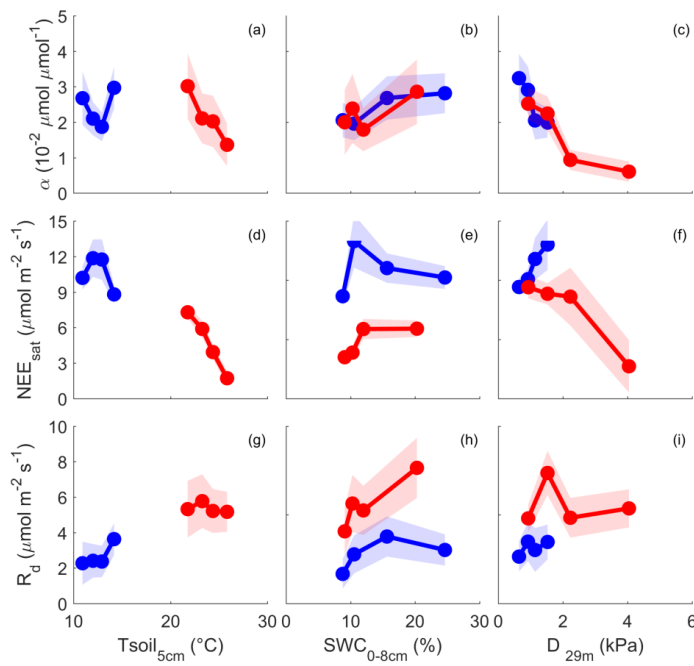
541 **Figure 3** Half-hourly measured NEE vs. ~~PAR~~PPFD, coloured by D (blue,  $D < 1.5$  kPa, cyan:  $D [1.5-3]$  kPa, red:  $D > 3$  kPa)  
542 for (a) summer, and (b) winter periods. Raw data are binned by light levels to show median (lines) and quartiles (white  
543 shades) for morning (continuous lines) and afternoon (dotted lines) hours separately.



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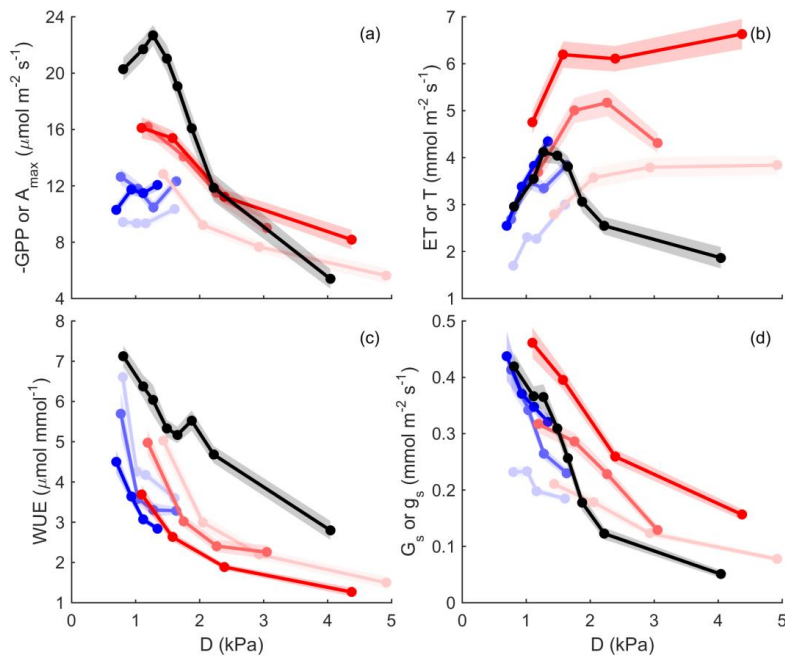
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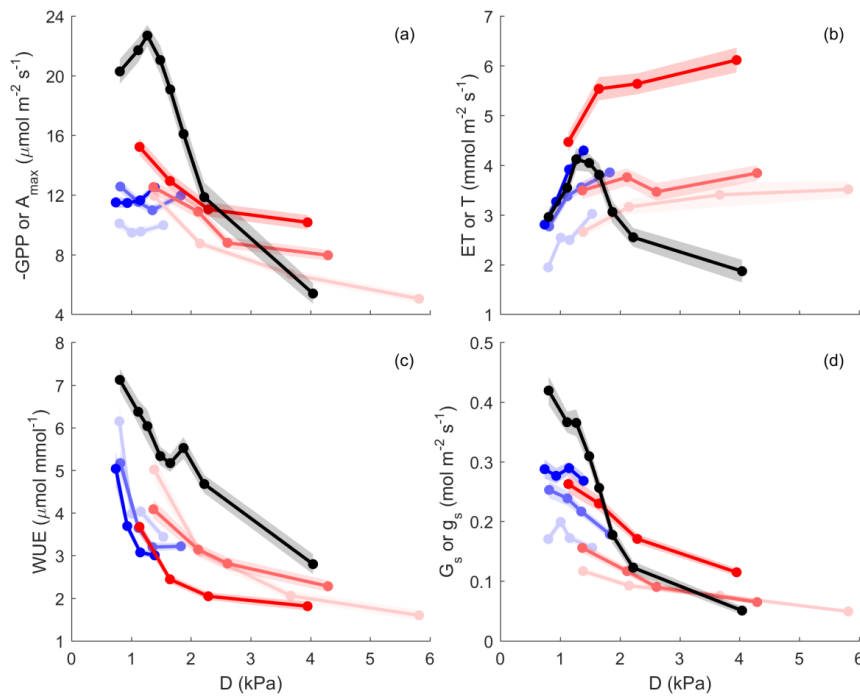
547 **Figure 4** NEE  $\mu\text{mol m}^{-2} \text{s}^{-1}$  light response parameters, calculated for different bins of climatic drivers (soil temperature ( $T_{\text{soil}}$ ,  
 548  $^{\circ}\text{C}$ ) at 5cm depth, soil water content (SWC, %) from 0 cm to 8 cm depth, and atmospheric demand (D, kPa) at 29 m  
 549 height), only raw, qc filtered daytime data is used. Light response curve was fitted using Mitscherlich equation (see  
 550 methods),  $\alpha$  is the initial slope, near PARPPFD = 0 ( $\mu\text{mol s}^{-1} \text{W} \mu\text{mol}^{-1}$ ),  $\text{NEE}_{\text{sat}}$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  is NEE at light saturation, and  
 551  $R_d$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  is the dark respiration (NEE when PARPPFD = 0). Blue indicates winter months, Red indicates summer  
 552 months. Dots are parameters value for each quartile of driver, plotted at  $x = \text{median}$  of driver for each bin. Shading is 95%  
 553 confidence interval of the parameter fit.



