



## Ecosystem physio-phenology revealed using circular statistics

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### Abstract.

Quantifying responses of vegetation phenology to climate variability is a key prerequisite to predict shifts in how ecosystem dynamics due to climate change. So far, many studies have focused on responses of classical phenological events (e.g. budburst or flowering) to climatic variability for individual species. Comparatively little is known on physio-phenological events such as the timing of the maximum gross primary production ( $\text{DOY}_{\text{GPPmax}}$ ). However, understanding this type of physio-phenological phenomena is an essential element in predicting the response of the terrestrial carbon cycle to climate variability. In this study, we aim to understand how  $\text{DOY}_{\text{GPPmax}}$  depends on climate drivers across 52 eddy-covariance (EC) sites in the FLUXNET network for different regions of the world. Most phenological studies rely on linear methods that cannot be generalized across both hemispheres and therefore do not allow for deriving general rules that can be applied for future predictions. Here we explore a new class of circular-linear (here called circular) regression approach that may show a path ahead. Circular regression allows relating circular variables (in our case phenological events) to linear predictor variables (e.g. climate conditions). As a proof of concept, we compare the performance of linear and circular regression to recover original coefficients of a predefined circular model on artificial and EC data. We then quantify the sensitivity of  $\text{DOY}_{\text{GPPmax}}$  to air temperature, short-wave incoming radiation, precipitation and vapor pressure deficit using circular regressions. Finally, we evaluate the predictive power of the regression models for different vegetation types. Our results show that the  $\text{DOY}_{\text{GPPmax}}$  of each FLUXNET site has a unique signature of climatic sensitivities. Overall radiation and temperature are the most relevant controlling factors of  $\text{DOY}_{\text{GPPmax}}$  across sites. The circular approach gives us new insights at the site level. In a Mediterranean shrub-land, for instance, we find that the two growing seasons are controlled by different climatic factors. Although the sensitivity of the  $\text{DOY}_{\text{GPPmax}}$  to the climate drivers is very site specific, it is possible to extrapolate the circular regression model across vegetation types. From a methodological point of view, our results reveal that circular regression is a robust alternative to conventional phenological analytic frameworks. In particular global analyses can benefit, where phase shifts play a role or double peaked growing seasons may occur.

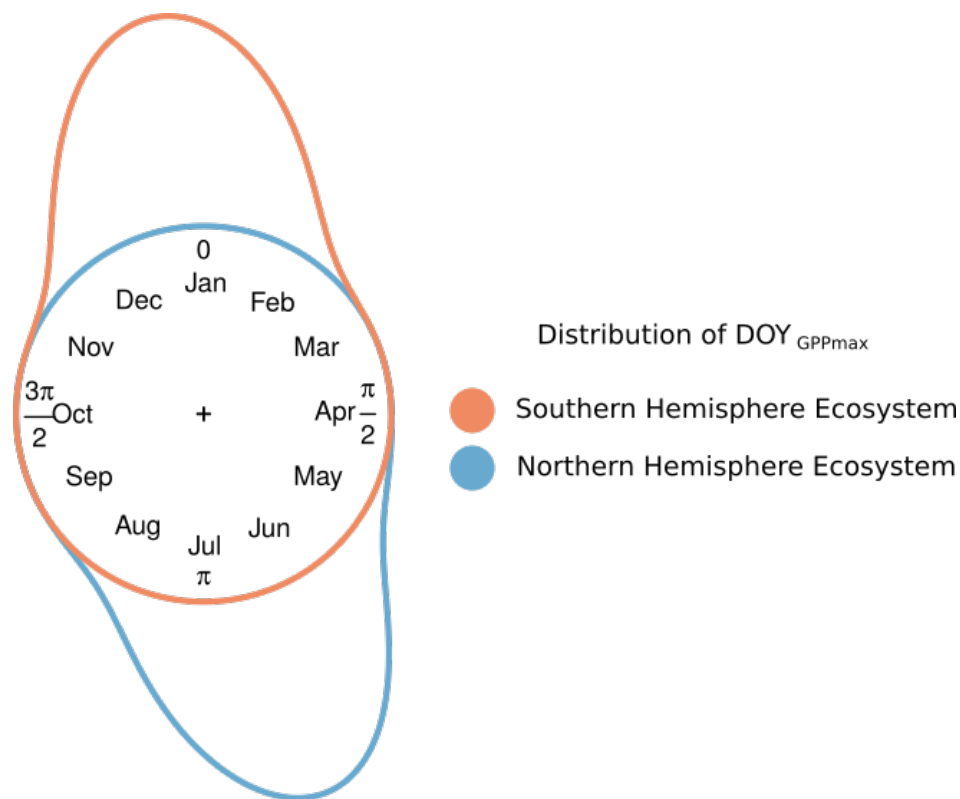


## 1 Introduction

Phenology is the study of the timing of biological events that can be observed either at the organismic level or at the ecosystem  
25 scale (Lieth, 1974). For the latter, phenology is the study of some integral behavior across phenological states of e.g. the inte-  
grated canopy reflectance captured by remote sensing (Richardson et al., 2009; Zhang et al., 2003), or ecosystem-atmosphere  
CO<sub>2</sub>-exchange fluxes (Richardson et al., 2010). In the last case we define these processes that integrate plant physiology and  
phenology as ecosystem physio-phenology given that related both the uptake of CO<sub>2</sub> by photosynthesis and the timing when  
30 plant photosynthesis start (beginning of the growing season), finish (end of the growing season) or reach its maximum potential  
(peak of the growing season). At the scale of ecosystems, phenology is influenced by climate conditions but simultaneously  
contributes to the regulation of different micro and macro meteorological conditions. Then, phenology influences the temporal  
dynamics of land-atmosphere water and energy exchange fluxes. Likewise, the terrestrial carbon cycle is affected by pheno-  
logical controls on CO<sub>2</sub> uptake and release (Peñuelas et al., 2009).

