Dear Professor Yakir,

I am writing to resubmit our manuscript entitled "*Examining the evidence for sustained transpiration during heat extremes*" for consideration for publication in Biogeosciences.

We have implemented our outlined revisions and feel that this will further improve the paper. However, in revision we do seek some advice on the suggested citations by the Associate Editor. We appreciate there is not an "instruction" to include these, but we wish to accommodate the advice where we can given that the Associate Editor has been thorough in providing advice.

With respect to the Kowalski paper, as we commented in our final response to the reviewer, the hypothesis they outlined from their work is actually consistent with our baseline theoretical expectation that E is proportional to GPPxD$^{0.5}$, where D increases with temperature. The hypothesis does not predict the divergence from proportionality under temperature conditions that we are interested in, and really isn't directly relevant to the work presented here. However, we seek to be flexible and if the editor has a suggested framing for how to include this we would welcome their advice.

We read through the Vesala et al. (2017 I assume, not 2015?) paper in relation to the Kelvin effect. We agree that this is an interesting paper. However, the response discussed is hypothesised to occur at low leaf water potentials with high relative humidity (specifically they looked at coastal redwood trees). These meteorological conditions are inconsistent with the high temperature ranges we are considering in our paper. We think it would be misleading to include this reference.

We also read through the Eder et al. paper. We are very happy to include a citation and a directed sentence from the reviewer but we need some assistance from the editor to do this. We could not identify what temperature ranges this site experienced and therefore the link between high temperatures and energy closure was not apparent. If we have missed something we would happily add the citation.

Thank you for your consideration.

Yours Faithfully,

Martin G. De Kauwe (on behalf of all the authors)

We thank the reviewer for their constructive comments and we address their various concerns below. Referee comments are highlighted in bold, with our response below in each case. We note that we made two earlier responses to the reviewer during revision, this response now incorporates the key points of those interactions to make things easier for the editor.

Prompted by recent observations from chamber measurements of a decoupling be- tween photosynthesis and transpiration at high temperatures, De Kauwe and col- leagues examine eddy covariance flux data to see whether such decoupling can be observed at the ecosystem scale. To my mind, this manuscript suffers from several important inadequacies, and requires major revision before it would be acceptable for publication. Anticipating that some of my criticisms will be viewed as controversial, I will nonetheless lay them all out, so that the editor can determine which (if any) deserve to be taken into consideration:

1. Both Tier-1 FLUXNET2015 data and OzFlux data suffer doubts regarding their validity due to their persistent failure to demonstrate conformity with the principle of energy conservation (i.e., to close the surface energy budget). Although it might be going too far to say that it is inappropriate to download and analyze such data as the authors have done, neither do I think it is correct for this issue to be neglected entirely. Specifically, I am not aware that anyone has looked at the effect of heat waves on the energy balance closure, but this would certainly seem to be germane to the scientific questions that the authors are posing in the context of dataset validity. Also, although the FLUXNET2015 database includes a GPP variable, this is not measured by flux towers and the procedure from which it is inferred is of dubious validity during conditions of extreme heat stress. Given that the authors are attempting to tease out subtle temperature dependencies of GPP (which is not measured directly) and LE (which fails energy conservation checks), it seems inappropriate to me that such issues are not mentioned at all in this paper.

We appreciate the Reviewers concerns on this issue.

We note in response to their statement about GPP that on page 6 of our original submission that we stated: "*Our analysis also relies on GPP which is not directly observed but is instead modelled using assumptions related to the extrapolation of night-time respiration (ER) and measured net ecosystem exchange. It is debatable whether these assumptions hold at very high temperatures, and examining these modelled GPP estimates at high temperatures warrants further investigation particularly as researchers leverage these data to explore the responses of the vegetation to temperature extremes.*"

In our revised discussion we have more fully addressed this concern: "*Our approach relies on GPP which is not directly observed but is instead modelled using assumptions related to the extrapolation of night-time respiration and measured net ecosystem exchange. It is debatable whether these assumptions hold at very high temperatures, and examining these modelled GPP estimate estimates at high temperatures warrants further investigation, particular as researchers leverage these data to explore the responses of the vegetation to temperature extremes. Eddy-covariance data are also known to have issues closing the energy balance (Foken 2008; Wilson et al. 2002; Hendricks-Franssen et al. 2010), which may introduce errors into the LE flux (see Wohlfahrt et al. 2009, for a detailed discussion). For the seven Australian flux sites that make up the majority of our analysis, we calculated the ratio of the sum of latent and sensible heat fluxes to the sum of the net radiation and ground heat flux, finding on average a ~17% imbalance in the ratio (range 7-30%). Importantly however, we did not find any difference in this imbalance in heatwave vs. non-heatwave days. This is in line with other studies   Despite these limitations, FLUXNET eddy covariance flux measurements still present our best ecosystem-scale estimates of vegetation responses to heat extremes and have been widely analysed to address these types of questions (Ciais et al. 2005; Teuling et al. 2010; Wolf et al. 2013; von Buttlar et al. 2018; Flach et al. 2018).*"

2. The paper draws no concrete conclusions, partly I think because the organisation of the manuscript is below standard.

We would disagree with this interpretation. We draw no concrete conclusions because the data do not allow us to do so. In our paper we tested whether a photosynthetic

decoupling mechanism identified in whole-tree chamber experiments (e.g. Drake et al. 2018, Global Change Biology), as well as other leaf-level experiments, was present at the ecosystem scale. As our results demonstrate, outside of the experimental environment, it is difficult to isolate such a mechanism. We did not find strong support for the original experimental result. However, absence of evidence is not evidence of absence and, given the caveats attached to the data, more concrete conclusions would be unwarranted. Instead, we discussed the need for new field-based studies to tackle this issue further. Although we are unable to draw concrete conclusions, we nonetheless believe the analysis is worth publishing as this is the first study to test for photosynthetic decoupling at an ecosystem scale and as such, discuss the associated uncertainties. Our revised Discussion section also includes a route forward section, which may help satisfy the reviewer on the merit of the study.

The paper contains about 1 page of introduction, 1.5 pages of methods, and 2.5 pages of "Results and discussion" to which will be added five figures and a table. This last section makes for difficult reading, in part because the authors appear to make little effort to distinguish between the facts and their inter- pretations thereof. Furthermore, the paper contains no equations whatsoever, despite the fact that the authors plot a variable (the product of GPP and the square root of the vapour pressure deficit) whose grouping cannot be justified (see comment number 3 below). All of these structural shortcomings make it particularly difficult for the reader to extract and evaluate the underlying message of the manuscript. I believe that the paper would be much better organised with a classical structure of 1. Introduction 2. Methods 3. Results 4. Discussion & 5. Conclusions.

We have now reorganised our manuscript as the reviewer suggested, adding an improved Methods and new Discussion and Conclusion sections.

3. According to the abstract, an important aspect of the paper addresses "the role of vapour pressure deficit" (D). The authors describe this in terms of the "theoretical expectation of the effect of D on g_s" (page 3, line 27), citing previous works in this regard. Although not explicitly appearing in this manuscript, the "equation" underlying this idea is eq. (7) from the 2011 paper by Medlyn et al.,

which is demonstrably in- correct. One of the major contributions to science of Joseph Fourier is the criterion of "dimensional homogeneity", which states that only quantities with the same dimen- sion can be compared, equated, added or subtracted. An obvious example would be the ridiculous statement that one kilometer is greater than one second. At the risk of sounding harsh, I must point out that equation (7) of the Medlyn et al. (2011) paper is equally absurd, and should not be considered as a "theoretical expectation". This ab- surdity seems to me to be a likely explanation for the fact that no units are included on the abscissa of Figure 5 of the De Kauwe et al manuscript, defined by a combination of variables (again: the product of GPP and the square root of the vapour pressure deficit; since it would be fitting for such a group of variables to be defined and assigned a symbol, I will call it Beta). The units of Beta would necessarily include the square root of a pressure unit such as mb or Pa (equivalent to the square root of a kg m-1 s-2). My guess is that the unpleasantness of such a unit caused it to be excluded in the axis label. I would argue that Beta should be rejected altogether based on the powerful tool of dimensional analysis, which invalidates eq. (7) from the 2011 Medlyn et al. paper.