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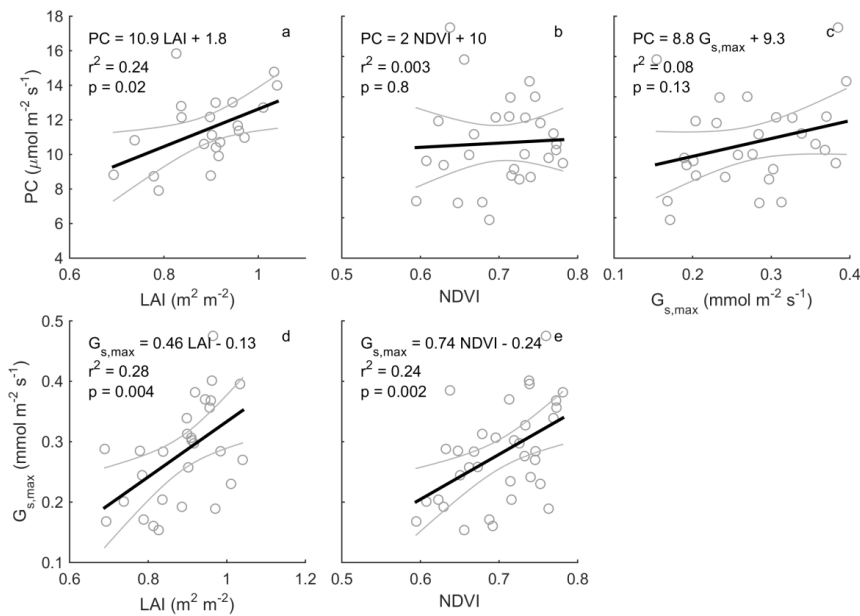
**Figure 5** Gross primary productivity or net assimilation (GPP or  $A_{max}$ ,  $\mu\text{mol m}^{-2} [\text{ground or leaf}] \text{ s}^{-1}$ ), evapotranspiration or leaf transpiration (ET or T,  $\text{mmol m}^{-2} [\text{ground or leaf}] \text{ s}^{-1}$ ), water use efficiency ( $\text{WUE} = \text{GPP}/\text{ET}$  or  $A_{max}/T$ ,  $\mu\text{mol mmol}^{-1}$ ) and surface conductance or leaf conductance ( $G_s$  or  $g_s$ ,  $\text{mmol m}^{-2} \text{ s}^{-1}$ ) vs. vapour pressure deficit (D). Leaf level is shown in black, ecosystem scale is shown in color; summer (red) and winter (blue), at saturated PARPPFD ( $>1000 \text{ W}\mu\text{mol m}^{-2} \text{ s}^{-1}$ ). D is binned into 4 quartiles for ecosystem and 8 for leaf; Y is mean value for each D bins, plotted at the median of D bin.

562 Shaded area indicates the standard error of the mean. The three color intensity show SWC quantiles (SWC < 0.33, SWC  
563 [0.33-0.67] and SWC [0.67-1.00] shown in decreasing color intensity).