The eddy covariance technique allows for continuously measuring the exchange of energy and matter between ecosystems  
35 and atmosphere (Aubinet et al., 2012). These measurements are available for several ecosystems around the world through  
the FLUXNET network (Baldocchi et al., 2001). The high temporal resolution of most eddy covariance observations (half-  
hourly), enables analyzing the seasonality of the exchange of CO<sub>2</sub> between ecosystems and the atmosphere in relationship  
with meteorological variables (i.e. radiation, temperature, precipitation, as well as with atmospheric humidity) and soil mois-  
ture (Migliavacca et al., 2015; Richardson et al., 2010). Specifically, one can monitor the trajectory of gross primary production  
40 (GPP) along the growing season and can derive phenological transition dates such as start and end of the growing season (e.g.  
(Luo et al., 2018)), as well as the timing of the maximum gross primary production, hereafter as referred to as DOY<sub>GPPmax</sub>  
(Zhou et al., 2016; Peichl et al., 2018; Wang and Wu, 2019).

Understanding how climate variability affects DOY<sub>GPPmax</sub> is fundamental given that it is the time when plants reach their  
maximum potential for CO<sub>2</sub> absorption. This optimum state require that several preconditions be achieved during the growing  
45 season and the preceding starvation phase. So far several studies have focused on studying the variability of GPPmax. For  
example Huang et al. (2018) reported the increase of GPPmax at global scale during the last decades. The authors found that  
the increase is mainly explained by the expansion of croplands, CO<sub>2</sub> fertilization and Nitrogen deposition. Zhou et al. (2017)  
studied how the variability of annual GPP is influenced by GPPmax and the start and the end of the growing season. They  
found that GPPmax better explains the variability of annual GPP than the days of the beginning and end of the growing sea-  
50 son. Bauerle et al. (2012) studied how photoperiod and temperature influence plants photosynthetic capacity. They found that  
photoperiod explains better the variability of photosynthetic capacity than temperature. So far, to the best of our knowledge  
only one study has focused on understanding the temporal variability of GPPmax. Wang and Wu (2019) used a combination  
of satellite, and eddy covariance data to explore how DOY<sub>GPPmax</sub> is controlled by climatic conditions. The authors reported  
that higher temperature advance DOY<sub>GPPmax</sub>, while the influence of precipitation and radiation were biome-dependent. Never-  
55 theless, this study was geographically located in China therefore, a global approach considering several ecosystems across the  
whole latitudinal gradient is still missing.



**Figure 1.** Conceptual distribution of GPPmax timing ( $DOY_{GPPmax}$ ) for two hypothetical ecosystems one in the Northern (Blue), and one in the Southern Hemisphere (Red). Each line represents the interannual variability  $DOY_{GPPmax}$ .  $DOY$ = day of the year.

The challenge of understanding phenology is generally to characterize a discrete event recurring with certain periodicity. Classically, phenological analyses have been performed using linear regression models (Morente-López et al., 2018; Rezaei et al., 2018; Zhou et al., 2016). Most of these studies analyze ecosystems with only one growing season (e.g. temperate or boreal forests), and when the summer is in the middle of the calendar year. However, the existing methods are not sufficiently generic to describe i) ecosystems in the Southern Hemisphere and ii) ecosystems with multiple growing seasons per year as often observed in e.g. semi-arid regions. Figure 1 illustrates the first problem from a conceptual point of view. Assume that some discrete event recurs annually, but the timing varies according to some external drivers. We would then know the interannual variability of phenology which essentially reflects the probability of this recurrent event in the course of the annual cycle.

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Figure 1 shows that linear regression models would be inappropriate to predict the day of the year ( $DOY$ ) of some phenological event in the Southern Hemisphere, as the actual target values to predict may flip between  $\gtrsim \frac{3\pi}{2}$  and  $\lesssim \frac{\pi}{2}$ . In recent years, circular statistics have gained some attention as they offer a solution to problems of this kind (Morellato et al., 2010; Beyene et al., 2018). Unlike classical statistics, the predicted variables are expressed in terms of angular directions (degrees or



70 radians) across a circumference (Fisher, 1995) allowing to perform statistical analysis where the data space is not Euclidean. In this framework, point events can be described as a von-Mises distribution (Von Mises, 1918) (the equivalent to the normal distribution in circular statistics, as shown in 1) with two parameters: The mean angular direction ( $\mu$ ) and the concentration parameter ( $\kappa$ ). Circular-linear (here called circular) regression technique allows to predict such circular responses (e.g. the timing of phenological events) from other linear variables (Morellato et al., 2010). Given that any phenological event can be  
75 interpreted as an angular direction and modeled alike, we assume that these circular regressions are well suited in this context. Despite this evident suitability, circular statistics have not yet been extensively applied in the study of phenology and will therefore be presented here as an alternative to conventional linear techniques.

In this paper, we aim to identify the factors controlling the phenology of the maximal seasonal GPP (GPP<sub>max</sub>). Specifically, we want to understand what are the climate controls of the timing of GPP<sub>max</sub> (DOY<sub>GPPmax</sub>) and provide a predictive framework  
80 using circular statistics. We explore this physio-phenological characteristic across different ecosystems around the globe using the FLUXNET 2015 dataset (Pastorello et al., 2017). The questions that we want to answer are: can circular statistics describe and predict DOY<sub>GPPmax</sub> per vegetation types? Can DOY<sub>GPPmax</sub> be explained using the climate conditions as cumulative factors? How is DOY<sub>GPPmax</sub> affected by the climatic conditions during the growing season? Based on these findings we discuss the potential of circular regressions beyond this specific application case in related phenological problems.

## 85 2 Methods

### 2.1 Data

We use 52 FLUXNET sites (with at least seven years of data) located through the latitudinal gradient of the globe (i.e. Northern, Southern hemisphere and tropical region) from the FLUXNET-2015 database (Table A1, <http://fluxnet.fluxdata.org/> (Pastorello et al., 2017)). Each FLUXNET site is identified with an abbreviation of the country and the name of the place e.g. AU-  
90 How means tower in Howard Springs, Australia. From the dataset we use the GPP data that was derived using the nighttime partitioning method and considering the variable  $u^*-t$  threshold to discriminate values of insufficient turbulence (Reichstein et al., 2005). In order to identify maximum daily GPP, we compute the quantile 0.9 for each day based on the half-hourly flux observations. As potential explanatory variables for DOY<sub>GPPmax</sub> we use on air temperature (T<sub>air</sub>), shortwave incoming radiation (SWin), precipitation (Precip), and vapor pressure deficit (VPD).

