Water stress induced breakdown of carbon-water relations: indicators from diurnal FLUXNET patterns

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Abstract. Understanding of terrestrial carbon and water cycles is currently hampered by an uncertainty in how to capture the large variety of plant responses to drought across climates, ecological strategies, and environments. In FLUXNET, the global network of CO2 and H2O flux observations, many sites do not uniformly report the ancillary variables needed to study drought response physiology such as soil moisture, sap flux, or species composition. In this sense, the use of diurnal energy, water, and carbon flux patterns to derive clues on ecosystem water limitation responses at a daily resolution could prove valuable, if nothing less than a benchmark to test current hypotheses. To this end, we propose two data-driven indicators derived directly from the eddy covariance data and based on theorized physiological responses to hydraulic and non-stomatal limitations. Hydraulic limitations (i.e. intra-plant limitations to water movement) are proxied using the relative diurnal centroid (C_{ET}^*), which measures the degree to which the flux of evapotranspiration (ET) is shifted toward the morning. Non-stomatal limitations (e.g. inhibitions of biochemical reactions, Rubisco activity, and/or mesophyll conductance) are characterized by the Diurnal Water:Carbon Index (DWCI), which measures the degree of coupling between ET and gross primary productivity (GPP) within each day. Globally, we found indications of hydraulic limitations in the form of significantly high frequencies of morning shifted days in dry/Mediterranean climates and savanna/evergreen plant functional types (PFT), whereas high frequencies of decoupling were dominated by dry climates and grassland/savanna PFTs indicating a prevalence of non-stomatal limitations in these ecosystems. Overall, both the diurnal centroid and DWCI were associated with high net radiation and low latent energy typical of drought. Using three water use efficiency (WUE) models, we found the mean differences between expected and observed WUE to be 0.59 to -0.14 umol/mmol and -0.56 to -0.69 umol/mmol for decoupled and morning shifted days respectively compared to mean differences -1.4 to -1.7 umol/mmol in dry conditions. These results suggest that morning shifts/hydraulic responses are associated with an increase in WUE whereas decoupling/non-stomatal limitations are not.

1 Introduction

Processes such as photosynthesis and transpiration are so intimately linked that knowledge and assumptions about one process are needed to accurately understand the other. Unfortunately, the relationship between carbon and water cycles is not fully understood (Tang et al., 2014), passing the biases and uncertainties of the carbon:water assumption back onto flux estimates specifically and global water and carbon cycle interactions and dynamics in general (Keenan et al., 2013; Schlesinger and Jasechko, 2014; Ito and Inatomi, 2012). One increasingly identified source of uncertainty is the diverse responses of plants to

water limitation (Zhou et al., 2013; Dietze et al., 2014; Rogers et al., 2017), which hampers the understanding and predictability of water and carbon cycles during drought. Here we highlight potential causes of uncertainty in carbon:water dynamics and outline data-derived indicators intended to reflect current theory.

1.1 Stomata, WUE, and the carbon:water relationship

5 Classically, vegetation water and carbon fluxes are linked by stomates, where an open stomate allows CO2 to enter the leaf and, consequentially, water is lost. From this, most theoretical frameworks make some form of assumption that carbon assimilation (A) and water losses (T) are both contingent primarily on leaf stomatal conductance (gs). This assumed relationship allows us to pass between the realms of carbon and water, based on the assumption that at any given time both A and T are proportional to the stomatal conductance multiplied by the difference in internal and external CO2 and water vapor concentrations. More

10 specifically,

$$A = g_s \cdot \Delta c \quad and \quad T = 1.6 \cdot g_s \cdot \Delta v \tag{1}$$

where Δc and Δv are the differences in inner and outer stomatal cavity concentrations of CO2 and water vapor, respectively.

By making some assumptions on how stomates react to environmental variables and how these changes affect water and carbon concentrations, we can come to a relatively consistent carbon:water ratio, generally expressed as a water use efficiency

15 ($WUE = A/T$). At the ecosystem level where direct measurements of A and T are not available, WUE is simply calculated as the ratio of gross primary productivity (GPP) to total evapotranspiration (ET) (Kuglitsch et al., 2008). Further, the effect of vapor pressure deficit (VPD) on stomatal response can be taken into account giving formulations such as

$$iWUE = \frac{GPP \cdot VPD}{ET} \quad and \quad uWUE = \frac{GPP \cdot \sqrt{VPD}}{ET} \tag{2}$$

for the intrinsic (iWUE) and underlying water use efficiencies (uWUE) respectively, both of which tend to be more constant

20 than WUE (Beer et al., 2009; Zhou et al., 2014). As ET is the sum of both T and non-biological evaportaion (e.g. soil and intercepted evporation), often periods during and shortly after rain events are excluded from WUE estimates to minimize the influence of non-plant evaporation. Ultimately, calculations of WUE provide a simple summary of the cost in water per carbon gain and becomes an indicator for how plants have and will adapt to the physical limitations of their changing environments (Keenan et al., 2013; Tang et al., 2014).

25 ## 1.2 Uncertainty during drought

Though assuming a rigid carbon:water relationship works well in conditions when ecosystems are moderately wet, conditions associated with the majority of carbon and water fluxes, an inflexible carbon:water assumption is unsatisfactory in that these assumptions may breakdown as plants shift from light to water limitations. Indeed, in a review of leaf level stomatal conductance models, Damour et al. (2010) concluded that the majority of stomatal models fail to adequately capture the effects of drought.