We have now clearly explained the theory that supports our analysis: "*As temperature increases, vapour pressure deficit (D) also increases, which will drive an increase in LE unless there is stomatal closure, but this effect is unrelated to the decoupling mechanism we seek to find. To disentangle the potentially contributing role of D, we also explored these data based on the theoretical expectation (Lloyd et al. 1991; Medlyn et al. 2011; Zhou et al. 2014) that transpiration (E) is approximately proportional to $GPP \times D^{0.5}$ (g C kPa$^{0.5}$ m^{-2} d^{-1}; Eqn. 7). This expectation is based the idea of optimal stomatal behaviour proposed by Cowan and Farquhar (1977) that stomata should be regulated so as to maximise photosynthetic carbon gain less the cost of transpiration. Medlyn et al. (2011) derived the optimal stomatal behaviour as:*

$$G_s = 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a} \tag{1}$$

where G_s is canopy stomatal conductance to CO_2 (mol m^{-2} s^{-1}), A is the net assimilation rate (μmol m^{-2} s^{-1}), C_a is the ambient atmospheric CO_2 concentration (μmol mol^{-1}), D is the vapour pressure deficit (kPa), the parameter g_1 (kPa$^{0.5}$) is a fitted parameter representing the sensitivity of the conductance to the assimilation rate and the factor 1.6 is the ratio of diffusivity of water to CO_2 in air. Assuming that transpiration is

largely controlled by conductance, this relationship can be rearranged to show that water-use efficiency (A/E) is approximately proportional to $1/\sqrt{D}$. This dependence has been remarked by many authors (e.g. Lloyd et al. 1991, Katul et al. 2009). Based on this dependence, Zhou et al. (2014, 2015) proposed an "underlying water-use efficiency" (uWUE) for eddy covariance data:

$$uWUE \approx \frac{GPP\sqrt{D}}{E} \tag{2}$$

Zhou et al. (2014) argued that the $D^{0.5}$ term provided a better linear relationship between GPP and E. Thus, to probe the effect of D, we focused on heatwaves (i.e. approach 2) and plotted LE expressed as evapotranspiration (mm day^{-1}), as a function of $GPP \times D^{0.5}$."

Both of our earlier responses to reviewer argued that there was in fact no problem with units, rather our original submission was simply not clear enough. We hope that our revised text will now satisfy the reviewer that there are no further issues. We refer the editor to earlier responses on this issue.

We have also added the requested units to the figure labels.

4. The ordinates of figures 3 and 4 are labelled with "density", a variable that normally would have units such as kg m-3. Rather, I believe that what the authors have plotted is a frequency of occurrence, which is a fractional, non-dimensional quantity that requires no units. However, since the values in figure 3 go well above unity, I suspect that they should be described in terms of percent (%). In any event, I think this needs to be clarified.

The plot is correct, and the confusion here relates to the normalisation of densities in the kernel density estimate. This is essentially the difference between probability mass functions (discrete variable) and probability density functions (continuous), the former no longer integrates to 1. We have now added "Probability density" to the figure label and added an interpretation sentence to each of the figure captions.

5. (This final comment may be viewed by the editor as excessively ego-centric on the part of the reviewer. Nonetheless I feel obligated to point it out.) I have applied the laws of physics to demonstrate that the paradigm underlying the definition of the "stomatal conductance" is fundamentally incorrect (Kowalski, Atmos. Chem. Phys., 17, 8177–8187, 2017), and furthermore to *predict* a decoupling of transpiration and

photosynthesis at high temperatures. The long-standing paradigm in ecophysiology presupposes all transport through stomata to be diffusive in nature, whereas my analy- sis, based on conservation of linear momentum, shows that non-diffusive transport also occurs in the form of "stomatal jets". In brief, because the exchange of water vapour dominates surface exchange of all gases, the evaporation rate defines a flow velocity away from the evaporating surface and consequent transport of all gases away from the evaporating surface. For the particular case of water vapour, the analysis shows that the specific humidity represents the fraction of water vapour transport that is non- diffusive. Students of thermodynamics know that, for a saturated environment such as that supposed by ecophysiologists within a stomatal cavity, the specific humidity increases nearly exponentially as a function of temperature. Thus, at extreme temper- atures the role of non-diffusive transport becomes non-negligible and a decoupling is expected between exchanges of water vapour (whose egress is aided by non-diffusive transport) and carbon dioxide (whose ingress is opposed by the outgoing Stefan flow). At the extreme limit of the boiling point, the vapour pressure inside the stomatal cavity would equal the total air pressure, meaning that (1) water vapour would be the lone gas inside the stomatal cavity, therefore (2) no diffusion could occur, and all transport would be non-diffusive (i.e., a specific humidity of 100%), and therefore (3) no photosynthesis would be possible (with no CO_2 present). Since my analysis is soundly based on the laws of physics and satisfactorily explains the decoupling between photosynthesis and transpiration at high temperatures, I believe that the authors should take it into account when exploring this "previously overlooked vegetation-atmosphere feedback that may in fact dampen, rather than amplify, heat extremes". However, I hardly think it is my place to insist that other scientists cite my papers, and so must leave judgement of this matter to the editor.

We thank the reviewer for their insight on this issue. Despite our back and forth discussion on this topic, we still maintain that that in order to argue for a paradigm shift ("*paradigm underlying the definition of the "stomatal conductance" is fundamentally incorrect*"), a certain weight of evidence, including measurements, will be required.

5

We further thank the reviewer for spelling out the hypothesis regarding the effect of temperature presented in their paper. Their hypothesis is that WUE should decline as temperature increases because of the change in specific humidity with temperature. This hypothesis is actually consistent with our baseline theoretical expectation that E

10   is proportional to GPP $\times$ D$^{0.5}$ where D increases with temperature. The hypothesis does not predict the divergence from proportionality under temperature conditions that we are interested in, and hence we maintain that it is not directly relevant to the work presented here. However, if the editor feels we should refer to this work, we will of course abide by their decision here.

We thank the reviewer for their constructive comments and we address their various concerns below. Referee comments are highlighted in bold, with our response below in each case.

5

Recent findings on a leaf and tree level indicated that during heatwaves the photosynthesis (A) may decouple from the stomatal conductance (gs). In line with gs, transpiration (E) may increase while A does not which impacts instantaneous water use efficiency (WUE). De Kauwe's et al paper aims to

10 **extend this evidence on the ecosystem level analyzing eddy covariance data from mostly Australian forested ecosystems. Because the topic is novel and because the correlation between A and gs became central to many models the topic may be in a scope of a large audience.**

Generally, the paper reads well. Data are demonstrated on figures which are

15 **mostly clear to understand.**

We thank the reviewer for this positive summary of our work.

But I do not think that the research questions stated in the last paragraph of the introduction section fit the rest of the paper. That means, the paper focuses more

20 **on changes in instantaneous WUE (A/E) that on a decoupling of the gs from A. Of course, both may be described in the same paper but the reasoning in the introduction and in a discussion as well as the structure of results should be adjusted accordingly.**

The reviewer is correct that whilst we do talk about a decoupling between A and g_s,

25 our analysis is focussed on the response of ecosystem-scale quantities: flux-derived GPP and the flux of latent heat. However, we do not see that the question as stated, was inconsistent with our analysis - the transpiration (or latent heat flux) is in part an outcome of the leaf-level stomatal response, which we feel this was clearly articulated: "*In this paper we therefore explore eddy-covariance measurements to*

30 *examine whether there is widespread field-based evidence that during heat extremes,*

trees decouple photosynthesis and g$_s$, leading to increased transpiration. We chose to focus on wooded ecosystems as the capacity to maintain transpiration throughout a heat extreme most likely requires deep soil water access and is in line with previous experimental evidence from trees (Drake et al., 2018; Urban et al., 2017)".

5 To further clarify this, we now also add to the above: "*In contrast to previous experimental studies (e.g. Urban et al. 2017), our focus is on the ecosystem-scale and so we analysed the photosynthetic decoupling between photosynthesis and transpiration.*"

10 **Further, I suggest a few points to work on: 1. Is it E or gs which decouples from A during heatwaves?**

We agree with the reviewer this is an important point to clarify and we will do so in our revised manuscript. We have changed our sub-heading in the methods 2.1 from "*Evidence of photosynthesis-canopy conductance decoupling*" to "*Evidence of*
15 *photosynthesis-transpiration decoupling*".

We have also added text to this section to explain our approach: "*A number of previous studies reporting photosynthetic decoupling experimentally, have focused on the coupling between A and G$_s$ (Weston and Bauerle, 2007; Ameye et al. 2012; von Caemmerer and Evans, 2015), as opposed to A and E (Drake et al. 2018). At the*
20 *ecosystem-scale (eddy-covariance), coincident measurements of G$_s$ and LE (or transpiration) are rarely available. Whilst it is possible to estimate the canopy G$_s$ by inverting the Penman-Monteith using measured LE, such an approach necessitates additional assumptions related to the canopy boundary layer conductance (Jarvis and McNaughton, 1986; De Kauwe et al. 2017), the canopy net radiation and the ground*
25 *heat flux (Medlyn et al. 2017). Here we avoid these assumptions by focusing our analysis on the measured LE flux, as opposed to an estimate of the canopy G$_s$.*"

Both are interlinked but for the modeling purposes, I believe that A/gs (i.e. intrinsic WUE) is more important than A/E (i.e. instantaneous WUE). On the

other hand, increase in E while A does not change or decline during the heatwave is the important issue, too.