95 Given that the past climate conditions affect the CO<sub>2</sub> exchange between the atmosphere (ecological memory, (Liu et al., 2019; Ryan et al., 2015)), we need to understand whether an aggregated form of these climatic variables would better predict the phenological responses. For this we aggregate the original times-series of the T<sub>air</sub>, SWin, Precip, and VPD using a half-life decay function (equation 1).

$$mean(x, N) = \frac{\sum_{i,t=1}^{365} x_i N_t}{\sum_{i,t=1}^{365} N_t} \quad (1)$$



100 where:  $N(t) = N_0 e^{\frac{\ln(2)}{t_{1/2}} t}$

We can then vary the half-time parameter ( $t_{1/2}$ ) from 2 to 365 days. We make these variables comparable via centering standardization to unit variance and identify the optimal  $t_{1/2}$  (S1.1).

## 2.2 Circular statistics

A basic circular regression model was proposed by (Fisher and Lee, 1992) as follows:

105  $y = \mu + 2 * \text{atan}(\beta_i x_i)$  (2)

where  $y$  is the target variable (i.e.  $\text{DOY}_{\text{GPPmax}}$ ),  $\mu$  is the mean angular direction of the target variable,  $x_i$  are the predictor variables, and  $\beta_i$  the regression coefficients. The parameters  $\mu$  and  $\beta_i$  are fitted via the maximum likelihood method using reweighted least squares algorithm as proposed by (Green, 1984).

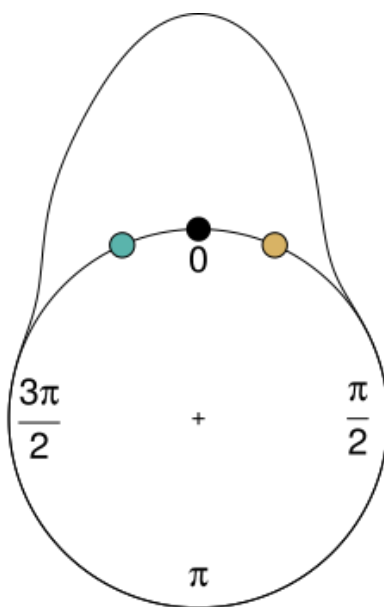
Circular regression models allow to interpret 1) the sign of the coefficient, 2) the statistical significance of the coefficient, and  
110 3) the accuracy of the prediction. Regarding the first point: Consider a negative sign of the coefficient, this would mean that an increasing value of the predictor would lead to an earlier  $\text{DOY}_{\text{GPPmax}}$  compared to the mean angular direction. Obviously the inverse would happen when the coefficient is positive. Figure 2 conceptually illustrates how the coefficients affect the predictions. Regarding the second aspect we can state that, if a coefficient is not significant, then its contribution would not be relevant to explain the phenological observation. In our case we define that the coefficient is significant if the median of the  
115 distribution of p-values is less than 0.05. Finally, we can estimate the accuracy of the prediction using the Jammalamadaka-Sarma (JS) correlation coefficient (Jammalamadaka and Sarma, 1988) implemented in the R package “circular” (Agostinelli and Lund, 2017). As in any other regression framework, this approach helps us to quantify the effect of each climate variable on the inter-annual variability of  $\text{DOY}_{\text{GPPmax}}$ .

To estimate the relative sensitivity of  $\text{DOY}_{\text{GPPmax}}$  to Tair, SWin, Precip, and VPD we use the implementation of equation  
120 2 in the “circular” R package (Agostinelli and Lund, 2017). To increase the robustness of the method we implement a block bootstrapping per growing season generating a model parameter average based on 1000 iterations. In each analysis, we estimate the accuracy of the model using the JS correlation coefficient.

## 2.3 Circular vs Linear Regression

We use equation 2, where we predefined two coefficient regressions ( $\beta_1 = 0.3$ ,  $\beta_2 = 0.1$ ). We generate two scenarios: 1) when  
125 the target timing occur at the beginning of the year ( $\mu = 0$ ) and 2) when the target timing occur at the middle of the year ( $\mu = \pi$ ). We simulate the variables  $x_1$  and  $x_2$  as normal distributions with a mean of 0, and 4 respectively, and a standard deviation of 1. For each scenario the amount of data is given by the equation 3 where  $N$  (rounded) is the amount of data for  $x_1$  and  $x_2$  and  $x$  take arbitrary values from 5 to 1000.

$N = e^{\log(x)}$  (3)



$\mu$	$\beta_1$	$X_1$	$\beta_2$	$X_2$
0	0	0.6	0.3	0.6
-0.413	0	1.3	0.3	0.6
6.697				
0.413	0	0.6	0.3	1.3

**Figure 2.** Interpretation of the coefficients in the circular regression. Consider a reference point (Black) generated with a circular-linear model with mean angular direction ( $\mu = 0$ ), two coefficients ( $\beta_1, \beta_2$ ) and two variables ( $X_1, X_2$ ), where one of the coefficients is negative ( $\beta_1$ ) and the other one is positive ( $\beta_2$ ). When the coefficient is negative and the value of the parameter increases (blue) the result is an earlier observation compared with the reference point (The equivalent of the negative radian is shown below the equation). On the other hand, when the coefficient is positive and the variable increase (yellow) the observation is later.

130 We use the simulated data from equation 1, and the original values of  $x_1$  and  $x_2$  to recover the original values of the regression coefficients  $\beta_1$  and  $\beta_2$  using the circular and linear regression. To increase the robustness of the analysis we simulate  $x_1$  and  $x_2$  1000 times for each  $n$ . We estimate the difference between the recovered and the original coefficient as the efficiency of the model (i.e. lower values mean higher efficiency).

