

Response to interactive comment by Anonymous Referee #3 on “Water stress induced breakdown of carbon-water relations: indicators from diurnal FLUXNET patterns”

Overall, I am supportive of the goals of this study. I agree that the asymmetry of the diurnal cycle of ET, and the correlation between GPP and ET, likely contain meaningful information about ecosystem response to drought. I also applaud the author’s efforts to link these metrics to insights informed by mechanistic theory.

1. The analysis presented here is very broad (i.e. results are synthesized across many sites, and often many PFTs). Cross-site syntheses like this are invaluable for understanding broad patterns in vegetation functioning; however, the objectives of this study would benefit from a more in-depth analysis of the results at a least few sites, preferably sites where there exist independent estimates of plant water relations during periods of hydrologic stress (i.e. from gas exchange, sap flux, isotope analysis of tree cores, etc). This sort of analysis would give the readers confidence that the C_{ET} and DWCI metrics are really reflecting stomatal and non-stomatal limitations to transpiration and carbon uptake, and aren’t unduly contaminated by the many sources of uncertainty in using eddy covariance measurements to infer GPP and water use efficiency (e.g. Knauer et al. 2017). Or, to put it differently the new metrics introduced in this manuscript merit some “proof of concept” before they are applied broadly.

As the reviewer has pointed out, the presented analysis is indeed takes a broad approach to ecosystem physiology. This broad approach was undertaken in part due to the lack of a congruent dataset of independent estimates of plant water relations with which to compare the FLUXNET dataset. While sites do exist with measurements such as sap flux and isotope composition, they are currently not well homogenized and synchronizes in a way that is conducive to do an analysis across ecosystems, though some are definitely in the pipeline such as the SAPFLUXNET initiative. However, in an effort to give the presented manuscript a more in-depth analysis, we have included a new section in the manuscript which focuses on 6 European sites and compares average monthly values to the monthly values in 2003 when the continent was hit by a heat wave and drought. As seen in Figure 3 (here R1), the sites show diverse responses in the summer of 2003, with some exhibiting distinct morning shifts and some decoupling, but each of the sites show some response to the high temperatures and low water conditions of the heatwave. This new figure is accompanied by the following text in the Results section:

As a case study, C_{ET}^* and DWCI time-courses for eight sites from Europe are shown in Figure 3, with an emphasis on 2003 when the continent was struck by a heatwave that was shown to effect both the carbon and water cycles [1, 9, 2]. For DWCI, forest sties showed high water:carbon coupling throughout the growing season, with the exception of Peuchebon (FR-Pue) which showed

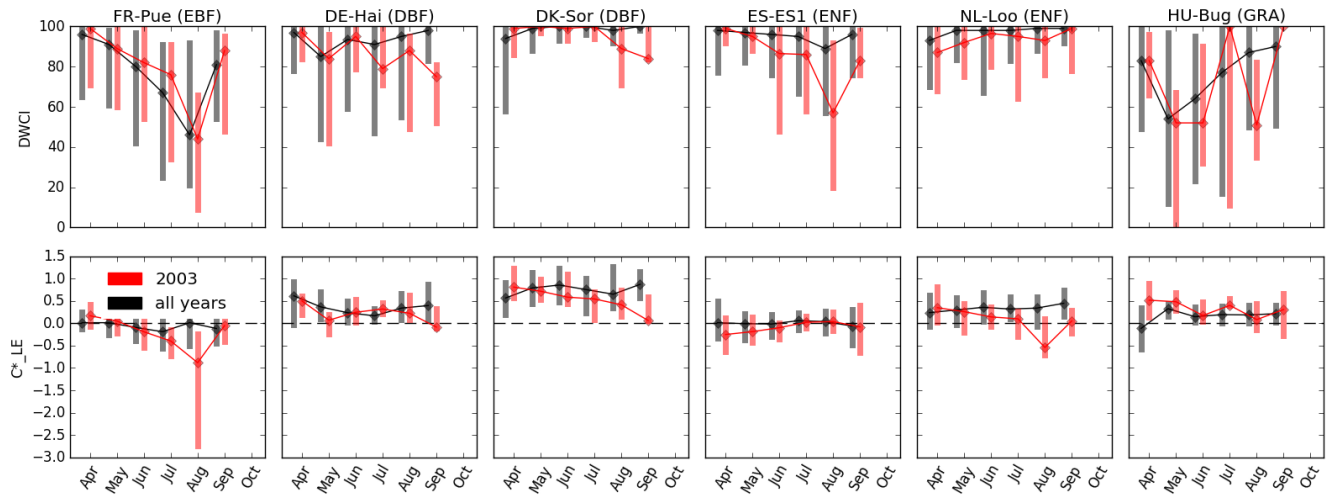


Figure R 1: Monthly median diurnal water carbon index (DWCI, lower panels) and diurnal centroids (C_{ET}^* , upper panels) for 6 sites in Europe. Data from all years available (black) is compared to 2003 (red) during which a drought event resulted in high temperatures and low precipitation throughout the summer. Note DWCI of 0-100 indicate lowest-highest probability of diurnal carbon:water coupling and C_{ET}^* of -1-1 indicate one hour morning shifted-one hour afternoon shifted ET. Vertical bars represent interquartile range. Sites from 5 plant functional types: evergreen broadleaf (EBF), deciduous broadleaf (DBF) and evergreen needleleaf (ENF) forests, as well as grasslands (GRA). Ecosystems show tendencies of morning shifts (e.g. DK-Sor and IT-Mal) and carbon:water decoupling (e.g. ES-ES1 and HU-Bug) during the drought year.