This failure to capture the effects of drought is not only disconcerting as this is when ecosystems are most at risk, but this incomplete framework tends to propagates errors and uncertainties into estimates of the water and carbon cycles. For instance, these uncertainties are reflected in one recent meta-analysis of T to ET partitioning studies which included EC, sap-flow and isotopic methods, which puts the state of the art estimated global T/ET at a notably uncertain 61% ±15% s.d.(Schlesinger and
5   Jasechko, 2014). Similarly, using estimates from models based on global remote-sensing products, Miralles et al. (2016) found global T/ET estimates varied from 24-76%. This high uncertainty is disconcerting, as transpiration is the largest and most dynamic component of the global water cycle, which likely controls the variability in global ET.

In addition to the uncertainty in water cycles, estimates of are GPP also sensitive to carbon:water assumptions. In outlining a road map for improved modeling of photosynthesis, Rogers et al. (2017) noted as key recommendations both improving
10   information about water:carbon relations (in the form of the stomatal slope parameter g1) as well as improving understanding of the response of carbon assimilation to drought. Similarly, in an analysis of parameter uncertainties for a terrestrial biosphere model, Dietze et al. (2014) found that two of the top five parameters contributing to the predictive uncertainty of net primary productivity we associated with plant water regulation. This is reflected in the stomatal conductance parameterization exercise from Knauer et al. (2015), where the authors were able to improve model performance in predicting EC measured GPP and
15   ET by including atmospheric effects (in the form of VPD) on stomatal conductance, but concluded that further improvement required global understanding of water limitation response variation across plant functional traits and growing conditions which is currently unavailable.

1.3 Sources of uncertainty

Two ideas to account for the errors in carbon:water assumptions under dry conditions have begun to emerge: that hydraulic
20   limitations in transporting water from root to leaf change stomatal responses and thus limit transpiration under high demand, or that changes in the intra-leaf processes of carbon transport and fixation under drought conditions result in non-stomatal limitations that impact carbon assimilation independently of water fluxes (Novick et al., 2016).

1.3.1 Hydraulic limitation

As soil water potentials in the root zone become increasingly negative, the long-term plant strategy may turn from optimizing
25   carbon fixation to preventing damage to hydraulic architecture (Tyree and Sperry, 1988). As such, stomata and transpiration are likely to increasingly respond not just to atmospheric conditions, but also soil moisture. To account for water limitations in LSMs, the water to carbon ratio is generally scaled in relation to available soil moisture. Though this method should link the leaf physiology to the soil and thus capture some hydraulic limitation, it has been criticized for not capturing the variety of drought responses found in different plant species and ecosystems (De Kauwe et al., 2015). This diversity in plant responses
30   has been pointed to as a key point of uncertainty in earth system models (Dietze et al., 2014).

1.3.2 Non-stomatal limitation

Though ecosystem water and carbon fluxes are predominantly controlled by stomates, non-stomatal or bio/photo-chemical inhibitions to carbon assimilation are worth considering as they have the capacity to decouple the water-carbon exchange. This decoupling could include conditions where the stomates are transpiring water but intra-leaf factors are slowing carbon

5 fixation, changing the intrinsic water use efficiency directly. Intra-leaf factors could include effects such as production of reactive oxygen species (Lawlor and Tezara, 2008); environmental limitations to the photosynthetic pathways, such as leaf temperature (Medlyn et al., 2002); or declines in mesophyll conductance (Flexas et al., 2012). Non-stomatal limitations have been observed at ecosystem scale (Reichstein et al., 2002; Migliavacca et al., 2009), though the exact mechanism is difficult to elucidate (Reichstein, 2003). These effects likely vary between species, as well as with the rate of onset of drought, access to

10 water, and other environmental conditions.

1.4 Objectives

There seems to be a collective conclusion that the breakdown of carbon:water assumptions needs to be better characterized in general, and specifically for implementation in modeling frameworks (De Kauwe et al., 2015; Manzoni, 2014; Zhou et al., 2013; Flexas et al., 2012; Egea et al., 2011). Though the problem is becoming clear, the way forward is hampered by an uncertainty

15 in how to capture the large variety in the response to drought across climates, strategies, and species. 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, if nothing less than a benchmark to test current hypotheses. To this end, we propose two data-driven indicators, the diurnal water:carbon index (DWCI) and the relative diurnal centroid in LE (C_{ET}^*). Both metrics are derived directly from the EC data and based on expected physiological responses to hydraulic and non-stomatal limitations.

20 Using these data-driven indicators we then characterize the distribution of these limitations across a global spread of climate and vegetation types. Finally, we explore the ability of these indicators to detect the disagreements between modeled and observed water use efficiency, and explore how these biases may be attributed to hydraulic and non-stomatal limitations.

2   Methods and Materials

2.1   Data

25 Carbon, water, and evergy fluxes measured with EC, as well as meteorological data, were obtained from the FLUXNET database (Baldocchi, 2008). Half-hourly latent heat and net ecosystem exchange (NEE) fluxes were collected and processed using standard QA/QC procedures (Papale et al., 2006), gap-filling and partitioning algorithms (Reichstein et al., 2005). From the database, half-hourly gross primary productivity (GPP) and ET data (derived from latent heat flux measurements) were downloaded and used for the following analysis. The list of selected sites and interactive map of sites used can be found in file

30 S1.

Potential ET (PET) was calculated as the daily fraction between the measured ET and estimated ET via a Priestly-Taylor model (Priestley and Taylor, 1972) using site measured net radiation (Rn) and air temperature (T_{air}). The slope (alpha parameter) was fit for each site-year using 95th quantile regression (Koenker and Bassett Jr, 1978) instead of using the original 1.26 value derived for a "well watered crop" (Priestley and Taylor, 1972). Evaporative fraction (EF) was calculated as the fraction

5 of actual ET for PET.