## 2.4 Analysis setup

135 The target variable  $DOY_{GPP_{max}}$  is the day of the year when GPP reaches its maximum during the growing season. Given that different ecosystems present more than one growing season per year (e.g. semi-arid ecosystems) it is necessary to identify the number of growing seasons per year. To identifying the number of growing seasons we apply a Fast Fourier Transformation (FFT) (Cooley and Tukey, 1965) to the mean seasonal cycle of the GPP time series. The number of growing seasons is



equal to the maximum absolute value of the first four FFT coefficients (excluding the first one). For each FLUXNET site,  
140 we reconstructed the GPP time series taking the real numbers of the inverse FFT. We used these reconstructed time series to  
calculate the expected mean timing of  $\text{DOY}_{\text{GPPmax}}$  and use this value as a template). To recover the real  $\text{DOY}_{\text{GPPmax}}$  from the  
original time series we define a window around the template of length inversely proportional to the number of cycles (180 days  
/ Number of growing seasons). Finally, to increase the robustness of the analysis we identify the days with the 10 greatest GPP  
values. Finally, given that most of the sites are located in the northern hemisphere we expect that in most cases  $\text{DOY}_{\text{GPPmax}}$   
145 will be reached at the middle of the year.

To understand possible similarities in the regression coefficients across sites, and if these are related to the vegetation types  
or climate classes, we visualize the coefficients in a reduced dimensional space. For this dimensionality reduction we use  
t-Distributed Stochastic Neighbor Embedding (t-SNE) analysis (Maaten and Hinton, 2008) using the “dimRed” R package  
(Kraemer et al., 2018). To quantify the contribution of each climate variable, we count the number of sites per vegetation type  
150 where the regression coefficient is statistically significant. We perform a one-leaf-out cross validation per vegetation type to  
evaluate the predictive power of the circular regression using climate conditions. We only consider vegetation types with more  
than five sites. In this case the standardization of the climate variables is not applied. Finally, we use the mean of the optimum  
half-time parameter per vegetation type to weigh the climate conditions.

### 3 Results

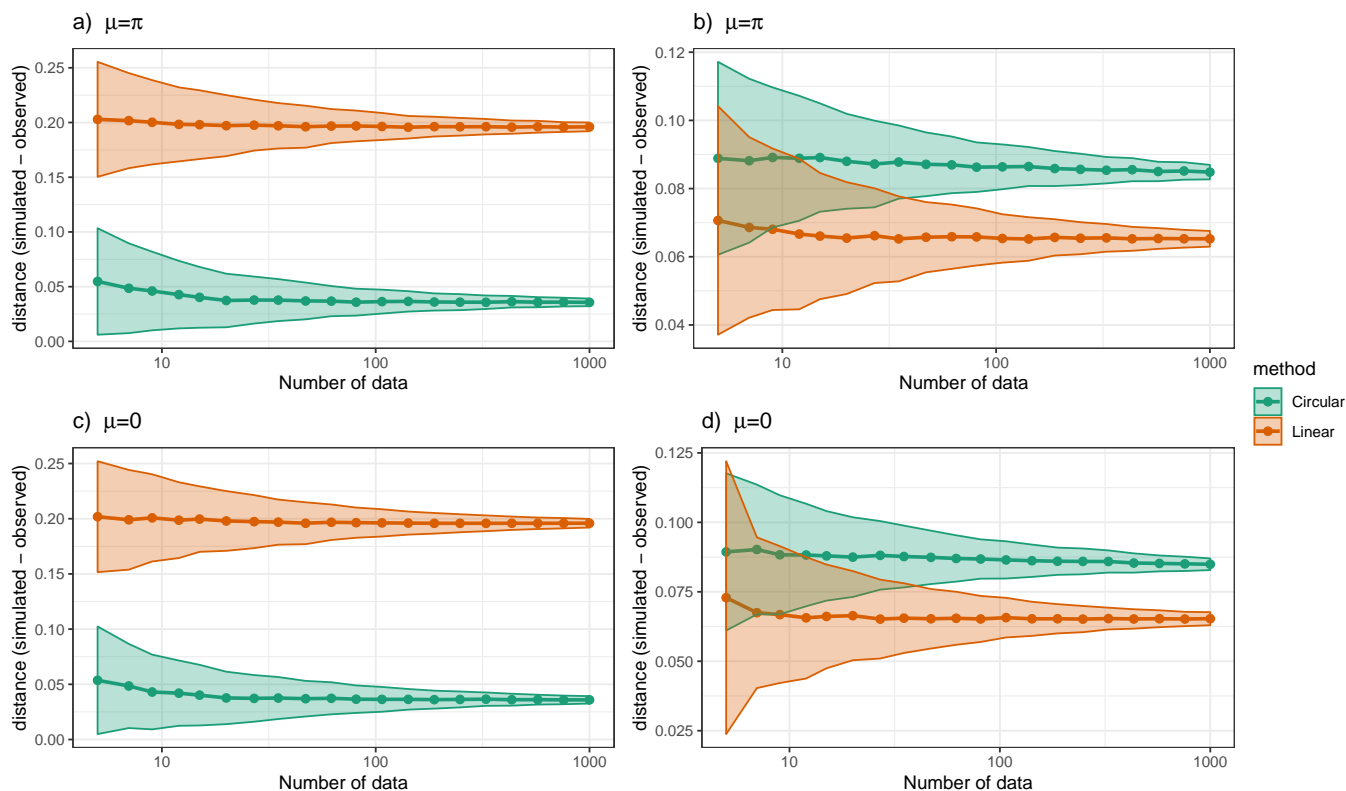
155 Here, we first report results from simulated data to describe the performance of the circular regression approach compared to  
a linear model. Second, we compare the performance of circular and linear regression using empirical data. Third, we analyze  
the sensitivity of  $\text{DOY}_{\text{GPPmax}}$  across vegetation types and climate classes. Finally, we show the results of the predictive power  
of circular regression per vegetation type.

#### 3.1 Circular vs Linear Regression

160 Figure 3 shows that for  $\mu = 0$  ( $\text{DOY}_{\text{GPPmax}}$  at the beginning of the year) and  $\mu = \pi$  ( $\text{DOY}_{\text{GPPmax}}$  at the middle of the year)  
the circular regression method is generally more efficient as it has a lower distance in case of  $\beta_1$ . For  $\beta_2$  linear regression  
performs better than circular regression when the number of data is higher than 100. Nevertheless, the differences between  
both regressions for  $\beta_2$  are of the order of 0.01 while the differences for  $\beta_1$  are of the order of 0.1.