a regular seasonal cycle of decoupling. The grassland site (HU-Bg) showed a higher variability in DWCI compared to the forest sites (all others). All sites showed either a decrease in median DWCI or an increase in variability during 2003, generally in July or August, particularly at Hainich (DE-Hai), Bugacpuszta (HU-Bug), and El Saler (ES-ES1). This increase in decoupling during 2003 is consistent with the hypothesis of non-stomatal limitations being expressed in hot, dry conditions. Median diurnal centroid values across all years varied in absolute magnitude, but were generally near or above zero, i.e. the water cycle showed no shift or an afternoon shift. One exception would be the Mediterranean oak forest of Puechabon, which shows a slight seasonal cycle of morning shifts going from a slight afternoon shift to a slight morning shift during June, July, and August. During drought years, sites that showed distinctive morning shifts were Puechabon (FR-Pue), Soroe (DK-Sor), and Loobos (NL-Loo). The framework that morning shifts are associated with water stress from soil moisture depletion would be supported by the increase in morning shifts during 2003, though factors such as species composition and access to soil water would play a significant factor and could account for the differences among sites. All sites which had significantly different ($p < 0.05$, Wilcoxon rank-sum test) DWCI values between 2003 and all other years except Puechabon, whereas with C_{ET}^* only Puechabon, Soroe, and Loobos showed significant differences.

Furthermore, we hope that by demonstrating the response of the metrics across a large number of sites, and providing the equations and associated code, we can provide the tools to those with both the access

and expertise of these particular sites with independent measurements. In this regard, we have taken the suggestion given by reviewer #1 to give a direct call for such an analysis, with the following text being added to the Discussion section “Looking beyond sums and means”:

Given the broad nature of the analysis here, the metrics and hypothesis presented would benefit from site specific validations such as looking to see if the morning shifts and decoupling are indeed associated with lower soil moisture levels, leaf water potentials, and/or decreases in sap flux. Sap flux in particular could give some interesting insights, as the diurnal patterns in sap flux velocity will also have an offset to incoming radiation related to tree capacitance, therefore relating sap flow diurnal centroids to the ET diurnal centroid could give some information on changes in plant water recharge. Furthermore, the diurnal centroid base metrics complement the hysteresis quantification methods such as those employed by Zhou et al. [13] and Matheny et al. [7], with the advantage of C_{ET}^* being compensation for cloudy conditions and possibly less influence of noise, though an intercomparison would be useful to explore the strengths and weaknesses of the different approaches. By providing both the equations and related code of the metrics, we the authors hope the metrics will be used by the community for both validation and to further ecophysiological understanding.

Finally, we have added Figure 5 (R2) highlighting the tree vs. grass responses based on evaporative fraction, which shows both the effect of decoupling and morning shifts in forest, savanna, and grassland sites with lower evaporative fraction, as well as showing the divergent responses. We hope these added analyses will give the reader confidence that the metrics are reflecting water stress responses.

2. I also had a few concerns about the presentation and interpretation of the water use efficiency theory. First, the authors attributed the afternoon decline in ET to “hydraulic limitation” driven specifically by challenges of moving liquid water from roots to the leaves as soil dries (e.g. Lines 24-25). While I agree that hydraulics are an important control on stomatal functioning, stomates may also close directly in response to rising VPD even if soil moisture is unchanged (as discussed at length in the stomatal optimization literature), and the mechanisms responsible for the VPD response are still not yet clear. Thus, it may be more appropriate to describe the afternoon decline in ET as simply “stomatal limitations.”