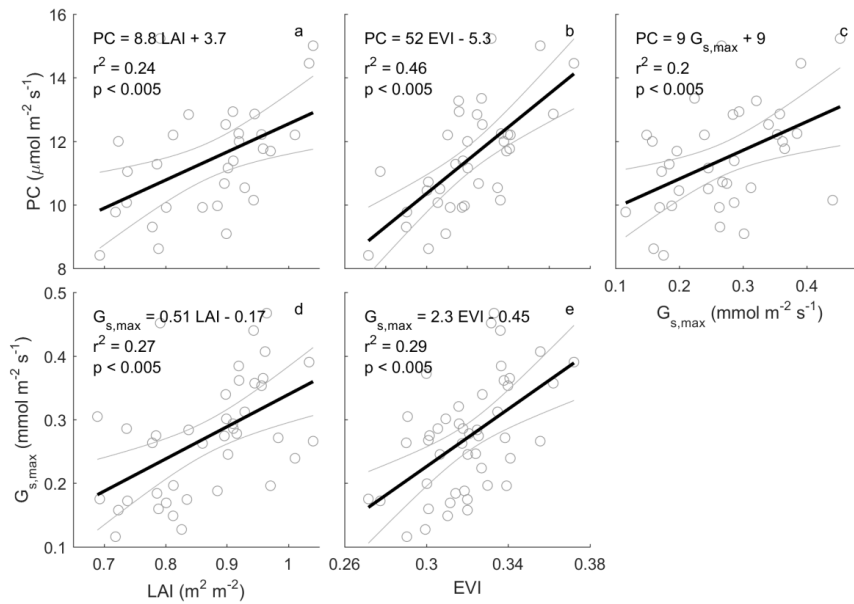


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568 **Figure 6** Relationships between monthly photosynthetic capacity (PC,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ), 250  $\text{m}^2$   
569 **normalized enhanced** vegetation index (NDVI/EVI), and maximum surface conductance ( $G_{s,max}$ ). Monthly PC /  $G_{s,max}$  are  
570 calculated as the median / 75% quantile of half-hourly GPP /  $G_s$  when PARPPFD [800-1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ] and D [1-1.5  
571 kPa]; rain events are filtered for  $G_{s,max}$  estimation, to minimise evaporation contribution to evapotranspiration (see methods).  
572 Monthly LAI is calculated as mean of LAI smoothed by a spline. Thick black line shows a linear regression. **PC vs. LAI was**  
573 **significant** ( $r^2 = 0.58$ ,  $p = 3.7 \times 10^{-5}$ , slope =  $20.1 \pm 3.8$ ).  **$G_{s,max}$  vs. LAI was also significant** ( $r^2 = 0.28$ ,  $p = 0.004$ , slope =  $0.46$   
574  $\pm 0.15$ ). For PC calculation, GPP data is only used when quality-checked NEE is available (GPP = NEE measured - ER  
575 estimated by a neural network, see method).

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581 **References**

582 Aubinet, M., T. Vesala, and D. Papale, 2012: *Eddy Covariance A Practical Guide to Measurement*  
583 *and Data Analysis*. Springer.

584 Aubinet, M., B. Chermanne, B.M. Vandenhoute, M.B. Longdoz, B.M. Yernaux, M., and E. Laitat,  
585 E.:2001: Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes.,  
586 *Agricultural and Forest Meteorology*, **108**, 293-315, [10.1016/S0168-1923\(01\)00244-1](https://doi.org/10.1016/S0168-1923(01)00244-1), 2001.

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587 Aubinet, M., Vesala, T., and Papale, D.: *Eddy Covariance A Practical Guide to Measurement and*  
588 *Data Analysis*, edited by: Aubinet, M., Vesala, T., and Papale, D., Springer, 2012.

589 Baldocchi, D., Y. Ryu, Y., and T. Keenan, T.:2016: Terrestrial Carbon Cycle Variability.,  
590 *F1000Research*, **5**, 2016.

Formatted: Font: Italic

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591 Baldocchi, D. D., B. B. Hicks, B. B., and T. P. Meyers, T. P.: *Measuring biosphere-atmosphere*  
592 *exchanges of biologically related gases with micrometeorological methods*, 1988: **MEASURING**  
593 **BIOSPHERE-ATMOSPHERE EXCHANGES OF BIOLOGICALLY RELATED GASES WITH**  
594 **MICROMETEOROLOGICAL METHODS**. *Ecology*, **69**, 1331-1340, [10.2307/1941631](https://doi.org/10.2307/1941631), 1988.

Formatted: Font: Italic

Formatted: Font: Bold

595 Barr, A., Richardson, A., Hollinger, D., Papale, D., Arain, M., Black, T., Bohrer, G., Dragoni, D.,  
596 Fischer, M., and Gu, L.: Barr, A., and Coauthors, 2013: Use of change-point detection for friction-  
597 velocity threshold evaluation in eddy-covariance studies., *Agricultural and Forest Meteorology*, **171**,  
598 31-45, 2013.