To illustrate the method in practice, we compare the circular and linear models using data from two sites: US-Ha1 (Northern  
165 Hemisphere deciduous Broadleaf forest), and AU-How (Southern Hemisphere woody savanna). We relate the climate variables  
with  $\text{DOY}_{\text{GPPmax}}$  (See methods) and reconstructed the  $\text{DOY}_{\text{GPPmax}}$  using the linear and circular regression models. We compare  
observed and predicted  $\text{DOY}_{\text{GPPmax}}$  using JS correlation for circular model and Pearson-Product Moment for linear model.  
For US-Ha1 both methods shows similar performance predicting  $\text{DOY}_{\text{GPPmax}}$  (Figure 4), while for AU-How circular model  
recover better the original data than the linear model. In the case when  $\text{DOY}_{\text{GPPmax}}$  is reached at the beginning of the year,  
170 linear methods produce a strong bias predicting the timing across all year (Figure 4,b).





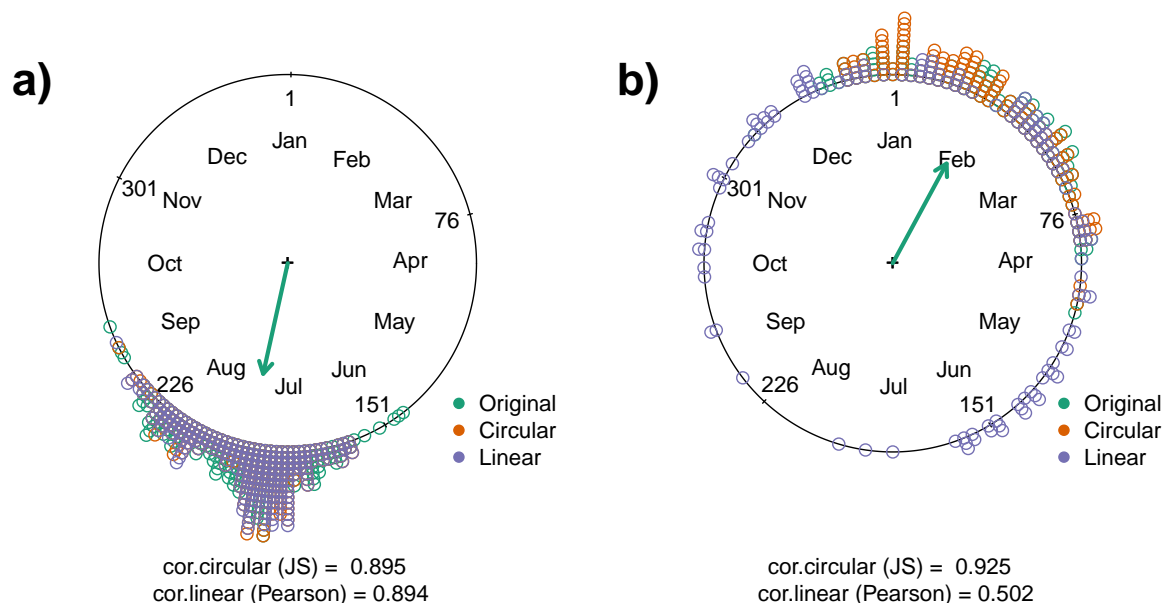
**Figure 3.** Efficiency of linear and circular regression models recovering the original coefficients of a circular regression to the number of data (lower values mean higher efficiency). Upper side:  $\mu = \pi$  (Maximum at the middle of the year). Bottom side  $\mu = 0$  (Maximum at the beginning of the year). The effect is analyzed for each regression coefficient individually. a. and c. correspond to the regression coefficient  $\beta_1$  and b. and d. correspond to the regression coefficient  $\beta_2$ .

### 3.2 Sensitivity of $\text{DOY}_{\text{GPPmax}}$ to climate variables

From 52 sites analyzed in this study, only one site (ES-LJu) shows a bimodal growing seasons (see S1.2). As expected in most cases  $\text{DOY}_{\text{GPPmax}}$  occurs at the middle of the calendar year (Figure S6), reflecting the uneven site distribution in FLUXNET (Schimel et al., 2015). However some ecosystems in the Northern Hemisphere do reach  $\text{DOY}_{\text{GPPmax}}$  at the beginning of the year, these are Mediterranean sites such as, US-Var and ES-LJu. In general terms, most of the sites have a standard deviation between 10 [days] and 40 [days]. The maximal std is 46.9 [days] for AU-Tum site. A detailed table with the mean angular direction and standard deviation of  $\text{DOY}_{\text{GPPmax}}$  of each site is presented in Supplement 1.2.

For most of the sites, the JS correlation coefficients are between 0.98 and 0.85 (Figure S5) showing that the interannual variability of  $\text{DOY}_{\text{GPPmax}}$  is mainly explained by the cumulative effect of the climate variables. Only five sites have a JS coefficient less than 0.8: US-Ton, IT-MBo, IT-Ro2, US-Wkg, and BR-Sa1. For ES-LJu the JS coefficient for the first growing season is 0.94 and 0.93 for the second one (Table S2).





**Figure 4.** Correlation coefficient between the observed and predicted  $DOY_{GPPmax}$  using climatic variables. Two sites are presented: a. US-Ha1, and b. AU-How. Observed  $DOY_{GPPmax}$  (Green) is compared with the data recovered using Circular (Orange) and Linear (Purple) regressions. Two correlation coefficients are used: Jammalamadaka-Sarna (JS) and Pearson product-moment (Pearson). In the circular plot the months and the day of the year (DOY) are also represented every 75 days. The green arrow indicate the mean angular direction of the distribution.

Across all sites we find that shortwave incoming radiation appears as the dominant driver worldwide in 34 sites (66 %). Air temperature is the main driver at another 14 sites (27 %), while precipitation is the main driver for US-Wkg and VPD for AU-How. For one site (IT-So1) any climatic variable is significant. In terms of the sign of the coefficients, shortwave incoming radiation and precipitation are predominantly negative, while for VPD is predominantly positive (Table 1). This means that higher integrated values of radiation and precipitation lead to an earlier  $DOY_{GPPmax}$ , while an increase of VPD will lead to a later  $DOY_{GPPmax}$ . For air temperature we find no clear tendency, as its signs are almost equally distributed between positive and negative (Table 1). Individual sensitivities per site are shown in Supplement 2.