The reviewer makes a very good point and highlights the complexities of the problem. Indeed, the key control mechanism a plant has in the soil-plant-atmosphere continuum is via the stomates, especially at the diurnal scale. Likewise, we agree that the stomates have been shown to have a primary response to VPD, indeed we introduce the $VPD^{-0.5}$ term when calculating the DWCI in an effort to mitigate the VPD effects on decoupling diurnal GPP and ET. However, the closure of stomates due to VPD would cause an afternoon decrease in GPP but not necessarily in ET as VPD is also a driver of ET. In other words, as the stomate is closing in response to VPD, VPD is also pulling harder at the water in the leaf. So the

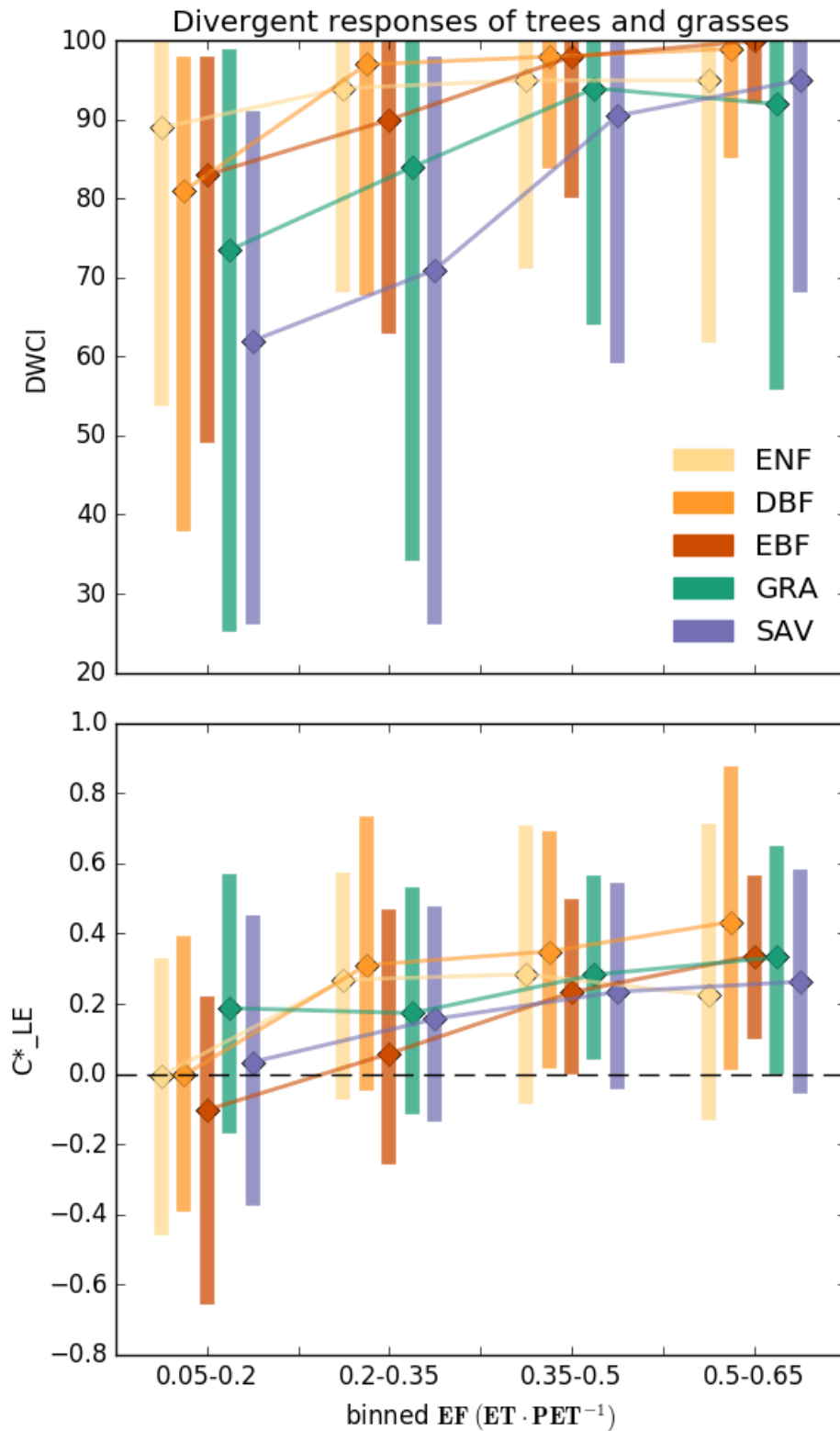


Figure R 2: Median diurnal water carbon index (DWCI, upper panel) and diurnal centroid (C^*_{ET} , lower panel) of plant functional types binned by evaporative Fraction (EF, low values indicate dry conditions). Note DWCI of 0-100 indicate lowest-highest probability of diurnal carbon:water coupling and C^*_{ET} of -1-1 indicate one hour morning shifted-one hour afternoon shifted ET. Evergreen needleleaf (ENF), deciduous broadleaf (DBF), and evergreen broadleaf (EBF) forests show increased morning shifts (low C^*_{ET}) with decreasing EF when compared to grassland (GRA) sites which tended to have decreased carbon:water decoupling (low DWCI) with decreasing EF. Savanna ecosystems (SAV) show a high degree of decoupling and intermediate levels of morning shifts. Vertical bars represent interquartile range.

hypothesis driving the diurnal centroid is then that the plant is responding to some form of hydraulic limitation of moving water, with the assumption that if the plant had unlimited access to water, and the ability to move it to the leaves, it would continue to keep the stomates open and take up carbon (the carbon cost of water would be zero as water is infinite). Though the reviewer makes a good point and this is simply a hypothesis for the metrics. As a further test, we have added additional subplots to Figure 4 (Figure 6a,d in the new manuscript, here R3a,d) which shows the response (as color) along the axes of evaporative fraction ($EF=ET/ET_{pot}$) and VPD.