We agree with the reviewer; however, outside of an experimental setting we do not have access to measurements of g_s. Here we are seeking to examine the evidence at the ecosystem-scale and as such, our focus is on the response of E. We agree, that a decoupling of A/g_s may not translate to A/E at the canopy/ecosystem-scale due to the level of control stomata have on transpiration ("decoupling", Jarvis and McNaughton, 1986) and environmental drivers (net radiation, wind speed, VPD). In our revised methods (see above) and discussion text we explain this point more fully.

The point the reviewer highlights speaks to the novelty of our approach, which considers responses at the ecosystem-scale and attempts to contextualise previous experimental work (e.g. Drake et al. 2018 and Urban et al. 2017).

Many papers were published on E/gs which assumed stomatal regulation to maximize the A for a fixed amount of water transpired over the long time period. This idea was recently challenged (i.e. Wolf et al. 2016, PNAS; Sperry et al. 2017, PCE) and De Kauwe et al. may want to work with this evidence, should they decide to aim their paper this way.

In our revised discussion (4.2 Implications for models), we have addressed the point raised by the reviewer: "*The implications for modelling studies that focus on heat extremes are clear, particularly for studies in Australia. None of the current generation of land surface models have the capacity to decouple transpiration from the down-regulation of photosynthesis with increasing temperature. Instead models assume photosynthesis and g_s (and consequently transpiration) remain coupled at all times. As a result, climate models will underestimate the capacity of the vegetation to dampen heat extremes in simulations for Australia. This is also true of more sophisticated plant hydraulic models (Williams et al. 2001) and profit-maximisation approaches (Wolf et al. 2015; Sperry et al. 2016) that hypothesise the cost of water is not fixed in time, but instead increases with increasing water stress. For these latter approaches to account for a photosynthetic decoupling they would need to prioritise maintaining an optimum canopy temperature above a net carbon gain. However,*

mechanisms to capture this within models should likely wait for further supporting evidence of photosynthetic decoupling."

Furthermore, I do not believe that trees should keep a fixed A/E ratio in a short time (i.e. a few days of a heatwave). That said, imagine the temperature is fixed to a specific value (i.e. 25 oC) and vapor pressure deficit (VPD) increases from near zero to a couple thousand Pa (scenario unlikely to happen in nature but good to demonstrate the change in WUE). Photosynthesis would decline due to stomatal closure as a response to the increase in VPD, but the transpiration would increase.

This is why we also analysed the eddy-covariance data from the perspective of WUE, to attempt to disentangle any decoupling from the response to increasing VPD.

2. Should authors want to focus more on A/gs relationship, I believe the analysis which clearly demonstrates the change in (or lack of) the response should be presented.

As mentioned above, it is not possible to show the A/g_s relationship from eddy-covariance data. To do so would require inverting the Penman-Monteith equation from measured LE flux. Whilst this approach has been used, it requires a series of assumptions related to the canopy aerodynamic conductance, it is far clearer to analysis the measured flux. See added text above.

While I do not challenge the approach of GPPxDˆ0.5 here, I do not think it is enough illustrative. Many readers, including me, are not familiar with this approach.

We agree that we were not clear enough in our explanation of this approach, a point that the other reviewer also highlighted. In our revised methods, we now explain why we took this approach: "*As temperature increases, vapour pressure deficit (D) also increases, which will drive an increase in LE unless there is stomatal closure, but this*

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effect is unrelated to the decoupling mechanism we seek to find. To disentangle the potentially contributing role of D, we also explored these data based on the theoretical expectation (Lloyd et al. 1991; Medlyn et al. 2011; Zhou et al. 2014) that transpiration (E) is approximately proportional to GPP × $D^{0.5}$ (g C $kPa^{0.5}$ m^{-2} d^{-1}; Eqn. 7). This

5 *expectation is based the idea of optimal stomatal behaviour proposed by Cowan and Farquhar (1977) that stomata should be regulated so as to maximise photosynthetic carbon gain less the cost of transpiration. Medlyn et al. (2011) derived the optimal stomatal behaviour as:*

$$G_s = 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a} \tag{1}$$

where G_s is canopy stomatal conductance to CO_2 (mol m^{-2} s^{-1}), A is the net assimilation

10 *rate (μmol m^{-2} s^{-1}), C_a is the ambient atmospheric CO_2 concentration (μmol mol^{-1}), D is the vapour pressure deficit (kPa), the parameter g_1 ($kPa^{0.5}$) is a fitted parameter representing the sensitivity of the conductance to the assimilation rate and the factor 1.6 is the ratio of diffusivity of water to CO_2 in air. Assuming that transpiration is largely controlled by conductance, this relationship can be rearranged to show that*

15 *water-use efficiency (A/E) is approximately proportional to $1/\sqrt{D}$. This dependence has been remarked by many authors (e.g. Lloyd et al. 1991, Katul et al. 2009). Based on this dependence, Zhou et al. (2014, 2015) proposed an "underlying water-use efficiency" (uWUE) for eddy covariance data:*

$$uWUE \approx \frac{GPP\sqrt{D}}{E} \tag{2}$$

20 *Zhou et al. (2014) argued that the $D^{0.5}$ term provided a better linear relationship between GPP and E. Thus, to probe the effect of D, we focused on heatwaves (i.e. approach 2) and plotted LE expressed as evapotranspiration (mm day^{-1}), as a function of GPP×$D^{0.5}$."*

25 **It would be much better to demonstrate directly how A changes with a change in gs (or canopy conductance, gc). There are approaches to calculate gc from sap flow measurements (which I use). I do not know how reliable are approaches to calculate gc from eddy covariance data but if gc can be somehow derived I would be in favor of using it.**

See response above.

3. The timescale of the temperature vs. GPP data. Why did the authors decide to use the maximal daily temperature and compare it to the daily sum of the GPP? Would not it be more appropriate to work with half an hour (or hour) resolution in both temperature and GPP?

The suggested approach is of course a viable analysis framework; however, it would increase the time-resolution (and so the noise in the data) without necessarily adding any additional insight. Our approach analysed multiple heat-extreme events, across multiple site, this would not be possible (or would be harder) if we disaggregated this into diurnal, 4-day events. Here, we are seeking to see the broader patterns at behaviour at the ecosystem-scale.

4. What is the temperature optimum of photosynthesis for the plants in studied ecosystems? The temperature of 37oC for a part of the day may not be high enough to visibly affect the daily GPP. 5.

The temperature optima for leaf and canopy photosynthesis in Eucalypts in southern Australia are well below 30 degrees (see Duursma et al. 2014; Drake et al. 2016; Kumarathunge et al. in review), suggesting that days above 37 degrees should induce a decline in GPP. We also analysed heatwave events (defined as least three consecutive days where the maximum daily temperature exceeded 35°C).

We have addressed this point in our new discussion sub-section (4.1 Why did we not find supporting evidence for ecosystem-scale photosynthetic decoupling?), specifically: "*One could ask whether our analysis considered hot enough temperatures (> 37 °C) to trigger a photosynthetic decoupling mechanism. For example, during an imposed heatwave, Ameye et al. (2012) probed the decoupling mechanism at daily maximum temperatures between 47 and 53°C. Similarly, Zhu et al. (2018) found that most of the 62 species sampled across Australia exhibited maximum critical temperatures near 50°C. However, the temperature optima for leaf and canopy photosynthesis in Eucalypts in southern Australia are well below 30*

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degrees (see Duursma et al. 2014; Drake et al. 2016; Kumarathunge et al. in review),
suggesting that days above 37°C should induce a decline in GPP. Our analysis also
included events with daily maximum temperatures of greater than 40°C and
consecutive heatwave days > 35°C. Therefore, we would argue that insufficiently high

5 *temperatures are unlikely to explain why we did not see clear evidence when looking*
at eddy covariance data."

**Is there any information available how much trees and understory (grasses)
contribute to the LAI and to the GPP?**

10 Across all of these flux sites we analysed, the simple answer is no. We have now added
a statement on this issue of leaf area adjustment to our new discussion: "*Finally,*
although Drake et al. (2018) did not find evidence of increased litterfall during their
heatwave experiment, it is of course possible that at our sites, there was some reduction
in leaf area in response to high extremes. Any leaf area reduction would in turn reduce

15 *transpiration and thus may offset ecosystem-scale estimates of a photosynthetic*
decoupling."