In order to get high quality data and minimize the influence of abiotic evaporation (hereafter just evaporation), all data was filtered with the aim to include only non-gap filled data in the growing season with dry surface conditions. Specifically, days with GPP < 5 $g \cdot m^{-2} \cdot d^{-1}$ or daily mean air temperature < 15 °C were removed. In an effort to minimize contributions of evaporation, a conservative soil wetness index (CSWI) was employed which was designed to force a positive water storage for

10 any time-step with any amount of precipitation. So by calculating the storage at time t (S_t) as,

$$S_t = min\left(S_{t-1} + P_t - ET_t, S_o\right) \tag{3}$$

where ET_t and P_t are the ET and precipitation at time-step t respectively, S_t is effectively capped at a maximum storage value of S_o, which was set to 5 mm. Furthermore, to make the metric conservative in regards to assumed water inputs, any precipitation event will refill the storage from 0 mm,

15 $$CSWI = max\left(S_t, min\left(P_t, S_o\right)\right) \tag{4}$$

which has the effect of requiring all precipitation up to 5 mm to be evaporated from the system before negative storage can occur. Any gaps in the precipitation data were assumed to be a precipitation event of 5 mm. Code and further outline of the algorithm can be found in file S2. Evaporation was assumed to be negligible when $CSWI$<0. This method was used over the more standard method of removing 1-5 days after a rain event, as it does not make the assumption that the surface will dry in

20 a fixed amount of time, instead relying on a minimum amount of evaporation.

2.2 Relative diurnal centroid (C_{ET}^*)

As soils dry, it becomes more difficult to transport stem and root zone moisture to the leaf, causing hydraulic limitations. This daily cycle of wetting and drying acts as a capacitor in the hydraulic circuit, allowing water stores to be more easily transported in the morning and depleting in the afternoon. As bulk soil moisture declines, this effect can be strong enough to shift the

25 diurnal cycle of ET significantly toward the morning. This phenomenon can be quantified using the diurnal centroid: defined as the flux weighted mean hour, or

$$C_{flux} = \frac{\sum flux_t \cdot t}{\sum flux_t} \tag{5}$$

where t is a regular, sub-daily time interval. The resulting C_{flux} is the weighted mean hour of the diurnal cycle of that particular flux. For example, if a calculated C_{ET} for a given day (using measurements at an hourly interval) equals 12, this
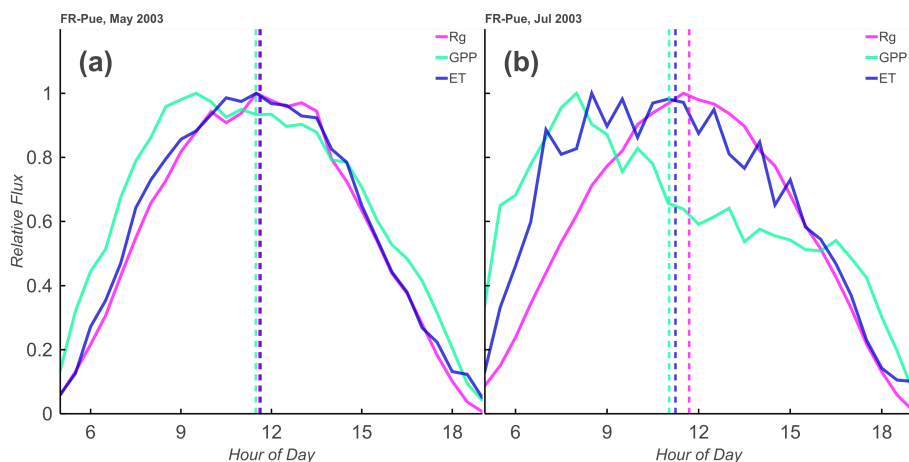
Figure 1. One month average cycle (soild lines) and accompanying diurnal centroid (vertical dashed lines) of incoming shortwave radiation (Rg), evapotranspiration (ET), and gross primary productivity (GPP) at the Peuchabon, France ('FR-Pue') site during 2003. May is relatively wet (32 mm rainfall, left) and July is relatively dry (0 mm rainfall, right). While ET and Rg correspond well in the wet month, the dry month shows a distinct phase shift in both GPP and ET fluxes towards the morning, as well as a midday depression in GPP.

would entail that the weighted mean for that day is at noon. Fig. 1 shows an example of the shifts in the monthly average cycle from a wet month to a dry month. As analyzed in Wilson et al. (2003), a shift in ET towards dawn can be indicative of afternoon stomatal closure. In order to isolate a shift, we then had to control for variations in global radiation (Rg), both fluctuations due to clouds and differences in the timing of solar noon. Therefore, the difference between the diurnal centroids of ET (C_{ET}) and

5 Rg (C_{Rg}) was calculated as

$$C_{ET}^* = C_{Rg} - C_{ET} \qquad (6)$$

giving C_{ET}^* as the diurnal centroid of ET relative to Rg. The resulting values of C_{ET}^* are not tied to the carbon cycle, which can be affected by non-stomatal limitations and generally shows a more prominent midday depression. Annotated code for this calculation can be found in file S3. Though a diurnal centroid can be calculated for any diurnal cycle, basing a metric on the

10 morning shift of ET relative to Rg has the advantage of targeting the non-atmospheric drivers of the water flux, of which there are few ancillary variables.