Formatted: Font: Italic

Formatted: Font: Bold

599 Beringer, J., Hutley, L. B., McHugh, I., Arndt, S. K., Campbell, D., Cleugh, H. A., Cleverly, J., de  
600 Dios, V. R., Eamus, D., Evans, B., Ewenz, C., Grace, P., Griebel, A., Haverd, V., Hinko Najera, N.,  
601 Huete, A., Isaac, P., Kanniah, K., Leuning, R., Liddell, M. J., Macfarlane, C., Meyer, W., Moore, C.,  
602 Pendall, E., Phillips, A., Phillips, R. L., Prober, S. M., Restrepo Coupe, N., Rutledge, S., Schroder, I.,  
603 Silberstein, R., Southall, P., Yee, M. S., Tapper, N. J., van Gorsel, E., Vote, C., Walker, J., and  
604 Wardlaw, T.: Coauthors, 2016: An introduction to the Australian and New Zealand flux tower network  
605 - OzFlux., *Biogeosciences*, **13**, 5895-5916, [10.5194/bg-13-5895-2016](https://doi.org/10.5194/bg-13-5895-2016), 2016.

Formatted: Font: Italic

Formatted: Font: Bold

606 de Dios, V. R., Fellows, A. W., Nolan, R. H., Boer, M. M., Bradstock, R. A., Domingo, F., and  
607 Goulden, M. L.: A semi-mechanistic model for predicting the moisture content of fine litter,  
608 *Agricultural and Forest Meteorology*, 203, 64-73, 2015.

609 Breiman, L., 2001: Random forests. *Machine learning*, **45**, 5-32.

610 Dixon, R. K., S. Brown, S., R. e. a. Houghton, R. e. a., A. Solomon, A., M. Trexler, M., and J.  
611 Wisniewski, J.:1994: Carbon pools and flux of global forest ecosystems., *Science (Washington)*, **263**,  
612 185-189, 1994.

Formatted: Font: Italic

Formatted: Font: Bold

613 Duursma, R. A., Barton, C. V., Lin, Y. S., Medlyn, B. E., Eamus, D., Tissue, D. T., Ellsworth, D. S.,  
614 and McMurtrie, R. E.: Duursma, R. A., T. E. Gimeno, M. M. Boer, K. Y. Crous, M. G. Tjoelker, and  
615 D. S. Ellsworth, 2016: Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond  
616 to elevated atmospheric CO2 but tracks water availability. *Global Change Biology*, **22**, 1666-1676.

617 Duursma, R. A., and Coauthors, 2014: The peaked response of transpiration rate to vapour pressure  
618 deficit in field conditions can be explained by the temperature optimum of photosynthesis.,  
619 *Agricultural and Forest Meteorology*, **189**, 2-10, 2014.

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Formatted: Font: Bold

620 Duursma, R. A., Gimeno, T. E., Boer, M. M., Crous, K. Y., Tjoelker, M. G., and Ellsworth, D. S.:  
621 Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond to elevated  
622 atmospheric CO2 but tracks water availability, *Global Change Biology*, **22**, 1666-1676,  
623 [10.1111/gcb.13151](https://doi.org/10.1111/gcb.13151), 2016.

624 Fan, S.-M., S. C. Wofsy, P. S. C., Bakwin, P. S., D. J. Jacob, and D. J. and R. Fitzjarrald, D. R.:1990:  
625 Atmosphere-biosphere exchange of CO<sub>2</sub> and O<sub>3</sub> in the central Amazon forest,1990.

626 Foken, T., 2008: The energy balance closure problem: an overview. *Ecological Applications*, **18**,  
627 1351-1367.

628 Foken, T., F. Wimmer, M. Mauder, C. Thomas, and C. Liebethal, 2006: Some aspects of the energy  
629 balance closure problem. *Atmospheric Chemistry and Physics*, **6**, 4395-4402.

630 Foken, T., M. Gockede, M., Mauder, M., L. Mahrt, L., B. Amiro, B., and W. Munger, W.:2004: Post-  
631 field data quality control, *Handbook of Micrometeorology: A Guide for Surface Flux Measurement*  
632 and *Analysis*, **29**, 181-208,2004.

633 Foken, T., Wimmer, F., Mauder, M., Thomas, C., and Liebethal, C.: Some aspects of the energy  
634 balance closure problem, *Atmospheric Chemistry and Physics*, **6**, 4395-4402, 2006.

635 Foken, T.: The energy balance closure problem: an overview, *Ecological Applications*, **18**, 1351-  
636 1367, 2008.

637 Gash, J., and A. Culf, A.:1996: Applying a linear detrend to eddy correlation data in realtime,;  
638 *Boundary-Layer Meteorology*, **79**, 301-306,1996.