Examining the evidence for sustained transpiration during heat extremes

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Abstract. Recent experimental evidence suggests that during heat extremes, wooded ecosystems may decouple photosynthesis and transpiration, reducing photosynthesis to near zero but increasing transpiration into the boundary layer. This feedback may act to dampen, rather than amplify, heat extremes in wooded ecosystems. We examined eddy-covariance databases (OzFlux and FLUXNET2015) to identify whether there was field-based evidence to support these experimental findings. We focused on two types of heat extremes: (i) the three days leading up to a temperature extreme, defined as including a daily maximum temperature > 37°C (similar to the widely used TXx metric) and (ii) heatwaves, defined as three or more consecutive days above 35°C. When focussing on (i), we found some evidence of reduced photosynthesis and sustained or increased latent heat fluxes in seven Australian evergreen wooded flux sites. However, when considering the role of vapour pressure deficit and focusing on (ii), we were unable to conclusively disentangle the decoupling between photosynthesis and latent heat flux from the effect of increasing vapour pressure deficit. Outside of Australia, the Tier-1 FLUXNET2015 database provided limited scope to tackle this issue as it does not sample sufficient high temperature events with which to probe the physiological response of trees to extreme heat. Thus, further work is required to determine whether this photosynthetic decoupling occurs widely, ideally by matching experimental species with those found at eddy-covariance tower sites. Such measurements would allow this decoupling mechanism to be probed experimentally and at the ecosystem scale. Transpiration during heatwaves remains a key issue to resolve, as no land surface model includes a decoupling mechanism, and any potential dampening of the land-atmosphere amplification is thus not included in climate model projections.

1 Introduction

In response to a warming climate, heatwaves have increased in frequency, magnitude and duration (Alexander et al., 2006; Perkins et al., 2012). Coupled climate models from the Coupled Model Intercomparison Project (CMIP5) project a marked increase in the frequency and severity of these heat extremes (Coumou and Robinson,

2013, Sillmann et al. 2013), highlighting the urgent need to understand the underlying driving mechanisms. Whilst heatwaves are commonly associated with large-scale, high-pressure synoptic systems (anticyclones) (Perkins, 2015), there is increasing evidence of the role of the land-surface in the amplification of heat extremes (Fischer et al., 2007; Teuling et al., 2010; Miralles et al., 2012; Kala et al., 2016; Donat et al. 2017). This land-atmosphere feedback is driven by drying soils and an increase in the sensible heat flux which further warms the boundary layer (Lorenz et al., 2010; Seneviratne et al., 2006). The combination of heat advection and heat storage in the boundary layer is recycled back to the surface over successive days and can lead to increasingly intense heatwaves, including "mega-heatwaves" (Miralles et al., 2014).

A number of studies have highlighted the contrasting functional traits of grasslands and forests as important controls on the role of the land surface in the amplification of heatwaves (Teuling et al. 2010; van Heerwaarden and Teuling, 2014). Grasses often have shallow root profiles, meaning that a relatively small reduction in soil moisture can stress a grassland, resulting in decreased transpiration (either directly via reduced stomatal conductance and/or indirectly via reduced leaf area), leading to a repartitioning of the available (radiant) energy towards sensible heat. Heatwaves also affect forests, but the deeper root profiles that characterise forests may make surface drying less likely to influence the surface energy balance. However, whilst this slower soil water depletion may buffer the transition to increased sensible heat flux, ultimately the decline in soil moisture may still result in heatwave intensification during prolonged dry spells (Teuling et al., 2010).

On the other hand, recent experimental evidence has highlighted a previously overlooked vegetation-atmosphere feedback that may in fact dampen, rather than amplify, heat extremes. A number of heatwave experiments carried out in well-watered, potted plants, have suggested that during temperature extremes, photosynthesis and stomatal conductance (g_s) become decoupled, such that photosynthesis is reduced to near zero, but transpiration is maintained (Ameye et al. 2012; von Caemmerer and Evans, 2015; Urban et al. 2017). For example, in a growth chamber study, Urban et al. (2017) found that g_s increased with rising temperature despite photosynthetic activity shutting down for both *Pinus taeda* and *Populus deltoides* x *nigra*. This result was also confirmed in a field-based whole tree-chamber study by Drake et al. (2018), who reported that transpiration was increased and decoupled from photosynthesis in 6-m tall *Eucalyptus parramattensis* trees during an imposed heatwave of four consecutive days with temperatures exceeding 43°C. Crucially, in the Drake et al. (2018) study, the plants were not well-watered. Instead, these trees had been subject to an imposed one-month drought prior to the experiment to reduce soil water stores. Evidence that transpiration increases during a heatwave, resulting in a cooler canopy temperature, would be consistent with an active mechanism (Trewavas et al. 2009) by trees to cool their canopies. Such a response to heat extremes would increase the latent heat flux into the boundary layer and have two major negative feedbacks on heat extremes: first, the increase in latent heat flux would be at the cost of the sensible heat flux, and a reduction in sensible heat flux would potentially reduce any land amplification on heatwaves over forested regions. Second, by moistening the boundary layer, the chance of clouds being formed would increase, leading to a decrease in solar radiation at the surface and a consequent cooling effect.

In climate models, including CMIP5 models, the land surface is represented by modules that assume photosynthesis and g_s (and consequently transpiration) are inherently coupled (De Kauwe et al., 2013). At high temperatures, models assume that photosynthesis is reduced due to: (i) the direct impairment of the photosynthetic biochemistry; (ii) increased respiration; and (iii) reduced g_s due to the associated high vapour pressure deficit.

Finding additional evidence of a decoupling between photosynthesis and g_s at high temperatures would therefore require revisiting existing assumptions embedded in all climate models and have important implications for model-based assessments of the role of the land surface in the amplification of heat extremes. In this paper we therefore explore eddy-covariance measurements to examine whether there is widespread field-based evidence that during heat extremes, trees decouple photosynthesis and g_s, leading to increased transpiration. In contrast to previous experimental studies (e.g. Urban et al. 2017), our focus is on the ecosystem-scale and so we analysed the photosynthetic decoupling between photosynthesis and transpiration. We chose to focus on wooded ecosystems as the capacity to maintain transpiration throughout a heat extreme most likely requires deep soil water access and is in line with previous experimental evidence from trees (Drake et al., 2018; Urban et al., 2017).

2 Materials and Methods

2.1 Evidence of photosynthesis-transpiration decoupling

A number of experimental studies reporting photosynthetic decoupling have focused on the coupling between A and g_s (Weston and Bauerle, 2007; Ameye et al. 2012; von Caemmerer and Evans, 2015), as opposed to A and E (Drake et al. 2018). At the ecosystem-scale (eddy-covariance), coincident measurements of G_s and LE (or transpiration) are rarely available. Whilst it is possible to estimate the canopy G_s by inverting the Penman-Monteith using measured LE, such an approach necessitates additional assumptions related to the canopy boundary layer conductance (Jarvis and McNaughton, 1986; De Kauwe et al. 2017), the canopy net radiation and the ground heat flux (Medlyn et al. 2017). Here we avoid these assumptions by focusing our analysis on the measured LE flux, as opposed to an estimate of the canopy G_s.

A range of definitions currently exist to identify an extreme temperature event (see Perkins et al. 2014 for a review). Most of these are defined from the context of the climate and may not reflect the physiological adaptations of the vegetation. Given this lack of a single unifying definition, we tested two approaches on the eddy-covariance measurements: (1) the change in GPP and latent heat flux during the four days leading up to and including a temperature extreme, where a temperature extreme was defined as being a day when the daily maximum temperature exceeded 37°C; and (2) the change in GPP and latent heat flux during a heatwave, defined as at least three consecutive days where the maximum daily temperature exceeded 35°C. The first approach can be viewed as analogous to the behaviour leading up to the hottest day of the year (commonly defined as TXx; Klein et al. 2009) and the imposed lower boundary of 37°C similar to selecting a number of "hot" days by using a percentile from the TXx but defined from a more physiological standpoint. This temperature threshold was selected to ensure the events were hot enough to stress the vegetation (Curtis et al. 2016; O'Sullivan et al. 2017; Zhu et al. 2018). For the Australian sites, 37°C was consistent with a site's climate-of-origin + threshold (mean summer maximum temperature; Tmax + 10°C) (Drake et al. 2017).

For each of these events we recorded the maximum daytime temperature, the mean daytime (6am – 8 pm) latent heat flux (LE), and the daytime summed gross primary productivity (GPP). We hypothesised that evidence of decoupling would present itself as a reduction in GPP and an increase LE as air temperatures increased. It is important to clarify that decoupling does not mean that g_s will increase as GPP declines, only that it will decline *less strongly* than current theory would predict if photosynthesis and g_s remained coupled. To test for evidence of decoupling in the flux behaviour we fitted a linear regression to the fluxes from each event leading up to a day where the maximum temperature exceeded 37°C (i.e. approach 1 above), showing events where the fitted slope

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was negative for GPP and positive for LE. We do not necessarily expect the response of GPP or LE to be linear with respect to increasing temperature, but selecting events based on their fitted (positive/negative) slopes allows us to identify patterns in the data. We do not seek to draw inference from the fitted slope being significant or not, given the small number of samples (n=4) in each event. We simply use this distinction to identify stronger positive or negative trends in these data.