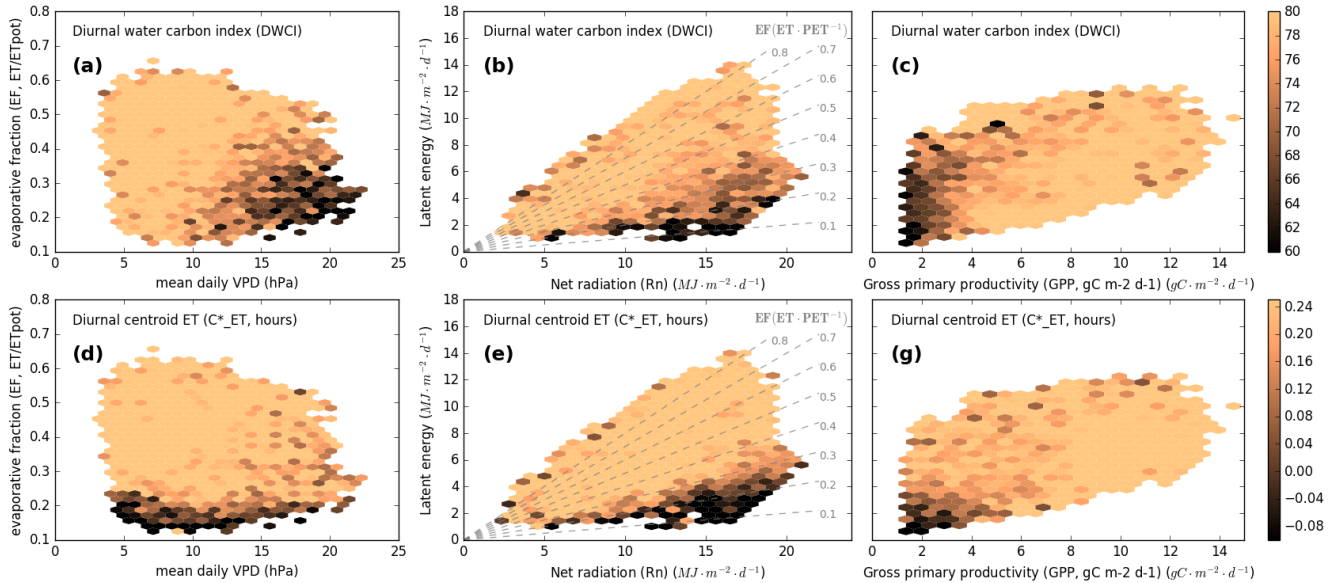


Figure R 3: Mean DWCI (upper panels) and C_{ET}^* (lower panels) with respect to evaporative fraction (EF) by vapor pressure deficit VPD (a,d), latent energy (LE) by Rn (b,e) and LE by GPP (c,g). Note DWCI of 0-100 indicate lowest-highest probability of diurnal carbon:water coupling and C_{ET}^* of -1-1 indicate one hour morning shifted-one hour afternoon shifted ET. Points with high Rn and low LE are associated with both low DWCI and C_{ET}^* , indicating that both metrics are related to water limitations. Though both metrics are associated with low EF, DWCI shows a much higher response to atmospheric demand as measured by VPD, with C_{ET}^* showing very limited response. Both metrics, and DWCI in particular, show low values with high ET and low Rn, though these points are also associated with over closed energy balances ($LE+H>Rn-G$). Both metrics are associated with low GPP, but the C_{ET}^* is restricted to both low GPP and ET, indicating water and carbon can decouple over a wider range of water stress. This also holds when points with energy balance over-closer are excluded (data not shown).

From the new subplot (Figure 6a,d (R3a,d)), one can see that the diurnal centroid in fact is not very responsive to mean daily VPD, instead being almost entirely responsive to EF. This would support our hypothesis that the morning shift is significantly driven by hydraulic limitations rather than simply the VPD response. In contrast, the same subplots shows that the DWCI is much more responsive to high VPD, indicating that decoupling is happening during high atmospheric demand. This is highlighted in the Results section with the text:

Apart from the response to periods of high LE and low Rn, the metrics showed diverging response when looking at EF (ET/PET which is similar to LE/Rn) and VPD, with DWCI showing a much stronger response to VPD and C_{ET}^* showing a much stronger response to EF (Figure

6a,d). This difference in response would indicate that DWCI is more responsive to atmospheric demand (estimated via VPD) and C_{ET}^* is more responsive to water limitations.