639 Jimeno, T. E., Jimeno, T. E., K. Y. Crous, K. Y., J. Cooke, J., O'Grady, A. A. P. O'Grady, A., ;  
640 Osvaldsson, A., B. E. Medlyn, B. E., and D. S. Ellsworth, D. S.:2016: Conserved stomatal behaviour  
641 under elevated CO<sub>2</sub> and varying water availability in a mature woodland, *Functional Ecology*, **30**,  
642 700-709,2016.

643 Graham, E. A., S. S. Mulkey, S. S., K. Kitajima, K., N. G. Phillips, N. G., and S. J. Wright, S. J.:2003:  
644 Cloud cover limits net CO<sub>2</sub> uptake and growth of a rainforest tree during tropical rainy seasons,;  
645 *Proceedings of the National Academy of Sciences*, **100**, 572-576,2003.

646 Griebel, A., D. M. Watson, and E. Pendall, 2017: Mistletoe, friend and foe: synthesizing ecosystem  
647 implications of mistletoe infection. *Environmental Research Letters*.

648 Griebel, A., L. T. Bennett, L. T., D. S. Culvenor, D. S., G. J. Newnham, G. J., and S. K. Arndt, S-  
649 K.:2015: Reliability and limitations of a novel terrestrial laser scanner for daily monitoring of forest  
650 canopy dynamics, *Remote Sensing of Environment*, **166**, 205-213,2015.

651 Griebel, A., Watson, D. M., and Pendall, E.: Mistletoe, friend and foe: synthesizing ecosystem  
652 implications of mistletoe infection, *Environmental Research Letters*, 2017.

653 Hill, M. J., U. Senarath, U., A. Lee, A., M. Zeppel, J. M., ; Nightingale, R. D. J. M., Williams, R. D. J.,  
654 and T. R. McVicar, T. R.:2006: Assessment of the MODIS LAI product for Australian ecosystems,;  
655 *Remote Sensing of Environment*, **101**, 495-518,2006.

656 Hinko-Najera, N., Isaac, P., Beringer, J., van Gorsel, E., Ewenz, C., McHugh, I., Exbrayat, J. F.,  
657 Livesley, S. J., and Arndt, S. K.:and Coauthors, 2017: Net ecosystem carbon exchange of a dry  
658 temperate eucalypt forest, *Biogeosciences*, **14**, 3781-3800,10.5194/bg-14-3781-2017, 2017.

659 Hsu, K. I., Gupta, H. V., Gao, X., Sorooshian, S., and Imam, B.: Self-organizing linear output map  
660 (SOLO): An artificial neural network suitable for hydrologic modeling and analysis, *Water Resources*  
661 *Research*, **38**, 2002.

662 Hutyra, L. R., Munger, J. W., Saleska, S. R., Gottlieb, E., Daube, B. C., Dunn, A. L., Amaral, D. F.,  
663 De Camargo, P. B., and Wofsy, S. C.:and Coauthors, 2007: Seasonal controls on the exchange of

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Formatted: Font: Bold

Formatted: Font: Italic

Formatted: Font: Bold

Formatted: Font: Italic

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Formatted: Font: Bold

664 carbon and water in an Amazonian rain forest. *Journal of Geophysical Research: Biogeosciences*,  
665 **112**, 2007. Formatted: Font: Italic  
Formatted: Font: Bold

666 Isaac, P., J. Cleverly, J. I. McHugh, I. E. van Gorsel, E. C. Ewenz, C., and J. Beringer, J.: 2017,  
667 OzFlux Data: Network integration from collection to curation. *Biogeosciences*, **14**, 2903, 2017. Formatted: Font: Italic  
Formatted: Font: Bold

668 Jones, T. L., D. E. Tucker, and D. E., and R. Ort, D. R.: 1998: Chilling delays circadian pattern of  
669 sucrose phosphate synthase and nitrate reductase activity in tomato. *Plant Physiology*, **118**, 149-158,  
670 1998. Formatted: Font: Italic  
Formatted: Font: Bold

671 Karan, M., Liddell, M., Prober, S. M., Arndt, S., Beringer, J., Boer, M., Cleverly, J., Eamus, D.,  
672 Grace, P., and Van Gorsel, E.: Coauthors, 2016: The Australian Supersite Network: a continental,  
673 long-term terrestrial ecosystem observatory. *Science of the Total Environment*, **568**, 1263-1274,  
674 2016. Formatted: Font: Italic  
Formatted: Font: Bold

675 Keeling, C. D., S. C. Piper, S. C., R. B. Bacastow, R. B., M. Wahlen, M., T. P. Whorf, T. P., M.  
676 Heimann, M., and H. A. Meijer, H. A.: 2001: Exchanges of atmospheric CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> with the  
677 terrestrial biosphere and oceans from 1978 to 2000. I. Global aspects. *Scripps Institution of*  
678 *Oceanography*, 2001. Formatted: Font: Italic

679 Keith, H., E. van Gorsel, E., K. L. Jacobsen, K., L., and H. A. Cleugh, H. A.: 2012: Dynamics of carbon  
680 exchange in a Eucalyptus forest in response to interacting disturbance factors. *Agricultural and*  
681 *Forest Meteorology*, **153**, 67-81, 10.1016/j.agrformet.2011.07.019, 2012. Formatted: Font: Italic  
Formatted: Font: Bold

682 Kljun, N., Calanca, P., Rotach, M. W., and Schmid, H. P.: A simple parameterisation for flux  
683 footprint predictions, *Boundary-Layer Meteorology*, **112**, 503-523,  
684 10.1023/b:boun.0000030653.71031.96, 2004.