As temperature increases, vapour pressure deficit (D) also increases, which will drive an increase in LE unless there is stomatal closure, but this effect is unrelated to the decoupling mechanism we seek to find. To disentangle the potentially contributing role of D, we also explored these data based on the theoretical expectation (Lloyd et al. 1991; Medlyn et al. 2011; Zhou et al. 2014) that transpiration (E) is approximately proportional to GPP $\times$ D$^{0.5}$ (g C kPa$^{0.5}$ m^{-2} d^{-1}; Eqn. 7). This expectation is based the idea of optimal stomatal behaviour proposed by Cowan and Farquhar (1977) that stomata should be regulated so as to maximise photosynthetic carbon gain less the cost of transpiration. Medlyn et al. (2011) derived the optimal stomatal behaviour as:

$$G_s = 1.6\left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a} \tag{1}$$

where G_s is canopy stomatal conductance to CO_2 (mol m^{-2} s^{-1}), A is the net assimilation rate (μmol m^{-2} s^{-1}), C_a is the ambient atmospheric CO_2 concentration (μmol mol^{-1}), D is the vapour pressure deficit (kPa), the parameter g_1 (kPa$^{0.5}$) is a fitted parameter representing the sensitivity of the conductance to the assimilation rate and the factor 1.6 is the ratio of diffusivity of water to CO_2 in air. Assuming that transpiration is largely controlled by conductance, this relationship can be rearranged to show that water-use efficiency (A/E) is approximately proportional to $1/\sqrt{D}$. This dependence has been remarked by many authors (e.g. Lloyd et al. 1991, Katul et al. 2009). Based on this dependence, Zhou et al. (2014, 2015) proposed an "underlying water-use efficiency" (uWUE) for eddy covariance data:

$$uWUE \approx \frac{GPP\sqrt{D}}{E} \tag{2}$$

Zhou et al. (2014) argued that the D$^{0.5}$ term provided a better linear relationship between GPP and E. Thus, to probe the effect of D, we focused on heatwaves (i.e. approach 2) and plotted LE expressed as evapotranspiration (mm day^{-1}), as a function of GPP$\times$D$^{0.5}$.

2.2 Flux data

Half-hourly eddy covariance measurements of the exchange of carbon dioxide, energy, and water vapour were obtained from the OzFlux (http://www.ozflux.org.au/) and FLUXNET2015 (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset) and releases. We confined our FLUXNET2015 analysis to sites classified as wooded according to the International Geosphere–Biosphere Programme, namely: evergreen needleleaf forest; evergreen broadleaved forest; and deciduous broadleaved forest (albeit noting that these names have an inherently Northern Hemisphere bias, and would be better classified as evergreen coniferous, evergreen angiosperm, and deciduous angiosperm forest, respectively). We excluded sites classified as savanna due to the associated complication of needing to attribute the total transpiration flux to grasses and trees; however, we do acknowledge that many of the Australian sites are also relatively open (see screening step below). We also excluded sites classified as mixed forest from our analysis, or those that did not meet our physiological threshold

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of a daily maximum temperature that exceeded 37°C. We also excluded sites that experienced burning. A total of nine sites met these criteria in the Tier 1 (freely available) FLUXNET 2015 database. FLUXNET data were pre-processed using the FluxnetLSM R package (Ukkola et al., 2017). For OzFlux, we used Level 6 gap-filled data following Isaac et al. (2017). These data were then screened to only keep measured and good-quality gap filled data. Events were ignored if a rainfall event greater than 0.5 mm day^{-1} was observed during, or in the two days prior to a heat event in the eddy covariance data as this could bias the LE flux by leading to an increase in LE not associated with the mechanism we wished to identify (i.e. due to soil/canopy evaporation).

2.3 Accumulated heat stress

To characterise a measure of the annual heat accumulated stress experienced by the vegetation we calculated the average number of growing degree days above our upper threshold of 37°C per year (GDD$_{37}$). We used surface air temperature from the 6-hourly, re-analysis by the Global Soil Wetness Project Phase 3 (GSWP3; http://hydro.iis.u-tokyo.ac.jp/GSWP3 and Dirmeyer et al. 2006) dataset during the period of 1970-2015 at a 0.5° spatial resolution. We opted to use this coarser dataset to estimate GDD$_{37}$ rather than the observed flux record due to the longer temporal record, which is likely to be more reflective of longer-term conditions.

2.4 Analysis code

All analysis code is freely available from: https://github.com/mdekauwe/heat_extremes_decoupling.

3 Results

We first focus on the Australian sites as these experienced more temperature extremes due to the warm climate. We found significant evidence of thermal heat stress (Table 1), with 85.8 GDD$_{37}$ at Alice Springs, 85.1 GDD$_{37}$ at Great Western Woodlands, 68.3 at Calperum, 31.7 at Gingin, 13.5 at Cumberland Plains, 13.4 at Whroo and 3.1 at Wombat.

Figure 1 shows a consistent reduction in the flux-derived GPP with increasing daily maximum temperature for each of the events (4-day events, where the maximum temperature > 37°C). We emphasise (see methods) that one should only interpret differences between significant negative slopes (dark blue lines) and negative slopes (dark green lines) as indicative of (possibly) stronger or more consistent reductions in GPP as a function of temperature. This reduction in GPP follows theory related to biochemical, respiratory and stomatal drivers (Lin et al., 2012). With the exception of the Whroo site, GPP was reduced to close to zero at temperatures greater than 40°C. Figure S1 shows the limited occurrences where the fitted slopes indicated a positive (or arguably flat) response with increasing temperature.

Evidence for the hypothesised decoupling between photosynthesis and g$_s$, which would lead to an increase in LE with temperature (but a concomitant decline in GPP, Fig. 1), is shown in Fig. 2. Despite variability in the measured data, at each of the seven sites, LE is found to increase or be sustained as the temperature increases in the lead up to the maximum temperature of each heat event. This increase is steepest at the Wombat State Forest site but is based on only one GDD$_{37}$ event (Table S1). At the other sites, the magnitude of the increase is smaller. However, it is clear that the LE flux is not reduced in line with GPP (Fig. 1) and instead remains sustained with temperature throughout the extreme events. Figure S2 shows the occurrences where the fitted slopes indicated a negative response with increasing temperature. In many cases these events were broadly flat in response to increasing

temperature, again indicating a sustained LE flux. Taken together, Figs. 1, 2 and S2 provide consistent evidence of a decoupling between photosynthesis and transpiration during significant heat extremes across a range of Australian wooded ecosystems.

We now seek to explore the strength of this apparent decoupling in more detail by looking at the ratio of positive to negative fitted slopes shown in Figs 1 and 2 and Figs S1 and S2. Figures 3 and 4 shows the distribution of fitted positive and negative slopes as a function of temperature across the Australian sites for GPP and LE, respectively. Whilst the fitted slopes for GPP are predominately negative (Figure 3), there does not appear to be a consistent pattern in the frequency of positive vs. negative fitted LE slopes, with some sites having more positive slopes (e.g. Gingin, Great Western Woodlands) and some registering more negative slopes (Calperum, Whroo), while others are about even (Alice Springs, Cumberland Plains) (Figure 4). This result is not surprising given our hypothesis that significant transpiration during a heatwave is dependent upon the available supply of soil moisture. As soil water supply becomes limiting, we would expect to find more frequent negative slopes. Consistent with this link to soil moisture, there is a small drop in the proportion of positive slopes (i.e. increased LE) towards the end of summer, which is coincident with an increase in the frequency of negative slopes (Fig S3).

Evidence for an increase in LE with temperature and for photosynthetic decoupling during heat extremes was much weaker across the seven FLUXNET2015 sites (excluding Australian sites; Fig. S4 and S5) that exceeded our 37°C threshold. The number of concomitant negative GPP slopes (Fig. S4) and positive LE slopes (Fig. S5) was noticeably lower when compared to Australian sites, making it harder to draw clear inferences. On the one hand, the weaker evidence from across the larger FLUXNET2015 dataset may point to this decoupling behaviour being species or climatic zone specific (i.e. located in very hot environments). However, we would caution against that interpretation as it is as likely to also point to the lack of representation of FLUXNET sites in regions, other than Australia, that experience very hot temperature extremes (e.g. the average GDD_{37} for the non-Australian sites was >1 at only two sites, Table 1). Given the limited signal in the results obtained from FLUXNET2015 sites, we continue to focus our analysis on Australian sites. However, given the extremely hot summer experienced across Europe in 2018, future studies may wish to revisit this analysis as these updated flux data become available.