Each site shows a unique  $DOY_{GPPmax}$  sensitivity to the different climate variables which leads to a range of unique patterns (Figure S7). In fact, these patterns of regression coefficients do not show any systematic relationship with vegetation type or climate class where the ecosystem is located (Figure S7). Considering the frequency per vegetation type, shortwave incoming



**Table 1.** Number of FLUXNET sites where each regression coefficient is statistically significant to explain the phenology of GPPmax ( $DOY_{GPPmax}$ ), and if the coefficient is positive or negative. We each category we present the number of sites. SWin = Shortwave incoming radiation, Tair = Air temperature, Precip = Precipitation, VPD = Vapor pressure deficit.

Sign	Climatic variable			
	SWin	Tair	Precip	VPD
(+)	1	21	2	17
(-)	48	17	21	5

radiation has the highest frequency in Evergreen Needleleaf Forest, Deciduous Broadleaf Forest, Grassland, Mixed Forest (MF), and Evergreen Broadleaf Forest, (Figure 5). VPD is not significant for Permanent Wetlands (WET) and Open Shrublands (OSH). While for Closed Shrublands (CSH), and Savannas (SAV) all the climate variables have the same frequency.

195 A special case to understand the sensitivity of  $DOY_{GPPmax}$  to climate variables is the site: "Llano de los Juanes", Spain (ES-LJu). It is the only clearly bimodal ecosystem in our study (Figure 6. In this case neither SWin nor Precip are statistically significant. While Tair and VPD are significant for both seasons. Furthermore, in the first growing season air temperature has a positive coefficient, while in the second growing season air temperature has a negative sign. On the other hand, VPD has a negative sign (the inverse of temperature) during the first growing season and positive during the second one.

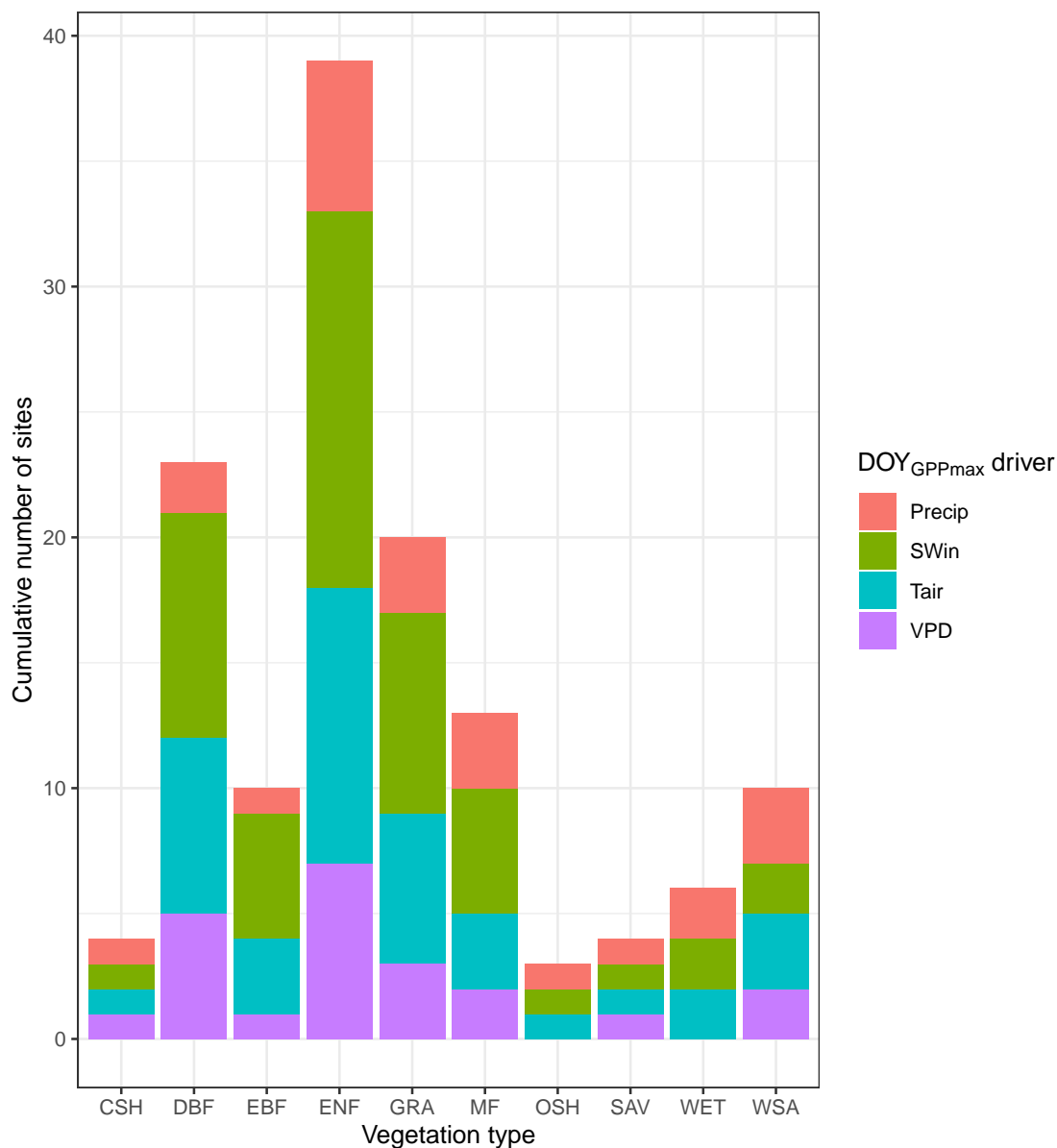
200 The leave-one-site-out cross-validation for several vegetation types shows that the power of the prediction of the model for GRA is zero. For DBF and EBF is 0.49 and 0.19, respectively, while for MF and ENF the power prediction of the model is 0.68 and 0.7, respectively (Figure 7).