2.3 Diurnal water carbon index (DWCI)

If transpiration and assimilation are predominantly controlled by stomatal conductance, it follows that their diurnal cycles should be largely in sync. In other words, regardless of a plants maximum T or A, if the stomates start to close, both rates should

15 be decrease by a similar percentage. On the other hand, non-stomatal limitations that inhibit carbon assimilation independent

of water have the capability to alter the diurnal cycle on just one flux, causing them to decouple. In an effort to quantify the degree of carbon:water coupling for an individual day, we examined the relationship of GPP and ET, where,

$$ET \propto GPP \cdot \sqrt{VPD} \tag{7}$$

or,

$$ET = i \cdot GPP \cdot \sqrt{VPD} \tag{8}$$

This relationship incorporates the assumption that, at least over short time scales, the amount of carbon that enters the leaf is proportional to the amount of water that leaves, and also incorporates the non-linear response of stomates to VPD (Katul et al., 2009; Zhou et al., 2014). This model, though simple, has been shown to work well across a variety of EC sites (Zhou et al., 2015). Fig. 2(ab) shows a comparison between the daily cycles in a wet and dry month. By calculating a daily correlation between the normalized daily cycles of ET and $GPP \cdot \sqrt{VPD}$, we come to a correlation coefficient for each day (see Fig. 2(cd), lower). For well watered days in the growing season the two signals tend to be well correlated ($\rho > 0.9$), but tends not to be correlated in periods of stress, a comparison of which can be seen seen in Fig. 2(cd).

As it is, this daily correlation coefficient is dependent on the signal strength, or magnitude, of the flux. Low correlation values could just as easily be from carbon:water decoupling as to a low signal to noise ratio. Therefore, to produce a more robust metric and account for these statistical decreases in correlation, we turned the daily correlation coefficient into an index based on its rank in a distribution of correlation coefficients from artificial datasets. These artificial datasets are constructed using the diurnal signal from potential radiation, with Gaussian noise ($\mathcal{N}(0, \sigma)$) added according to the standard deviation random uncertainty of the ET and NEE fluxes, or

$$flux_{artificial} = \frac{Rg_{pot}}{\overline{Rg_{pot}}} \cdot \overline{flux} + \mathcal{N}(0, \sigma^2_{flux}) \tag{9}$$

Uncertainties of the NEE and ET fluxes were estimated from the gap filling procedure of Reichstein et al. (2005), with the uncertainty equal to the standard deviation of flux measurements within a time window and similar meteorological conditions. As GPP is calculated from gap-filled values of NEE, the uncertainty from NEE was used for GPP. Furthermore, the correlation structure between the noises in LE and and NEE was preserved in the artificial dataset.

In essence, by using the underlying signal from potential radiation, both the artificial ET and $GPP \cdot \sqrt{VPD}$ are perfectly correlated when no noise is added. Adding noise then isolates the decoupling effect of signal to noise ratio. An artificial correlation coefficient can then be calculated from the two artificial datasets in the same manner as from the real dataset, and this experiment is repeated 100 times for each day, giving a daily distribution of artificial correlation coefficients. The rank of the real correlation coefficient in the distribution from the artificial set gives a probability that the carbon and water signals are actually coupled. The resulting index has a range of 0-100, with 100 indicating that the real correlation coefficient was greater
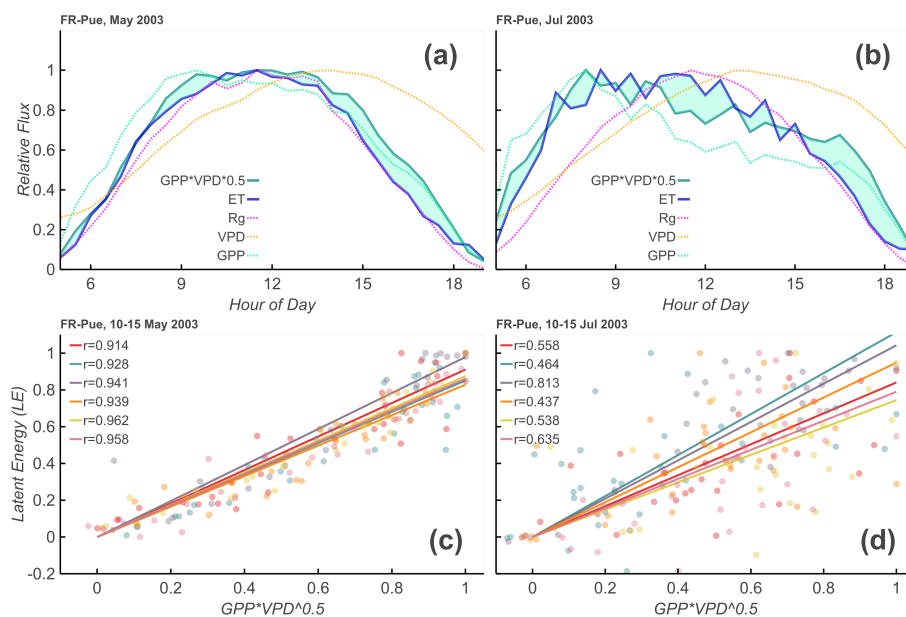
Figure 2. upper One month average diurnal cycle of incoming shortwave radiation (Rg), evapotranspiration (ET), vapor pressure deficit (VPD), gross primary productivity (GPP), and underlying water use efficiency (uWUE, $GPP * VPD^{-0.5}$) at the Peuchabon, France ('FR-Pue') site during 2003. Discrepancies between uWUE and ET increase from the relatively wet May (32 mm rainfall, left) to the relatively dry July (0 mm rainfall, right). lower These discrepencies are reflected in the daily correlation values between uWUE and ET, giving an indication of the appropriatness of the uWUE model for each day, as well as the degree of coupling between water and carbon signals.