Increasing temperature also usually leads to increasing D and as a result, even with perfect coupling between photosynthesis and g_s, we would still expect to see transpiration changing as a function of $GPP \times D^{0.5}$. Figure 5 shows this relationship for consecutive heatwave and non-heatwave days (note Wombat State Forest was excluded from this analysis as there were insufficient consecutive days > 35°C.) If the change in transpiration was being driven by a decoupling of g_s from the response of photosynthesis, we might expect to see increasing transpiration for a given $GPP \times D^{0.5}$, i.e. a spread in points vertically for heatwave days. If the change was being driven by increasing water use efficiency, we might expect to see an increased $GPP \times D^{0.5}$ for a given unit of transpiration, i.e. a spread horizontally for heatwave days. Across the sites there was not a clear difference in the behavior for heatwave vs. non-heatwave days. At Calperum, Cumberland Plains and Whroo the relationship between $GPP \times D^{0.5}$ and transpiration was fairly constant, whereas at Great Western Woodlands, transpiration for a given GPP x $D^{0.5}$ on heatwave days was slightly higher than on non-heatwave days and at Alice Springs and Gingin, slightly lower. At Alice Springs and Gingin, this seems to fit with our expectation of increasing D driving increasing water

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use efficiency, i.e. not the decoupling mechanism. At Great Western Woodlands, there is some indication the data spread vertically, which may be consistent with our expectation outlined for decoupling, but the pattern is not conclusive.

4 Discussion

Recent experimental studies (Drake et al., 2018; Urban et al., 2017) have identified that at very high temperatures (> 40°C), plant decouple photosynthesis and g_s and instead increase transpiration in an apparent active process to cool their canopies. Our results from across seven wooded ecosystems located in Australia were inconclusive. We found some indication (Figs. 1-4) that LE was increased or sustained as GPP decreased when exploring the behavior in the lead up to the hottest days of the year. However, when we focused on heatwave events (i.e. consecutive days > 35°C; Fig. 5) and considered the role of D, i.e. as a driver of increased LE, rather than a photosynthetic-decoupling that would increase the transpiration flux to cool the canopy (i.e. in response to leaf temperature), we found little clear support for photosynthetic decoupling.

4.1 Why did we not find supporting evidence for ecosystem-scale photosynthetic decoupling?

One interpretation of the apparent contradictions between the findings of previous studies and our lack of conclusive evidence at the ecosystem-scale, may simply relate to the interpretation scale. At the leaf-level, plants usually reduce g_s exponentially with increasing D (Oren et al. 1999). However, at high temperatures and with the associated high D, the increased atmospheric demand for water may drive an increase in the transpiration rate. In well-controlled environments, it may be possible to separate the direct response to temperature from that of D, but as our analysis shows, this is more complicated with ecosystem-scale data.

The recent work by Drake et al. 2018 demonstrated clear evidence of photosynthetic decoupling at the canopy scale using a series of whole-tree chambers, which would suggest that this mechanism is unlikely to simply be scale dependent. However, to infer the photosynthetic decoupling, Drake et al. (2018) demonstrating that the observed decline in g_s (and so transpiration) was weaker than predicted by a coupled leaf A-g_s model, which was specifically calibrated to the experimental data. This approach is not viable across multiple sites as it necessitates detailed site measurements for calibrations that are often prohibited by the tall canopy height of mature stands. Applying such a coupled model (e.g. a land surface model) to these site data simply demonstrates that the model is unable to capture the observed site responses (not shown). As a result, we could not reliably infer that the divergence from model behaviour points to evidence of photosynethetic-decoupling, as opposed to, for example, poor parameterization associated with stand level attributes such as leaf area index or root zone soil moisture.

One could ask whether our analysis considered hot enough temperatures (> 37°C) to trigger a photosynthetic decoupling mechanism. For example, during an imposed heatwave, Ameye et al. (2012) probed the decoupling mechanism at daily maximum temperatures between 47 and 53°C. Similarly, Zhu et al. (2018) found that most of the 62 species sampled across Australia exhibiting maximum critical temperatures near 50°C. However, the temperature optima for leaf and canopy photosynthesis in Eucalypts in southern Australia are well below 30 degrees (see Duursma et al. 2014; Drake et al. 2016; Kumarathunge et al. in review), suggesting that days above 37°C should induce a decline in GPP. Our analysis also included events with daily maximum temperatures of

greater than 40°C and consecutive heatwave days > 35°C. Therefore, we would argue that insufficiently high temperatures are unlikely to explain why we did not see clear evidence when looking at eddy covariance data.

Our approach relies on GPP which is not directly observed but is instead modelled using assumptions related to the extrapolation of night-time respiration and measured net ecosystem exchange. It is debatable whether these assumptions hold at very high temperatures, and examining these modelled GPP estimate estimates at high temperatures warrants further investigation, particular as researchers leverage these data to explore the responses of the vegetation to temperature extremes. Eddy-covariance data are also known to have issues closing the energy balance (Foken 2008; Wilson et al. 2002; Hendricks-Franssen et al. 2010), which may introduce errors into the LE flux (see Wohlfahrt et al. 2009, for a detailed discussion). For the seven Australian flux sites that make up the majority of our analysis, we calculated the ratio of the sum of latent and sensible heat fluxes to the sum of the net radiation and ground heat flux, finding on average a ~17% imbalance in the ratio (range 7-30%). Importantly however, we did not find any difference in this imbalance in heatwave vs. non-heatwave days. This is in line with other studies   Despite these limitations, FLUXNET eddy covariance flux measurements still present our best ecosystem-scale estimates of vegetation responses to heat extremes and have been widely analysed to address these types of questions (Ciais et al. 2005; Teuling et al. 2010; Wolf et al. 2013; von Buttlar et al. 2018; Flach et al. 2018).

Our analysis is also limited by the number of extreme events recorded in the existing record and the clear bias in these data towards Australian sites is due to the lack of representation of sites within the FLUXNET data collection that sample locations in extreme environments outside of Australia. In our analysis we focused on hot days and heatwaves with a very hot temperature range, i.e. consecutive days > 35°C, hence a fair criticism of our approach is that a lower threshold might be also relevant for different environments and species. Any choice of threshold is arguably arbitrary; we chose ours to ensure we were focusing on the vegetation response to a threshold that would lead to a degree of physiological limitation and is in line with studies that suggest this occur at temperatures above our chosen thresholds (Curtis et al. 2016; O'sullivan et al. 2017; Zhu et al. 2018).

Finally, although Drake et al. (2018) did not find evidence of increased litterfall during their heatwave experiment, it is of course possible that at our sites, there was some reduction in leaf area in response to high extremes. Any leaf area reduction would in turn reduce transpiration and thus may offset ecosystem-scale estimates of a photosynthetic decoupling.

4.2 Implications for models

The potential implications for modelling studies that focus on heat extremes are clear, particularly for studies in Australia. None of the current generation of land surface models have the capacity to decouple transpiration from the down-regulation of photosynthesis with increasing temperature. Instead models assume photosynthesis and g_s (and consequently transpiration) remain coupled at all times. As a result, climate models may underestimate the capacity of the vegetation to dampen heat extremes in simulations for Australia. This is also true of more sophisticated plant hydraulic models (Williams et al. 2001) and profit-maximisation approaches (Wolf et al. 2016; Sperry et al. 2016) that hypothesise the cost of water is not fixed in time, but instead increases with increasing water stress. For these latter approaches to account for a photosynthetic decoupling they would need to prioritise

maintaining an optimum canopy temperature above a net carbon gain. However, mechanisms to capture this within models should likely wait for further supporting evidence of photosynthetic decoupling.

4.4 Route forward

Our study did not find conclusive evidence for the experimentally observed photosynthetic decoupling using eddy-covariance data. However, it would be premature to interpret our results as evidence that such a mechanism does not scale from the leaf to ecosystem. Instead, understanding the response of transpiration during heatwaves remains an important issue to resolve. It is clear that further experimental results will be required to resolve this issue and these studies will need to be able to more clearly separate the decoupling mechanism from the response to D. To make progress on this photosynthetic-decoupling issue will likely require concurrent leaf-level gas-exchange measurements (photosynthesis and g_s) as well as canopy/ecosystem-scale transpiration. To date, most of our insight has been limited to the leaf-scale (Ameye et al. 2012; von Caemmerer and Evans, 2015; Urban et al. 2017), or a single canopy-scale study situated in whole-tree chambers (Drake et al. 2018). To bridge this gap in our knowledge, it would be desirable to align future experiments with measurements taken at eddy covariance sites (i.e. by using matching species) to allow us to more easily test whether this mechanism scales to the ecosystem.