685 Knauer, J., C. Werner, C., and S. Zaehle, S.: 2015: Evaluating stomatal models and their atmospheric  
686 drought response in a land surface scheme: A multibiome analysis. *Journal of Geophysical Research:*  
687 *Biogeosciences*, **120**, 1894-1911, 2015. Formatted: Font: Italic  
Formatted: Font: Bold

688 Knauer, J., Zaehle, S., Medlyn, B. E., Reichstein, M., Williams, C. A., Migliavacca, M., De Kauwe,  
689 M. G., Werner, C., Keitel, C., and Kolari, P.: Coauthors, 2017: Towards physiologically meaningful  
690 water-use efficiency estimates from eddy covariance data. *Global Change Biology*, 2017. Formatted: Font: Italic

691 Kolari, P., H. K. Lappalainen, H. K., Hänninen, H., and P. Hari, P.: 2007: Relationship between  
692 temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in  
693 southern boreal zone. *Tellus B*, **59**, 542-552, 2007. Formatted: Font: Italic  
Formatted: Font: Bold

694 Kormann, R., and F. X. Meixner, 2001: An analytical footprint model for non-neutral stratification.  
695 *Boundary-Layer Meteorology*, **99**, 207-224.

696 Lim, P. O., H. J. Kim, H. J., and H. Gil Nam, H.: 2007: Leaf senescence. *Annu. Rev. Plant Biol.*, **58**,  
697 115-136, 2007. Formatted: Font: Italic  
Formatted: Font: Bold

698 Lindroth, A., L. Klemetsson, L., A. Grelle, A., P. Weslien, P., and O. Langvall, O.: 2008:  
699 Measurement of net ecosystem exchange, productivity and respiration in three spruce forests in  
700 Sweden shows unexpectedly large soil carbon losses. *Biogeochemistry*, **89**, 43-60, 2008. Formatted: Font: Italic  
Formatted: Font: Bold

701 Lloyd, J., and J. A. Taylor, J. A.: On the temperature dependence of soil respiration, 1994: ON THE  
702 TEMPERATURE-DEPENDENCE OF SOIL RESPIRATION. *Functional Ecology*, **8**, 315-323,  
703 10.2307/2389824, 1994. Formatted: Font: Italic  
Formatted: Font: Bold

704 Medlyn, B. E., [Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., Crous,](#)  
705 [K. Y., De Angelis, P., Freeman, M., and Wingate, L.:Coauthors, 2011:](#) Reconciling the optimal and  
706 empirical approaches to modelling stomatal conductance. *Global Change Biology*, **17**, 2134-2144,  
707 [10.1111/j.1365-2486.2010.02375.x, 2011.](#)

708 Mitscherlich, E. A.: [1909:](#) Das Gesetz des Minimums und das Gesetz des abnehmenden  
709 Bodenertrages. *Landw. Jahrb.*, **38**, 537-552, [1909.](#)

710 Moncrieff, J., [R. Clement, R. J. Finnigan, J., and T. Meyers, T.:2004:](#) Averaging, detrending, and  
711 filtering of eddy covariance time series. *in: Handbook of micrometeorology*, Springer, [7-31, 2004.](#)

712 Moncrieff, J. B., [Massheder, J. M., deBruin, H., Elbers, J., Friberg, T., Heusinkveld, B., Kabat, P.,](#)  
713 [Scott, S., Soegaard, H., and Verhoef, A.:Coauthors, 1997:](#) A system to measure surface fluxes of  
714 momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, **189**, 589-611,  
715 [1997.](#)

716 Monteith, J. L.: [1965:](#) Evaporation and environment. *Symp. Soc. Exp. Biol.*, [1965, 4.](#)

717 Moore, C. E., [T. F. Keenan, T. F., R. A. Duursma, R., A., I. van Dijk, A. I., L. B. Hutley, L. B., J. R.](#)  
718 [Taylor, J. R., and M. J. Liddell, M. J.:2016:](#) Reviews and syntheses: Australian vegetation phenology:  
719 new insights from satellite remote sensing and digital repeat photography. *Biogeosciences*, **13**, 5085,  
720 [2016.](#)

721 Munné-Bosch, S., and [L. Alegre, L.:2004:](#) Die and let live: leaf senescence contributes to plant  
722 survival under drought stress. *Functional Plant Biology*, **31**, 203-216, [2004.](#)