than the entire artificial set, and therefore it is very likely that carbon and water are coupled. From this index we can now quantify if the water and carbon signals are coupled for any given day, and therefore shed light onto whether the two fluxes are only controlled by the opening and closing of stomates. Annotated code for this calculation can be found in file S4.

2.4 Models and parameter estimation

5   Three models were used as benchmarks of physiological understanding. The three models provide a spectrum of theoretical to empirical basis. The "Katul" model, as defined and used in calculation of the DWCI, is based in stomatal optimization theory (Katul et al., 2009; Zhou et al., 2015), 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. One step away from a theoretical basis is a revision of this model by Boese et al. (2017), the "Boese" model, where an additional radiation term was added such that,

10   $$ET = i \cdot GPP \cdot \sqrt{VPD} + r \cdot Rg \tag{10}$$

where i and r are parameters fit to each site-year. This relationship with Rg was shown to have a better predictive performance for EC data from 115 sites (Boese et al., 2017). The interpretation of this extra radiation term is not clear and is difficult to

reconcile with the current understanding of physiology. It is possible the term could be related to biophysical effects, e.g. VPD at leaf surface vs the measured ambient VPD. Nevertheless, the Boese model is an empirical and ecosystem scale model that complements the theoretical and originally leaf-level model from Katul.

Parameters of these models were estimated for each site-year. The Boese model parameters were fit using trimmed least
5   squares regression (TLS) which minimizes the 90th percentile of SSE to prevent influence of large outliers (Rousseeuw, 1983; Reth et al., 2005). As the error in both ET and GPP are assumed to be of similar magnitude, the i parameter in the Katul model was calculated using geometric mean regression, where the final slope was calculated as the geometric mean of the parameters from

$$ET = i_{GPP} \cdot GPP \cdot \sqrt{VPD} \; and \; GPP \cdot \sqrt{VPD} = \frac{ET}{i_{ET}} \tag{11}$$

10   Because both the Katul and Boese models are anchored in a theoretical understanding of leaf physiology, their inability to make accurate predictions may be a result of a failure of their underlying assumptions. Therefore a fully empirical and highly non-linear model can give insight into how much information is actually stored in the data while minimizing any assumptions. As a fully empirical model, a random forest regression (RandomForestRegressor from Pedregosa et al. (2011) based on Breiman (2001)) was fit to half-hourly ET data for each site using Rg, VPD, $Tair$, GPP and year as input parameters.
15   Values were estimated using 50 trees with predictions made using out-of-bag estimates to prevent over-fitted model predictions.

3   Results

3.1   Distribution of data driven indicators by vegetation type and climate

The frequency of low values of diurnal centroid and DWCI across climate groups and plant functional types is shown in Fig. 3. The thresholds of 10 and -0.5 for DWCI and C^*_{ET} respectively were chosen because: when DWCI<10 it is reasonably likely
20   that carbon and water are decoupled, and sites under water stress tended to have C^*_{ET}<-0.5. Using these thresholds we find that 7% and 8% of data points across all sites are decoupled and morning shifted respectively. Though there is a fairly large variance across climate groups and plant functional types, low values of both DWCI and C^*_{ET} occur at higher frequencies in savanna ecosystems and dry or Mediterranean climates. Conversely, lower frequencies of both metrics are seen in tropical, boreal, and temperate-continental climates. Overall, frequencies were highly variable within plant functional types. Interestingly, C^*_{ET}
25   seems to be more variable in moderately dry ecosystems with potentially deep roots, favoring woodier savannas and evergreen broad-leaf forests over grasslands and open shrub lands. In contrast, DWCI shows similarly high frequencies from savannas and grasslands. Strikingly, the arid and semi-arid climate group seems to be associated with the majority of low DWCI occurrences, with a mean frequency of about 15% of days being uncoupled.