5. Conclusion

A number of recent experimental studies have highlighted that during heat extremes, plants may decouple photosynthesis and transpiration: reducing photosynthesis to near zero but increasing transpiration into the boundary layer. In this study we used eddy-covariance measurements to examine the evidence for a photosynthetic-decoupling in wooded ecosystems at the ecosystem-scale during heat extremes. When focussing on the three days leading up to a temperature extreme (a daily maximum > 37°C), we found some evidence of reduced photosynthesis and sustained or increased latent heat fluxes in seven Australian evergreen wooded flux sites. However, when considering the role of vapour pressure deficit, we were unable to conclusively disentangle photosynthetic-decoupling from the effect of increase in transpiration due to increasing vapour pressure deficit during heatwaves (three or more consecutive days above 35°C). The response of transpiration during heat extremes remains a key issue to resolve and will require targeting measurements at both leaf and canopy/ecosystem scales. None of the current generation of land surface models has the capacity to decouple transpiration from the down-regulation of photosynthesis with increasing temperature and as a result, will not include any potential dampening of the land-atmosphere amplification in climate model projections.

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Data availability. All Eddy covariance data are available from: http://www.ozflux.org.au/ and http://fluxnet. fluxdata.org/data/fluxnet2015-dataset

Competing interests. The authors declare no competing financial interests.

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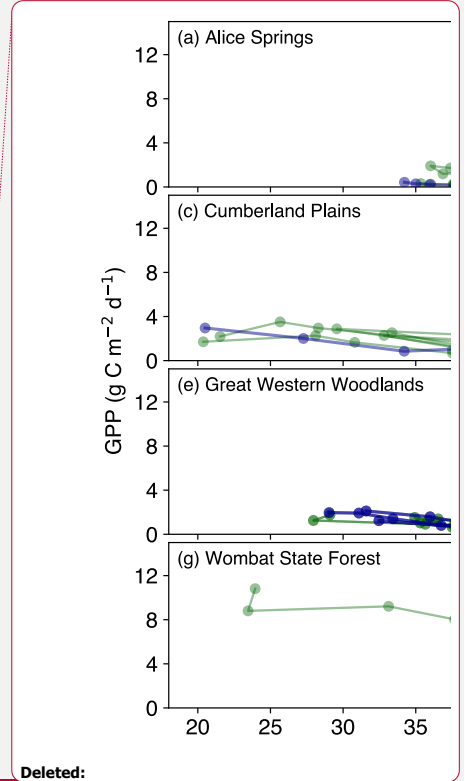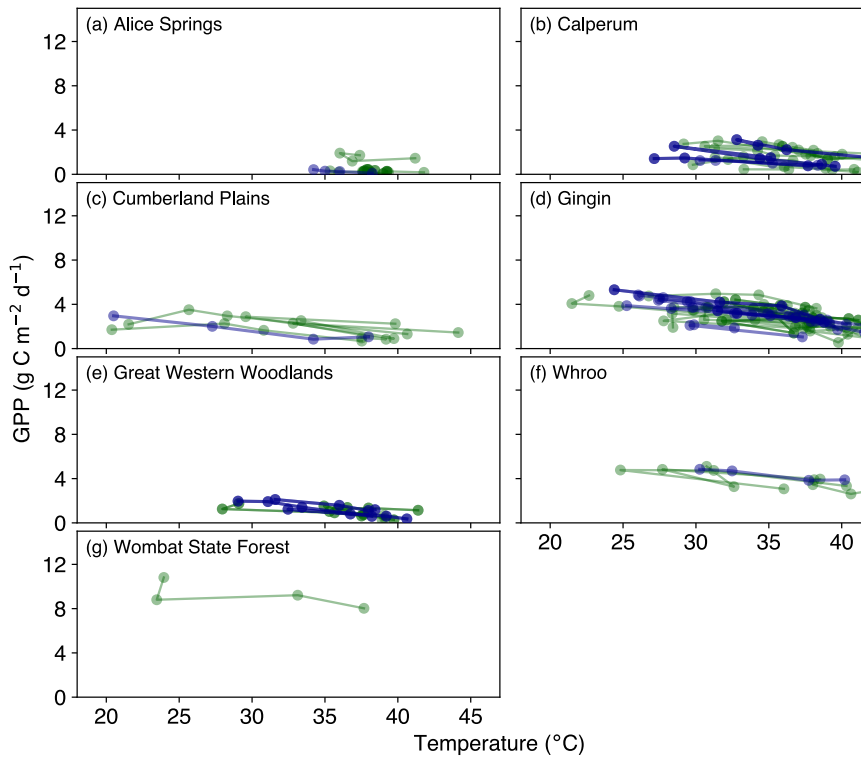
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Figures