So while the reviewer is correct in that this morning shift likely would ultimately be a stomatal control, we hope to highlight this underlying hypothesis which differentiates what we are looking for from the stomatal limitations often describing VPD effects on carbon uptake. To clarify this point in the introduction, we have added the following text:

Under this hydraulic limitation framework a plant will be reacting to the inability to transport water, even though the key control mechanism for a plant is via the stomata, possibly expressed as an increase in sensitivity. Such assumptions are consistent with the mechanisms encoded in some land surface and ecosystem models, which account for water limitations by scaling the water to carbon ratio in relation to available soil moisture.

3. Next, the function $ET = iGPP \sqrt{VPD}$, proposed by Zhou et al. (2015), is referred to in this manuscript as the “Katul” model; presumably this nomenclature originates from the theory presented in Katul et al. (2010), which presents arguments leading to the equation: $ET = GPP \times \sqrt{VPD} / \sqrt{1.6\lambda c_a}$ The parameter λ is the so-called “marginal water use efficiency” and c_a is atmospheric CO₂ concentration. This is similar to the Eq. 8 in the present manuscript: $ET = i \times GPP \times \sqrt{VPD}$ If $i = 1 / \sqrt{1.6\lambda c_a}$ I appreciate that the authors have attributed the model to Katul et al. (2010), who presented the theory on which the equation is based. However, before the authors attribute the model’s “inability to make accurate predictions” to “be a result of a failure of their underlying assumptions,” (Page 9, lines 10-11), care should be taken to make sure the underlying assumptions are properly stated and considered. The Katul et al. (2010) result relies on an assumption of Rubisco-limited photosynthesis (which generates a linear A-Ci curve). . .this assumption is not likely to hold in dense forests where understory vegetation is often light-limited. Second, and perhaps more importantly, stomatal optimization theory assumes that the parameter λ should hold constant over timescales of hours, but varies over longer timescales (days to weeks) as other slowly-evolving boundary conditions change (Manzoni et al. 2013, Palmroth et al. 2013). So in that regard, I disagree with the author’s assessment on Page 8, Line 5, that the “Katul” model “makes the assumption that the WUE is constant if corrected by the effect of VPD.” The potential for λ to vary may also help to explain the tendency of the Katul (and other) models to underestimate WUE during dry conditions (i.e. Figure 5), especially if the ‘i’ parameter is determined using observations from well-watered conditions.

We would like to thank the reviewer for so succinctly summarizing what is not always made clear in many manuscripts, including this one in present state. In regard to the initial comments, the reference to Katul 2010 is one that should be cited in this context and this reference has now been included in the appropriate places. Furthermore, the text has been changed so that the model is now initially introduced as:

These carbon:water links are fundamental to understanding how stomata are regulated and

underly key functioning in mechanistic plant and ecosystem models. One such set of models are those based on optimality theory which posit that plants tend to optimize carbon gains to water losses, such as those described by Katul et al. [4] and Katul, Palmroth, and Oren [3]. These concepts from Katul, which carry the assumptions of RuBISCO limitation, were built upon by Zhou et al. [13] and Zhou et al. [11] to give the equation,

$$uWUE = \frac{GPP \cdot \sqrt{VPD}}{ET}$$

where the \sqrt{VPD} accounts for the stomatal response to vapor pressure deficit (VPD). Accounting for the VPD response allows for a more stable metric of WUE that is temporally more stable and physiologically more meaningful, such as when comparing the diurnal cycles of carbon and water.

The point that the carbon cost of water is likely to change is further highlighted in the Materials and Methods where the subsection “Models and parameter estimation” has been expanded to say,

The “Katul” model, as defined and used in calculation of the DWCI, is based in stomatal optimization theory [4, 3, 11], which makes the assumption that the WUE is constant if corrected by the effect of VPD, using an inverse square root as the assumed relationship. Though the constant nature of uWUE may not be correct, with the optimal carbon cost of water changing over day or weeks [5, 8], a yearly parameter of uWUE was estimated which is consistent with other modeling exercises [12].

Note that an explanation of how these yearly parameters are calculated follows this statement, which hasn’t changed from the original submission. Finally, as the reviewer has pointed out, our statement that biases of the Katul model are a failure of underlying assumptions becomes misleading as we do not reference what assumptions we have made. As such, this has been amended to say:

Both the Katul and Boese models are theoretically based and here implemented have the underlying assumptions of RuBiSCO-limited conditions and constant carbon cost of water throughout the season which may not reflect reality.

4. Finally, when using the shape of the diurnal pattern of ET to infer stomatal limitation, I wondered why the authors focused only on the shift in the peak, and not the overall degree of asymmetry between morning and afternoon periods (for example, if the ET data from hours 0-12 are reflected about the solar noon axis, that is the area between the reflected and actual ET data).