## 4 Discussion

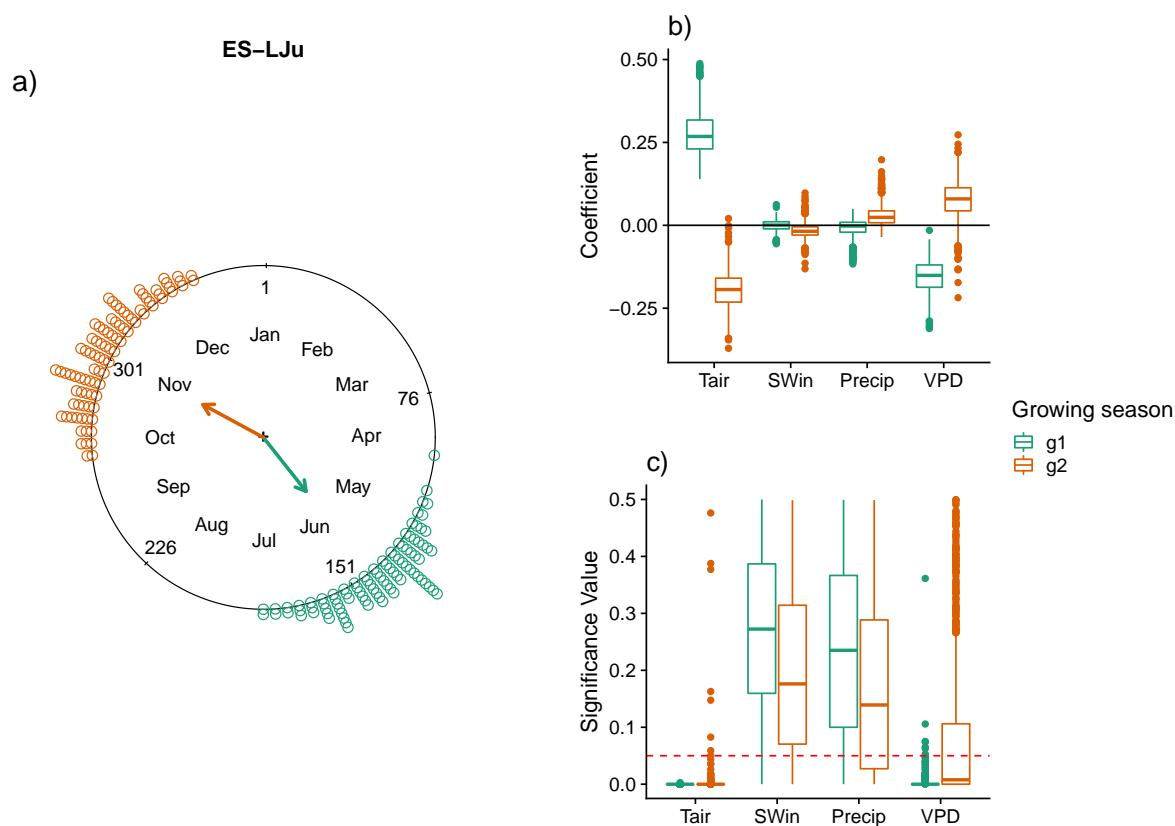
### 4.1 Circular vs Linear regression

205 We show that circular regression is a suitable tool to analyze phenological events. Our results suggest that circular regressions can recover the values of the predefined coefficients in the simulations with higher accuracy than linear regression (in the order of 0.1 to 0.01), presenting an advantage when analyzing the effect of climatic variables on phenological events. In addition, circular regression is able to analyze the phenology of ecosystems regardless of the day of the year when the event occurs, allowing to analysing phenological studies at global scale regardless of geographic location or the distribution of the  
210 observations during the year.

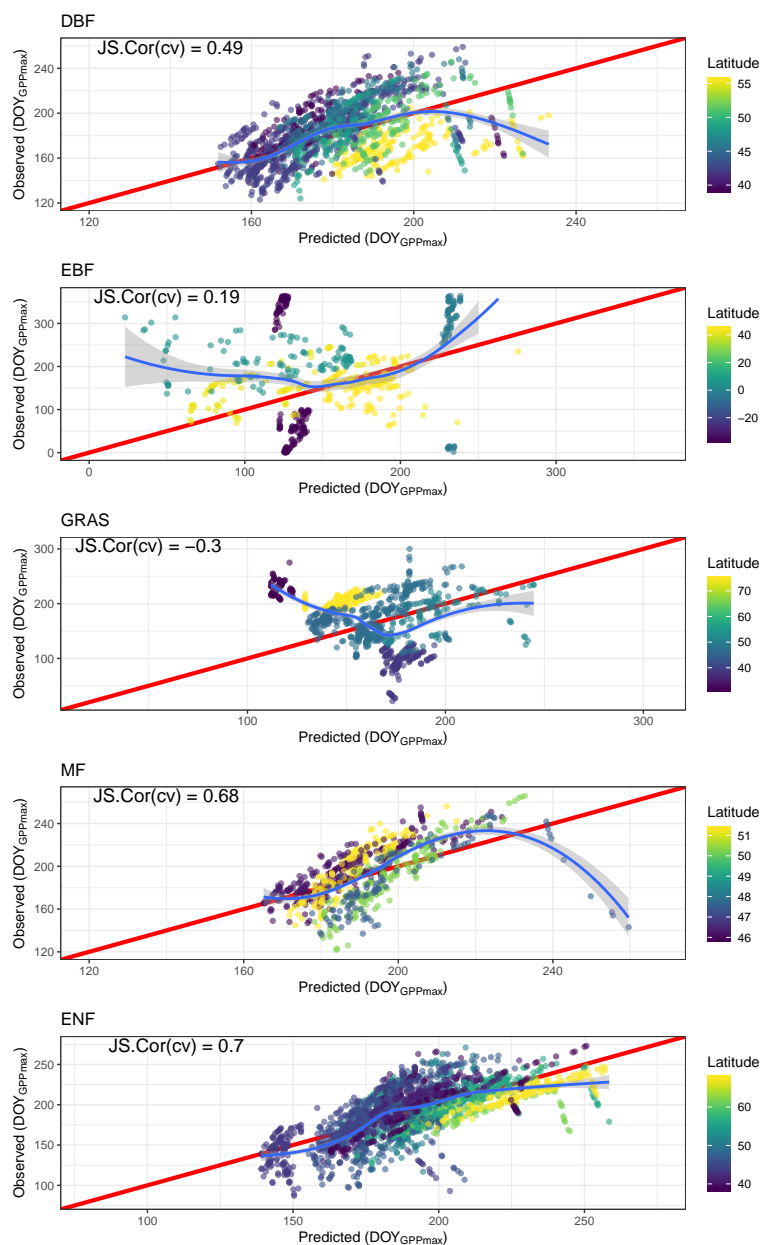
Richardson et al. (2013) concluded that phenology models need to be improved as a prerequisite to extending the prediction capacity of global-scale models. As we demonstrate here, circular statistics open new opportunities to do so. Besides, the results on phenological sensitivity of  $DOY_{GPPmax}$  in this study indicate the complexity of ecosystem responses to climate variability. This should be considered a first step to implement more complex statistical techniques like decision trees, Gaussian process  
215 or artificial neural networks.