Figure 1: Evolution of GPP in the three days prior to and including a hot temperature extreme (daily maximum temperature exceeded 37˚C). Dark blue lines represent events in which a fitted linear regression indicated a significant negative slope, whilst dark green lines represent events where the fitted slope was negative but not significant. Events where the fitted slope was positive are shown in Figure S1.
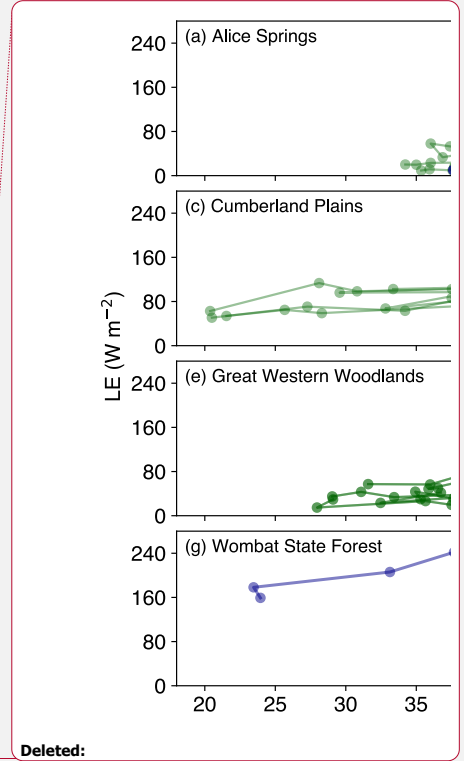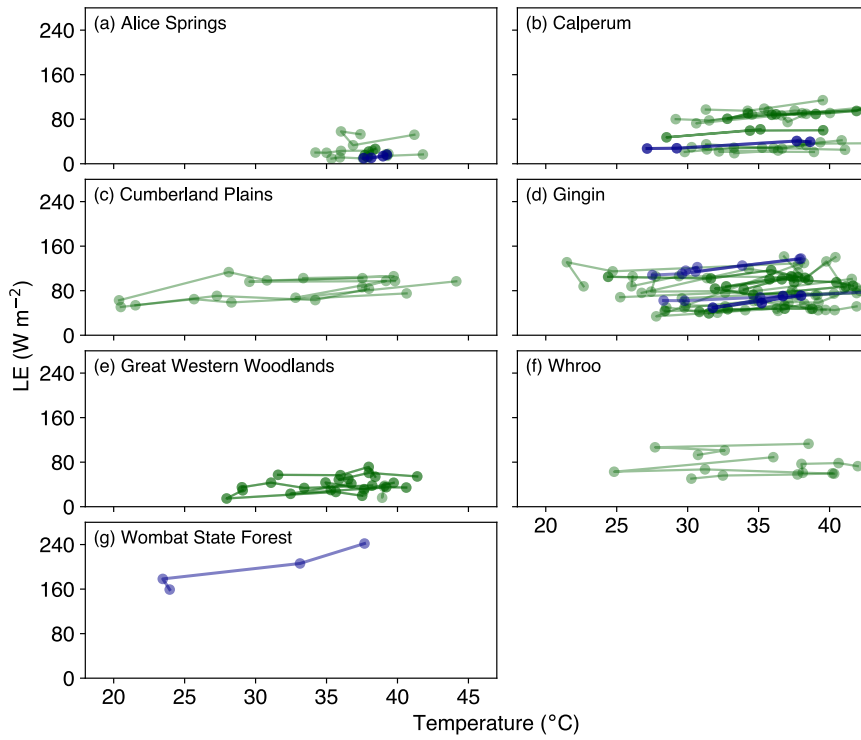
Figure 2: Evolution of LE in the three days prior to and including a hot temperature extreme (daily maximum temperature exceeded 37˚C). Dark blue lines represent events in which a fitted linear regression indicated a significant positive slope, whilst dark green lines represent events where the fitted slope was positive but not significant. Events where the fitted slope was negative are shown in Figure S2.
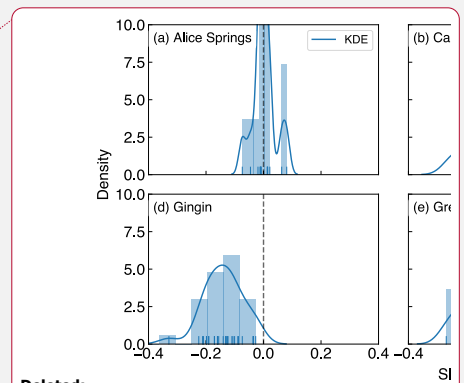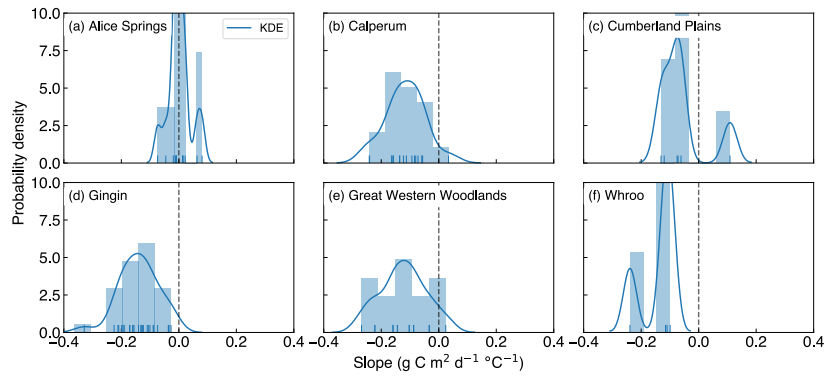
Figure 3: Probability density and histogram showing the distribution of fitted positive and negative GPP slopes across the OzFlux sites. The dark blue curve shows the fitted kernel density estimate (KDE) and the vertical blue lines along the x-axis are "rugs", which represent the individual occurrence of fitted slopes. Data from Wombat State Forest has been omitted from the graph as there was only one slope. Note, the sum of the bars can exceed one as the normalisation ensures that the sum of the bar heights multiplied by the bar widths equals one, which allows the normalised histogram to be compared to the KDE, which is normalised so that the area under the curve equals 1.
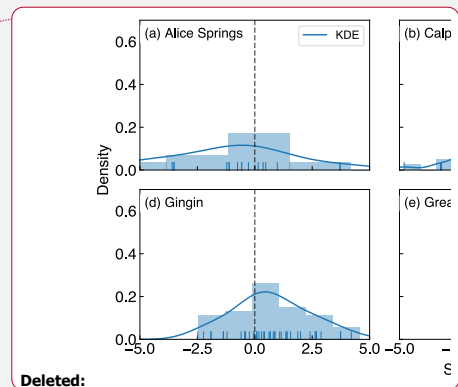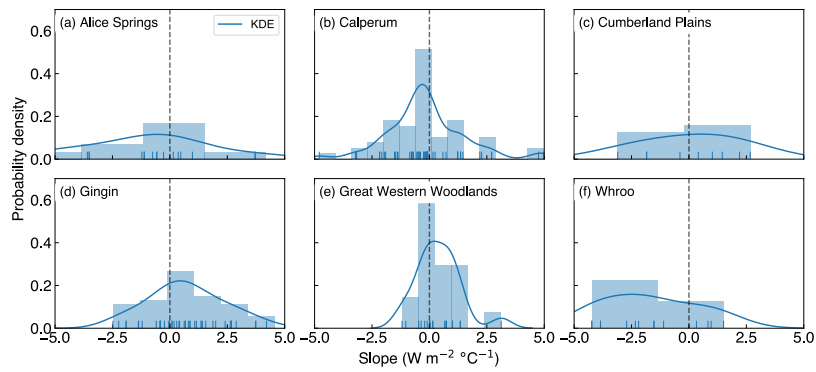
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Figure 4: Probability density and histogram showing the distribution of fitted positive and negative LE slopes across the OzFlux sites. The dark blue curve shows the fitted kernel density estimate (KDE) and the vertical blue lines along the x-axis are "rugs", which represent the individual occurrence of fitted slopes. Data from Wombat State Forest has been omitted from the graph as there was only one slope. Note, the sum of the bars can exceed one as the normalisation ensures that the sum of the bar heights multiplied by the bar widths equals one, which allows the normalised histogram to be compared to the KDE, which is normalised so that the area under the curve equals 1.
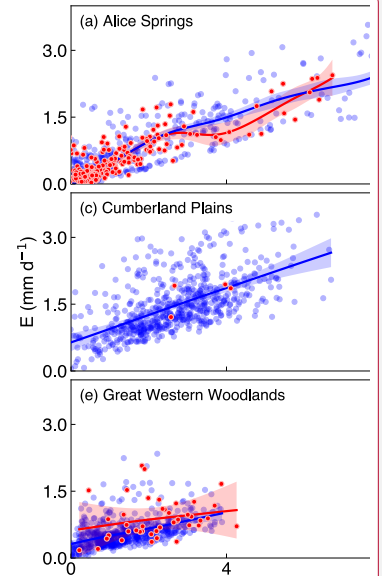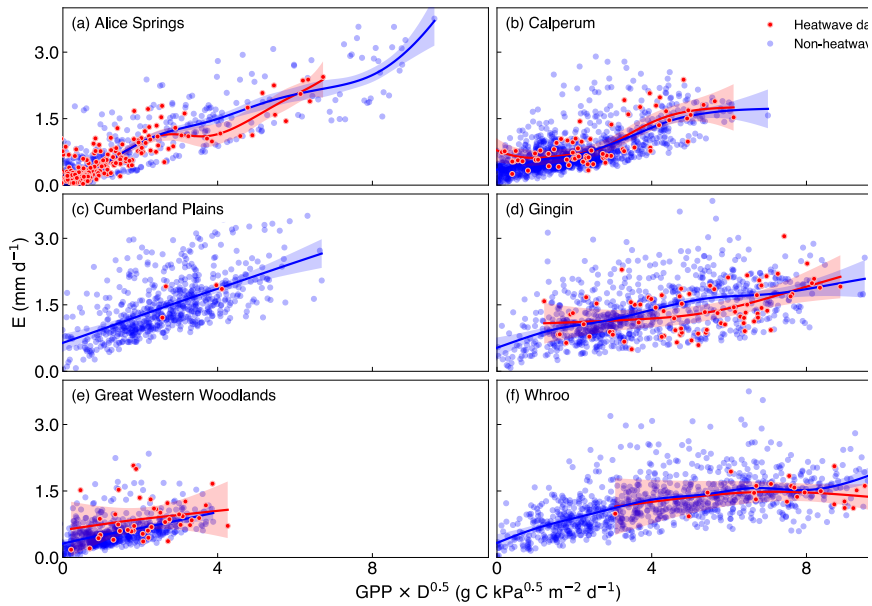
Figure 5: E as a function of GPP x $D^{0.5}$ on heatwave and non-heatwave days. The solid lines are smoothed time series using a generalized additive model (with a 95% confidence intervals). Note the generalized additive model was not fit to the heatwave days at Cumberland Plains due to the limited data.

Tables

Table 1. OzFlux and FLUXNET2015 site information. GDD_{37} is the average number of growing degree days above our threshold of 37°C. Plant Functional types (PFT) were: ENF - evergreen needleaf forest; EBF - evergreen broadleaved forest; and DBF - deciduous broadleaved forest. Note the FLUXNET sites Castel d'Asso 1 and 3 and Roccarespampani 1 and 2 have been combined in the table.

Site	Latitude	Longitude	GDD_{37}	Dominant Species	Years	Reference
OzFlux sites						
Alice Springs	-22.28	133.25	85.8	Acacia aneura	2010-2013	Cleverly et al. (2013)
Calperum	-34.00	140.59	68.3	Mallee	2011-14	Meyer et al. (2015)
Cumberland Plains	-33.61	150.72	13.5	Eucalyptus moluccana and Eucalyptus fibrosa	2013-14	Renchon et al. (2018)
Gingin	-31.37	115.71	31.7	Banksia	2012-14	Silberstein (2015)
Great Western Woodlands	-30.19	120.65	85.1	Eucalyptus salmonophloia	2013-15	Macfarlane (2013)
Whroo	-36.67	145.03	13.4	Eucalyptus microcarpa and Eucalyptus leucoxylon	2012-14	McHugh et al. (2017)
Wombat State Forest	-37.42	144.09	3.1	Eucalyptus obliqua, Eucalyptus radiata and Eucalyptus rubida	2011-14	Griebal et al. (2016)
FLUXNET2015 sites						
Castel d'Asso	42.38	12.02	0.1	Poplar species	2011-14	Sabbatini et al. (2016)
Le Bray	44.71	-0.77	0.5	Pinus pinaster	1996-08	Berbigier et al. (2001)
Mongu	-15.44	23.25	52.6	Brachystegia bakeriana and Brachystegia spiciformis	2000-09	Merbold et al. (2009)
Morgan Monroe State Forest	39.32	-86.41	21.5	Acer saccharum, Liriodendron tulipifera, Sassafras albidum, Quercus alba and Quercus nigra	1999-2014	Schmid et al. (2000)
Puechabon	43.74	3.60	0.4	Quercus ilex	2000-14	Rambal et al. (2004)
Qianyanzhou	26.74	115.05	20.9	Pinus elliottii and Pinus massoniana	2003-05	Yu et al. (2006)
Roccarespampani	42.39	11.92	0.2	Quercus Cerris L.	2000-12	Rey et al. (2002)