This idea was actually explored during the course of the analysis while looking for a metric to quantify

the asymmetry of the diurnal patterns, and would lead in the direction of hysteresis analysis that other researchers had done such as Zhou et al. [13] and Matheny et al. [7]. One issue with this type of analysis is that one tends to compare individual half hours of the morning to half hours in the evening which can be problematic. For example, in the case of the example the reviewer suggests, a cloud passing in afternoon would be indistinguishable to a physiological response to water limitation as both would reduce the water flux. So by using the diurnal centroid of ET vs Rg we are able to measure the asymmetry while correcting for changes in incoming energy. Previous experiences with hysteresis approaches showed that the quantifications could be very sensitive to noise, especially at the daily scale and the diurnal centroid may be a more robust metric. However, the reviewer makes a good point that hysteresis quantification and diurnal centroid based metrics are two approaches to explore the same effect, a point which we have added to the discussion:

Furthermore, the diurnal centroid base metrics complement the hysteresis quantification methods such as those employed by Zhou et al. [13] and Matheny et al. [7], with the advantage of C_{ET}^* being compensation for cloudy conditions and possibly less influence of noise, though an intercomparison would be useful to explore the strengths and weaknesses of the different approaches.

A few other comments include:

5. Page 2, lines 15-24. The presentation of the iWUE models would benefit from a more general explanation of what each of the three metrics actually describes and/or is sensitive too. E.g. WUE is useful for understanding broad patterns of ecosystem water use and carbon uptake, but is sensitive to non-biological drivers (e.g. VPD). The iWUE attempts to correct for the direct effect of VPD on transpiration, and is thus a more biologically relevant metric. The uWUE further attempts to correct for stomatal closure under high VPD, and therefore may be more closely linked to the “non-stomatal” limitations to gas exchange during drought.

In an effort to make this section more clean and concise, we have removed the reference to Beer et al. 2008 and iWUE as it was not further referenced in the manuscript. We have also taken the reviewers advice and expanded the section to give some context to the VPD term. The text now reads:

These carbon:water links are fundamental to understanding how stomata are regulated and underly key functioning in mechanistic plant and ecosystem models. One such set of models are those based on optimality theory which posit that plants tend to optimize carbon gains to water losses, such as those described by Katul et al. [4] and Katul, Palmroth, and Oren [3]. These concepts from Katul, which carry the assumptions of RuBISCO limitation, were built upon by Zhou et al. [13] and Zhou et al. [11] to give the equation,

$$uWUE = \frac{GPP \cdot \sqrt{VPD}}{ET}$$

where the \sqrt{VPD} accounts for the stomatal response to vapor pressure deficit (VPD). Accounting for the VPD response allows for a more stable metric of WUE that is temporally more stable and physiologically more meaningful, such as when comparing the diurnal cycles of carbon and water.

6. Page 4, Line 17: “the use of EC measured diurnal patterns of carbon, water, and energy fluxes to derive clues on ecosystem drought responses at a daily resolution could prove valuable, if nothing less than a benchmark to test current hypotheses.” As far as rationale for the work goes, I found this to be rather weak. Perhaps the authors could give specific examples of hypotheses that could be tested with these metrics.

We agree that this statement was rather vague, it has now been changed to be more explicit:

In this sense, the use of EC measured diurnal patterns of carbon, water, and energy fluxes to derive clues on ecosystem drought responses at a daily resolution could prove valuable both as a means to identify potential periods of ecosystem stress, inform machine learning algorithms on ecophysiological conditions not found in environmental variables, as well as benchmarking a models ability to capture sub-daily dynamics.

7. Page 9, line 20: “sites under water stress tended to have $C_{ET} < -0.50$.” How do the authors know that the sites were under water stress? This gets back to my original point about validating the metrics against independent observations of plant function.

The reviewer makes a good point, one which was also brought up by reviewer 1 (comment 9). As discussed in comment 1 of this review, evidence of metric response is seen in the case study of the European heatwave of 2003. Furthermore, to address the appropriateness of these thresholds, we have included a new sensitivity analysis which shows the relationship of frequency of uncoupled and morning shifted days based on different threshold levels (Figure S2. here R4). This analysis indicates that indeed these levels may have been slightly too strict and have been changed to $DWCI < 25$ and $C_{ET}^* < -0.25$, which gives a stronger response while does not change the patterns. The unchanged patters demonstrate both the robustness of the patterns, as well as that the absolute threshold levels are flexible with acceptable ranges of about 5-75 for DWCI and -1.0-0.0 for C_{ET}^* . This analysis is now discussed in the results section with the following text:

These thresholds were chosen to highlight frequency differences between sites and were shown to have large metric responses under dry conditions while having low frequencies under wetter conditions (see sensitivity analysis in supplementary figure S2). Furthermore, these thresholds

results in a similar median frequency of uncoupled and morning shifted days between all site-years being 8.7% and 9.4% of days respectively. The similarity in median frequencies across site-years allowed for easier inter-comparison between the two metrics. The frequency of decoupling and morning shifts using these thresholds for each site can be found in the map found in File S1.