The response of both variables to drought stress is further observed in Fig. 4, where low mean values of both DWCI and C^*_{ET}
30   are associated with conditions of high net radiation and low latent energy, indicative of drought. This pattern is much cleaner with the diurnal centroid than with DWCI, though mean values are generally above 50 for most bins, indicating that most days
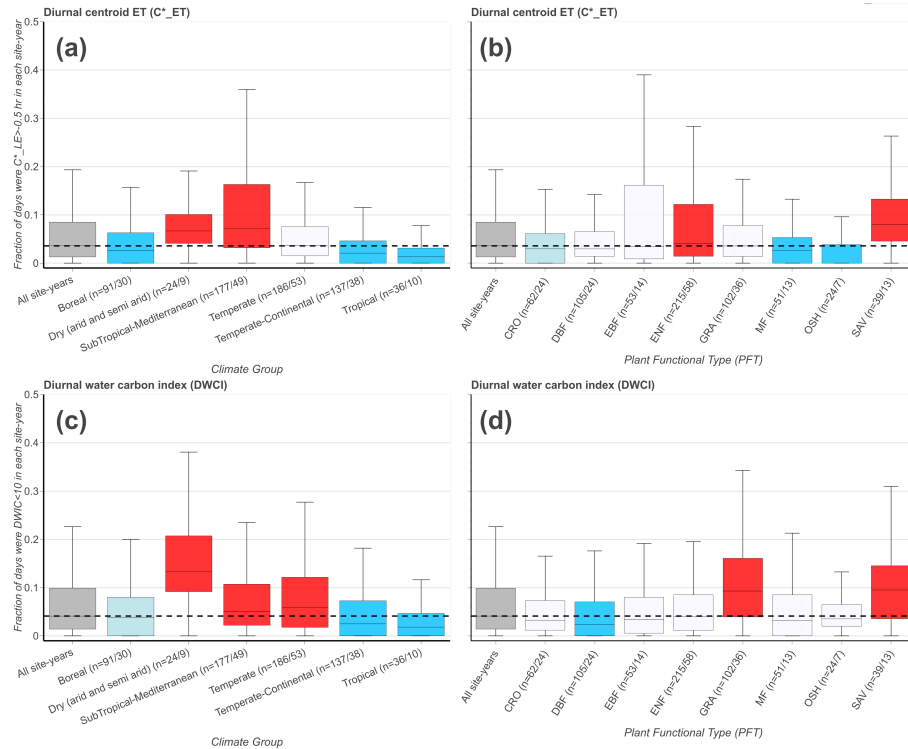
Figure 3. The frequency of morning-shifted Diurnal Centroids (CET<-0.5 hours, panels a-b) and low diurnal water carbon correlation (DWCI<10, panels c-d) for 651 fluxnet site-years/189 sites, grouped by climate group (left) and plant functional type (right). Group labels on x-axis indicate the number 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.

are well coupled. Low values of both indicators are also seen under conditions with low Rn and high latent energy (as seen by the dark streak at the top edged of in Fig. 4(a)), which is generally not associated with drought stress. Further analysis showed that these points are also associated with energy balance over closure, where the sum of latent and sensible heat is greater than net radiation (ET+H>Rn, see Fig. S5) and therefore likely represent a data problem rather than a physiological response.

5 Removing all days where the energy balance is over closed did not alter the patterns associated with drought. Both DWCI and C_{ET}^* also show a trend with low GPP, although in the case of the diurnal centroid the effect is limited to both low GPP and ET.

3.2 Difference between modeled and actual WUE

Fig. 5 shows the difference between expected and observed WUE from the Katul, Boese, and random forest (RF) models, with respect to conditions of drought as characterized by low evaporative fraction (EF<0.2), C:W decoupling (DWCI<10),
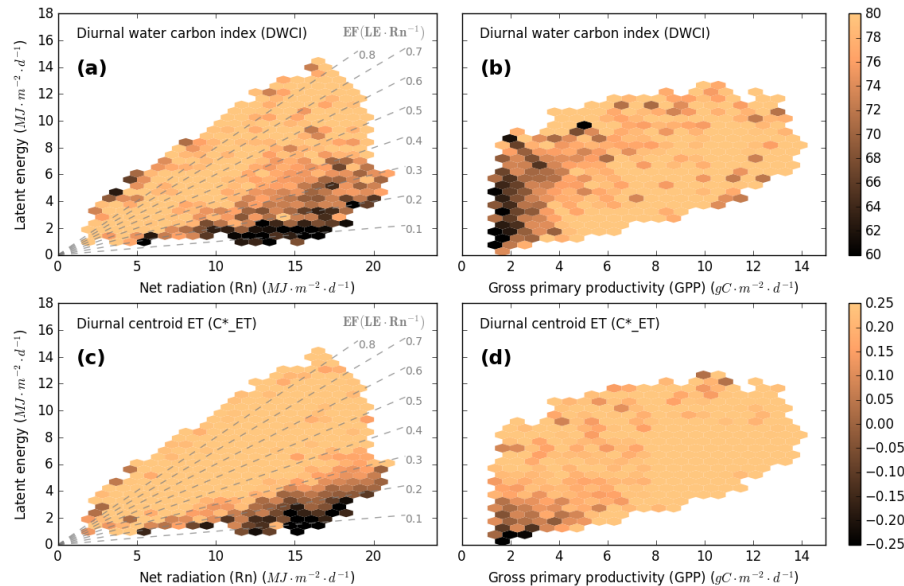
Figure 4. Mean DWCI (upper) and C^*_{ET} (lower) with respect to latent energy (LE) by Rn (left) and LE by GPP (right). Points with high Rn and low LE are associated with both low DWCI and C^*_{ET}, indicating that both metrics are related to water limitations. Both metrics, and DWCI in particular, show 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).

and morning shifts (C^*_{ET}<-0.5). For all models, the dry days show the largest average shift between expected and observed WUE, followed by morning shifted days. Uncoupled days show the smallest shifts for all models, with an overestimation of WUE for the Katul model and a slight mean underestimation of WUE the more empirical models (Boese and random forest). As all models were calibrated within a site-year, the over or under estimation of WUE indicate an inability of the model to
5 capture a change in the system. Cases of mean mis-estimation tended to be influenced by long tails in the distribution with median differences being less exaggerated. However, these long tails are indicative of major model error in periods where the ecosystem is likely under stress conditions.