723 Novick, K. A., [A. C. Oishi, A. C., E. J. Ward, E. J., M. B. S. Siqueira, M. B., S., J. Y. Juang, J. Y., and](#)  
724 [P. C. Stoy, P. C.:2015:](#) On the difference in the net ecosystem exchange of CO<sub>2</sub> between deciduous  
725 and evergreen forests in the southeastern United States. *Global Change Biology*, **21**, 827-842,  
726 [10.1111/gcb.12723, 2015.](#)

727 Novick, K. A., [Fieklín, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., Papuga, S. A.,](#)  
728 [Blanken, P. D., Noormets, A., Sulman, B. N., Scott, R. L., Wang, L. X., and Phillips, R. P.:Coauthors,](#)  
729 [2016:](#) The increasing importance of atmospheric demand for ecosystem water and carbon fluxes.  
730 *Nature Climate Change*, **6**, 1023-1027, [10.1038/nclimate3114, 2016.](#)

731 Pan, Y., [Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L.,](#)  
732 [Shvidenko, A., Lewis, S. L., and Canadell, J. G.:Coauthors, 2011:](#) A large and persistent carbon sink  
733 in the world's forests. *Science*, **333**, 988-993, [2011.](#)

734 Pook, E.: [1984:](#) Canopy dynamics of Eucalyptus maculata Hook. II. Canopy leaf area balance.  
735 *Australian Journal of Botany*, **32**, 405-413, [1984.](#)

736 Poulter, B., [Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G.,](#)  
737 [Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S., and van der Werf, G. R.:Coauthors, 2014:](#)  
738 Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*,  
739 **509**, 600-603, [10.1038/nature13376, 2014.](#)

740 Prior, L. D., and [D. M. Bowman, D. M.:2014:](#) Big eucalypts grow more slowly in a warm climate:  
741 evidence of an interaction between tree size and temperature. *Global change biology*, **20**, 2793-2799,  
742 [2014.](#)

743 [Reich, P. B., D. S. Falster, D. S. Ellsworth, I. J. Wright, M. Westoby, J. Oleksyn, and T. D. Lee, 2009:](#)  
744 [Controls on declining carbon balance with leaf age among 10 woody species in Australian woodland:](#)  
745 [do leaves have zero daily net carbon balances when they die? New Phytologist](#), **183**, 153-166.

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Formatted: Font: Bold

746 [Resco de Dios, V., A. W. Fellows, R. H. Nolan, M. M. Boer, R. A. Bradstock, F. Domingo, and M. L.](#)  
747 [Goulden, 2015: A semi-mechanistic model for predicting the moisture content of fine litter.](#)  
748 [Agricultural and Forest Meteorology, 203, 64-73.](#)

749 Restrepo-Coupe, N., [Huete, A., Davies, K., Cleverly, J., Beringer, J., Eamus, D., Gorsel, E. v., Hutley,](#)  
750 [L. B., and Meyer, W. S.:and Coauthors, 2016:](#) MODIS vegetation products as proxies of  
751 photosynthetic potential along a gradient of meteorologically and biologically driven ecosystem  
752 productivity. [Biogeosciences, 13, 5587-5608, 2016.](#)

753 Restrepo-Coupe, N., [Levine, N. M., Christoffersen, B. O., Albert, L. P., Wu, J., Costa, M. H.,](#)  
754 [Galbraith, D., Imbuzeiro, H., Martins, G., and Araujo, A. C.:Coauthors, 2017:](#) Do dynamic global  
755 vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model  
756 intercomparison. [Global change biology, 23, 191-208, 2017.](#)

757 Saleska, S. R., [Miller, S. D., Matross, D. M., Goulden, M. L., Wofsy, S. C., Da Rocha, H. R., De](#)  
758 [Camargo, P. B., Crill, P., Daube, B. C., and De Freitas, H. C.:Coauthors, 2003:](#) Carbon in Amazon  
759 forests: unexpected seasonal fluxes and disturbance-induced losses. [Science, 302, 1554-1557, 2003.](#)

760 Schimel, D. S., [House, J. I., Hibbard, K. A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B. H., Apps,](#)  
761 [M. J., Baker, D., and Bondeau, A.:Coauthors, 2001:](#) Recent patterns and mechanisms of carbon  
762 exchange by terrestrial ecosystems. [Nature, 414, 169-172, 2001.](#)

763 Thom, A. [: 1972:](#) Momentum, mass and heat exchange of vegetation. [Quarterly Journal of the Royal](#)  
764 [Meteorological Society, 98, 124-134, 1972.](#)

765 Tjoelker, M. G., [J. Oleksyn, J., and P. B. Reich, P. B.:2001:](#) Modelling respiration of vegetation:  
766 evidence for a general temperature-dependent Q<sub>10</sub>. [Global Change Biology, 7, 223-230, 2001.](#)