8. Figure 3: The text is small and hard to read.

The text size has been increase to improve readability (Figure R5).

9. Page 13, Lines 15-25: I found this discussion of the links between C_{ET} and isohydricity to be highly speculative, notably because isohydricity tends to describe plant response to declining soil moisture, yet the afternoon stomatal closure may be largely caused by increasing VPD.

To further the points discussed above, the VPD responses are likely tied to the concept of isohydricity. The review by Martínez-Vilalta and Garcia-Forner [6] makes the point that VPD and transpiration dynamics feed back into the rate of soil moisture depletion and how fast a plant will reach the point of hydraulic failure. Discussion of these points have been added to highlight these feedbacks, and the section now reads:

In this way, it seems that though C_{ET}^* is less noisy as a drought indicator (see Fig. 6), it may only be of use in tree systems that are more prone to hydraulic stress. However, this does put the metric in a rather unique position in that it could be used as a global scale hydraulic indicator, having potential application in exploring ecosystem level isohydricity [6]. Isohydricity is intrinsically a concept that relates to an individual plant, as dynamics of rooting depth, hydraulic conductances, and sensitivities to VPD can vary within individuals of the same species at the same location. However, these factors are all interrelated, as hydraulic and stomatal conductances drive transpiration dynamics which control the rate of depletion of root zone water which can then feed back to stomatal sensitivity, such as via ABA signaling [10].

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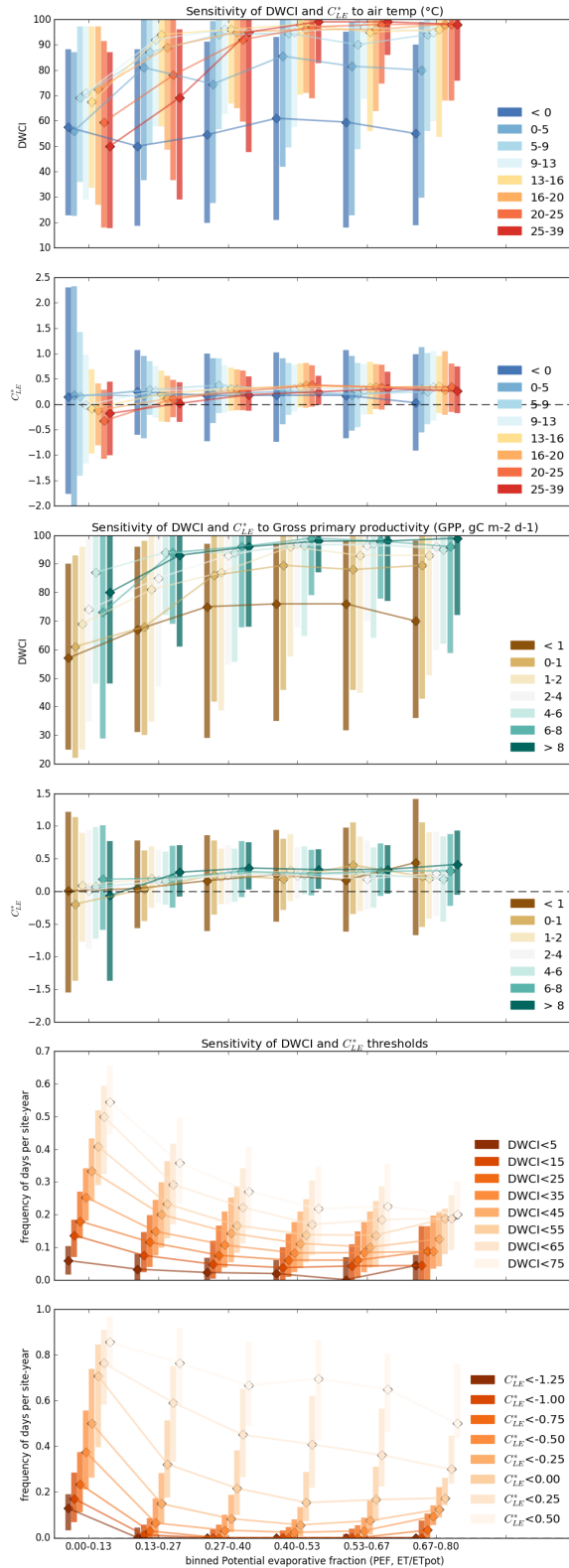


Figure R 4: Figure S1. Sensitivity analysis of DWCI and C_{ET}^* to evaporative fraction (EF=ET/potential ET) under different GPP and air temperature (T_{air}) values, as well as the sensitivity of frequency of decoupling (DWCI < threshold) and morning (C_{ET}^* < threshold) using various thresholds. Note DWCI of 0-100 indicate lowest-highest probability of diurnal carbon:water coupling and C_{ET}^* of -1-1 indicate one hour morning shifted-one hour afternoon shifted ET. Bins for GPP and T_{air} based on percentiles to give an equal number of points per bin, with the exception of $GPP < 1$ and $T_{air} < 0$, which are approximately double the size of the other bins and represent periods of low plant activity such as winter. Vertical bars represent interquartile range in all cases.