4 Discussion

4.1 Looking beyond sums and means

10 The proposed metrics DWCI and C^*_{ET} depart from more traditional summarizations from sub-daily to daily timescales such as sums and means. This departure is advantageous in that it extracts added information that may have been otherwise ignored by turning the focus from signal amplitude to the signal shape. However, these new metrics also come with their own set of caveats, most notably issues with data quality confounding interpretability. Both metrics are susceptible to noise, as one or
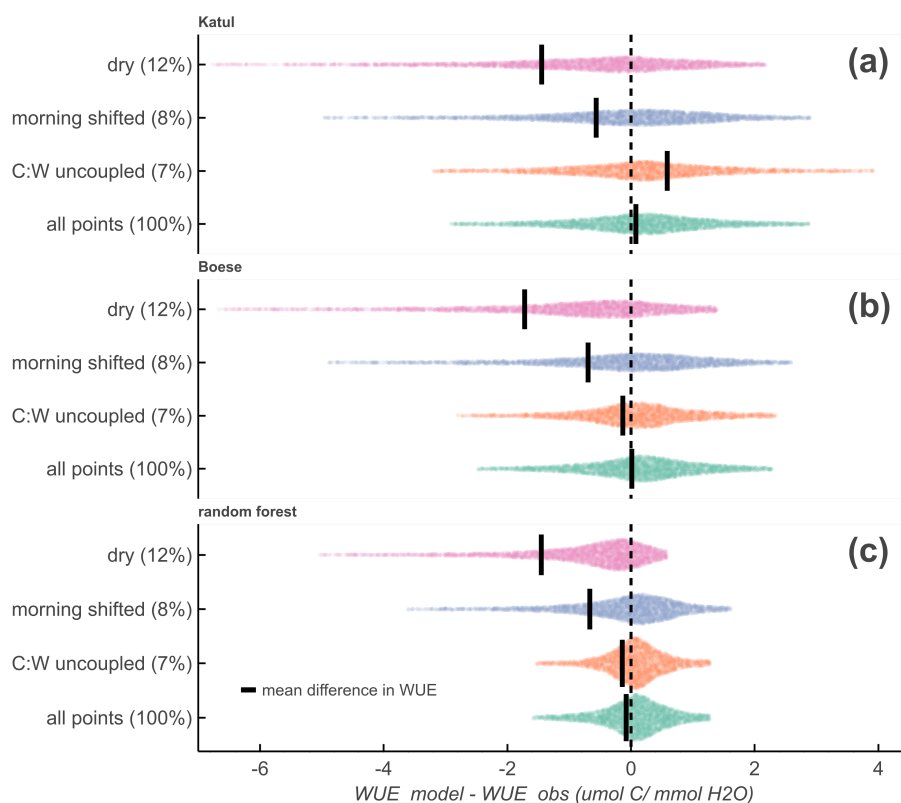
Figure 5. Difference in modeled and measured WUE for Katul (top), Boese (middle), and random forest (bottom) models. The random forest model was fit using Rg, VPD, T_{air}, GPP, and year. Thresholds designating dry, morning shifted, and C:W uncoupled were EF<0.2, * ET<-0.5, and DWCI<10 respectively for each day. The distributions span from the 10th to 90th percentiles, and the width of each gives an indication of the variance, which is larger in the sub groups compared to all points. Furthermore, the mean difference in WUE (black lines) tends to be shifted in dry and morning shifted days indicating a mean underestimation of WUE by the models mostly due to the long tails. Decoupled days show highter variance, but no clear pattern in under- or over-estimation. The percentage of days in each category are designated next to y-axis label in parenthesis.

two errant points within a day can be reflected as a decrease in correlation or a shift in diurnal centroid. This is evident from the existence of afternoon shifted C^*_{ET}, sometimes by more than an hour, which the authors have no proposed explanation for other than noise in the data. However, attributing afternoon shifted points as poor data requires further investigation. Despite the possible shortcomings, both metrics show a definite response to drought conditions across the broad array of sites, climates, and ecosystems contained in FLUXNET (see Fig. 4), and give valuable insight into the underlying physiology.

4.2 Trees, grass, and drought stress

By comparing climate groups and PFTs with the frequent occurrence of low DWCI and C_{ET}^* from Fig. 3, we can note two striking differences: evergreen broad- and needle-leaf forests show high variability of morning shifted days but not uncoupled days, whereas grasslands show significantly high uncoupled but not morning shifted days. This disparity may indicate an interaction of C_{ET}^* not only with drought, but hydraulic sensitivity. The shorter hydraulic system of grasses may not necessitate stomatal closure under high demands (Holloway-Phillips and Brodribb, 2011), thus causing less frequent phase shifts even under drought conditions. These ecosystems may only exhibit higher hydraulic stresses, associated with both dryness and a more sensitive hydraulic structure. Temperate-continental and tropical climates all showed a low frequency of morning shifted days, even though they are occupied by large trees with cavitation susceptible vascular systems (Konings and Gentine, 2016), suggesting that these ecosystems show limited drought stress even with the hydraulic susceptibility. Similarly, the high degree of variability in morning shifted frequencies between site-years in sub-tropical/Mediterranean and evergreen broad- and needle-leaf forests could either indicate variation in the response in hydraulic stress between sites, or that hydraulic stress is only expressed some years, leading to high and low frequencies within the same site.