767 Trenberth, K. E. [: 1983:](#) What are the seasons? [Bulletin of the American Meteorological Society, 64,](#)  
768 [1276-1282, 1983.](#)

769 [van Gorsel, E., Berni, J. A. J., Briggs, P., Cabello Leblie, A., Chasmer, L., Cleugh, H. A., Haeker, J.,](#)  
770 [Hantson, S., Haverd, V., Hughes, D., Hopkinson, C., Keith, H., Kljun, N., Leuning, R., Yebra, M.,](#)  
771 [and Zegelin, S.:van Gorsel, E., and Coauthors, 2013:](#) Primary and secondary effects of climate  
772 variability on net ecosystem carbon exchange in an evergreen Eucalyptus forest. [Agricultural and](#)  
773 [Forest Meteorology, 182-183, 248-256, 10.1016/j.agrformet.2013.04.027, 2013.](#)

774 Vickers, D., and [L. Mahrt, L.:1997:](#) Quality control and flux sampling problems for tower and aircraft  
775 data. [Journal of Atmospheric and Oceanic Technology, 14, 512-526, 1997.](#)

776 Webb, E. K., [G. I. Pearman, G. I., and R. Leuning, R.:1980:](#) Correction of flux measurements for  
777 density effects due to heat and water vapour transfer. [Quarterly Journal of the Royal Meteorological](#)  
778 [Society, 106, 85-100, 1980.](#)

779 Wilczak, J. M., [S. P. Oncley, S. P., and S. A. Stage, S. A.:2001:](#) Sonic anemometer tilt correction  
780 algorithms. [Boundary-Layer Meteorology, 99, 127-150, 2001.](#)

781 Wilson, K., [Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C.,](#)  
782 [Ceulemans, R., Dolman, H., and Field, C.:Coauthors, 2002:](#) Energy balance closure at FLUXNET  
783 sites. [Agricultural and Forest Meteorology, 113, 223-243, 2002.](#)

784 Wilson, K. B., [Baldocchi, D. D. D., Baldocchi, and P. J. Hanson, P. J.:2001:](#) Leaf age affects the  
785 seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous  
786 forest. [Plant Cell and Environment, 24, 571-583, 10.1046/j.0016-8025.2001.00706.x, 2001.](#)

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787 Windsor, D. M., 1990: Climate and moisture variability in a tropical forest: long-term records from  
788 Barro Colorado Island, Panama, 1990.

789 Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., Guan, K. Y.,  
790 Stark, S. C., Christoffersen, B., Prohaska, N., Tavares, J. V., Marostica, S., Kobayashi, H., Ferreira,  
791 M. L., Campos, K. S., da Silva, R., Brando, P. M., Dye, D. G., Huxman, T. E., Huete, A. R., Nelson,  
792 B. W., and Saleska, S. R.: Coauthors, 2016: Leaf development and demography explain photosynthetic  
793 seasonality in Amazon evergreen forests, *Science*, **351**, 972-976, [10.1126/science.1250668](https://doi.org/10.1126/science.1250668), 2016.

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794 Xia, J. Y., Niu, S. L., Ciais, P., Janssens, I. A., Chen, J. Q., Ammann, C., Arain, A., Blanken, P. D.,  
795 Cescatti, A., Bonal, D., Buchmann, N., Curtis, P. S., Chen, S. P., Dong, J. W., Flanagan, L. B.,  
796 Frankenberg, C., Georgiadis, T., Gough, C. M., Hui, D. F., Kiely, G., Li, J. W., Lund, M., Magliulo,  
797 V., Marcolla, B., Merbold, L., Montagnani, L., Moors, E. J., Olesen, J. E., Piao, S. L., Raschi, A.,  
798 Roupsard, O., Suyker, A. E., Urbaniak, M., Vaccari, F. P., Varlagin, A., Vesala, T., Wilkinson, M.,  
799 Weng, E., Wohlfahrt, G., Yan, L. M., and Luo, Y. Q.: Coauthors, 2015: Joint control of terrestrial  
800 gross primary productivity by plant phenology and physiology, *Proceedings of the National Academy  
801 of Sciences of the United States of America*, **112**, 2788-2793, [10.1073/pnas.1413090112](https://doi.org/10.1073/pnas.1413090112), 2015.

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802 Yi, C., Ricciuto, D., Li, R., Wolbeck, J., Xu, X., Nilsson, M., Aires, L., Albertson, J. D., Ammann, C.,  
803 and Arain, M. A.: Coauthors, 2010: Climate control of terrestrial carbon exchange across biomes and  
804 continents, *Environmental Research Letters*, **5**, 034007, 2010.

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805 Zhang, Y., Z. Tan, Z. Q. Song, Q. G. Yu, G., and X. Sun, X.: 2010: Respiration controls the  
806 unexpected seasonal pattern of carbon flux in an Asian tropical rain forest, *Atmospheric  
807 Environment*, **44**, 3886-3893, 2010.

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