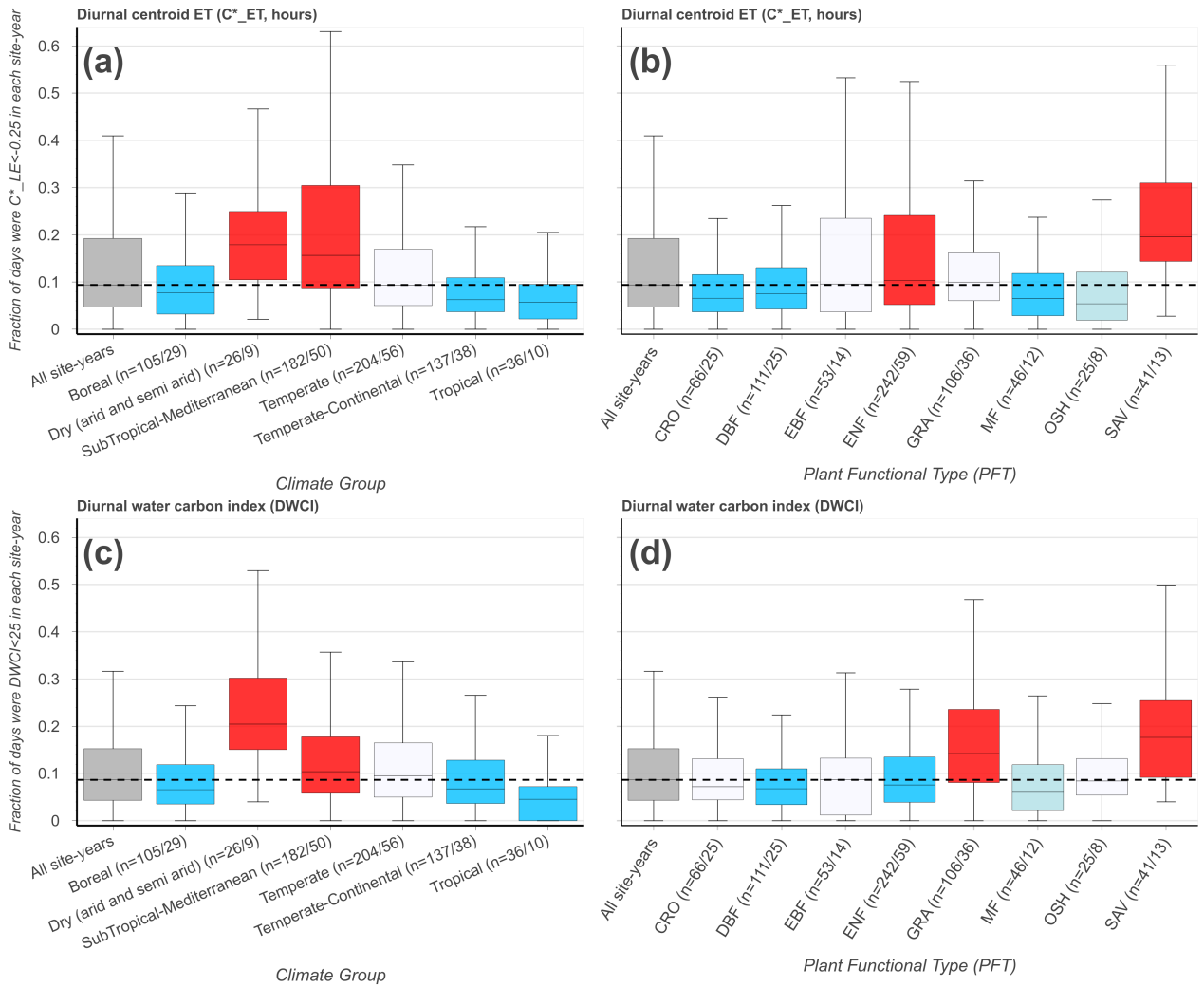


Figure R 5: The frequency of morning-shifted Diurnal Centroids ($C^*_{ET} < -0.25$ hours, upper figure) and low diurnal water carbon index ($DWCI < 25$, lower figure) for 690 fluxnet site-years/192 sites, grouped by climate group (left) and plant functional type (right). Group labels on x-axis indicate the number of site-years/sites (n=site-years/sites) for each category. Dashed line is the median for all site-years combined. Color shade indicates level of significance, with light colors and dark colors having p-values < 0.10 and < 0.05 respectively (Wilcoxon–Mann–Whitney two-sample rank-sum test), red and blue colors indicate distributions higher and lower respectively compared to data from all sites excluding the group. Only sites with at least 20 data points and groups with more than 5 site-years were included.

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