In this way, it seems that though C_{ET}^* is less noisy as a drought indicator (see Fig. 4), 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 (Martínez-Vilalta and Garcia-Forner, 2016). Current estimates of isohydricity require repeated quantification of leaf water potential, which are currently restrained to the individual scale, i.e. from actual leaf measurements (Martínez-Vilalta et al., 2014) or to global scale, but only 0.5 degree resolution estimates from radar (Konings and Gentine, 2016). This limitation of large and small scales leaves a knowledge gap at the size of an eddy covariance footprint, hindering the study of ecosystem response to drought. However, under the assumption that the morning shifts seen under low evaporative fraction are due to stomates closing throughout the day in response to root zone moisture depletion, it may be possible to compare the onset and speed with which the diurnal centroid shifts toward the mornings as ecosystems dry. In this way, one could infer the ecosystem response to soil moisture, without explicitly knowing the soil moisture. The resulting relationship could prove useful as a data derived ecosystem functional property, giving direct information on variations in water limitation response.

4.3 C:W decoupling and energy balance closure

In addition to error from single data points, both metrics, but especially the DWCI, show some relationship with energy balance over closure. Energy balance mismatch is a common phenomenon in EC measurements, with under closure (ET+H<Rn) being a more common concern (Leuning et al., 2012; Wilson et al., 2002). Issues with energy balance closure can be, among other causes, attributed to advection, where energy, water, and carbon are transported in and out of the tower footprint, complicating an absolute accounting of these quantities (Barr et al., 2006; Brötz et al., 2014; Wilson et al., 2003). The apparent association of DWCI and over closure could be due to transfer of moist air from the surrounding landscape, causing the DWCI to be more contingent on the mixing of source air and less from plant controls. In this scheme, the over closure seen in Fig. 4

could be caused by the mixing of outside moist air into the drier air from the EC site, causing an increase in latent energy. However, the infiltrating air sources could also have similar or drier moisture levels which would not necessarily be seen as over closure. In this scenario, this infiltrating air could contain varying carbon and water concentrations, again causing a carbon:water decoupling, but one that would not be associated with over closure. If this effect has no diurnal pattern, and thus

5   does not generally influence the mean diurnal centroid in ET, it could explain why the patterns with dryness are much clearer with C^*_{ET} compared to DWCI. This would have the implication that DWCI is then a mixture of advection and non-stomatal signals, complicating the biological interpretability. However, the association with dryness in both metrics gives credence that they do indeed reflect some physiology, if we assume EBC should not be influenced by dryness level. Furthermore, if potential stress conditions are removed, the DWCI could be useful as a metric of advection in the system, even when the energy balance

10 is relatively well closed.

4.4   WUE shifts associated with metrics and not captured by models

Fig. 5 demonstrates the strong tendency of the models to underestimation WUE in dry conditions. This is true even for the fully non-linear and empirical random forest model, indicating that the model under-performance is not necessarily due to an incomplete model framework, but due to a lack of information to constrain the problem. Given the association of both metrics

15 with drought (Fig. 4), one could expect that the models would underestimate WUE in uncoupled and morning shifted days. Though this is the case with morning shifted days, decoupling shows only small and inconsistent underestimations of WUE, with even a mean overestimation in the case of the Katul model. Given the limitations outlined in the previous sections, one could blame noise for the lack of WUE shift, but this does not reconcile with the higher frequency of decoupling during dry days which should bias the WUE estimates. Furthermore, as the more empirical models (Boese and RF) reduce the prediction

20 variability, they leave a slight WUE underestimation, indicating that some of the overestimation from the Katul model may be tied to limitations of the underlying theory, yet the distributions still lack the long tails of underestimation in the empirical models. Extending these findings to the underlying hypotheses of the metrics, namely hydraulic and non-stomatal limitations, we could conclude that the hydraulic controls do impose a greater water use advantage than non-stomatal limitations. In other words, the findings suggest that days with water:carbon decoupling, and possibly non-stomatal limitations, do not improve

25 WUE, whereas hydraulic responses can improve WUE. As WUE is a ratio, this does not shed any light onto the change in productivity, as low values of WUE may indicate that a plant is still productive, but at a higher water cost. However, solid conclusions would require further analysis with some site specifics measurements of actual plant function.

5   Conclusions

Both the DWCI and the C^*_{ET} demonstrate an ability to show consistent patterns with drought across a broad array of sites,

30 climates, and ecosystems, with the added advantage of being tied to theoretical underpinnings. Particularly, the demonstrated patterns give novel information about carbon water relations and hydrological dynamics that are not currently present at ecosystem scale across a database as large as FLUXNET. These metrics and their underlying theory provide a data derived example

differentiating the hydrological response of tree and grass plant functional types, as well as give evidence for the presence and absence of a WUE advantage from hydraulic and somatal limitations respectively. Going forward, these metrics can be used as a tool to further understand the diversity of ecosystem drought responses.

Code and data availability. Code for all metrics outlined in the manuscript are available as associated supplemental materials. All data can
5 be obtained through http://fluxnet.fluxdata.org/

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