**Figure 5.** Contribution of each climate variable to explain the interannual variation of  $DOY_{GPPmax}$  per vegetation type. CSH: Closed Shrublands ( $n = 1$ ), DBF: Deciduous Broadleaf Forest ( $n = 10$ ), EBF: Evergreen Broadleaf Forest ( $n = 5$ ), ENF: Evergreen Needleleaf Forest ( $n = 15$ ), GRA: Grassland ( $n = 8$ ), MF: Mixed Forest ( $n = 5$ ), OSH: Open Shrublands ( $n = 1$ ), SAV: Savannas ( $n = 1$ ), WET: Permanent wetlands ( $n = 2$ ), WSA: Woody Savannas ( $n = 3$ ). Each bar shows the cumulative number of sites where each climate variables are statistically significant.



**Figure 6.** DOY<sub>GPPmax</sub> sensitivity to different climate drivers in a Mediterranean ecosystem: "Llano de los Juanes", Spain (ES-Lju) with two growing seasons (green and orange). a) DOY<sub>GPPmax</sub> distribution across the year. The arrows indicate the mean angular direction of the growing season. b) regression coefficients for each growing season and c) the significance values for each variable. The red line in c) represents a p-value of 0.05.



**Figure 7.** Cross validation of the circular regression model to predict  $DOY_{GPPmax}$  for different vegetation types using air temperature, Short-wave incoming radiation, precipitation and Vapor pressure deficit (see methods). Deciduous Broadleaf Forest (DBF). Evergreen Broadleaf Forest (EBF). Grassland (GRA). Mixed Forest (MF), and Evergreen Needleleaf Forest (ENF). For each site the Jammalamadaka-Sarna (JS) correlation coefficient is shown. The red line represents the perfect fit. The blue line shows the tendency of the data.



## 4.2 Sensitivity of $DOY_{GPPmax}$ to climate variables

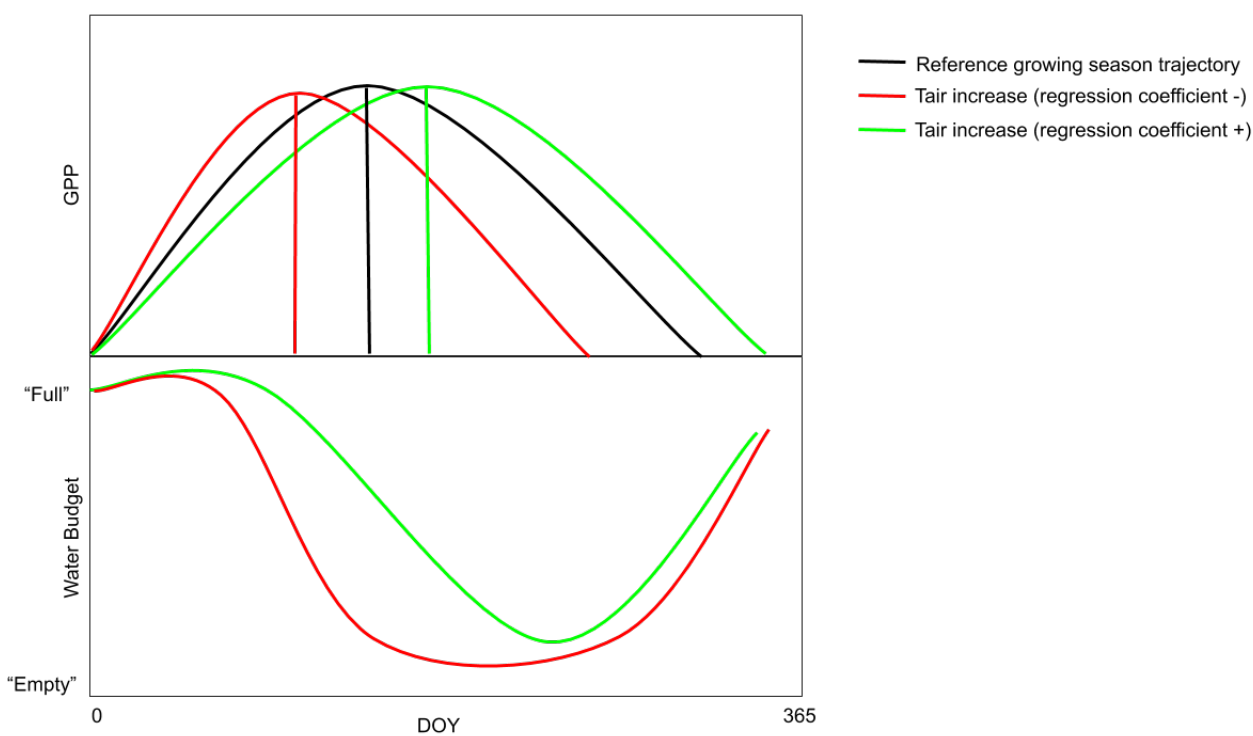
The geographical location of the FLUXNET 2015 sites represent an advantage to capture the  $DOY_{GPPmax}$  variability at global scale (Figure S6). Most of the analyzed sites (47) are located in the Northern Hemisphere. Two sites (GF-Guy and BR-Sa1) are located in the tropical region and, 3 sites (ZA-Kru, AU-How, AU-Tum) in the Southern Hemisphere. However, because  
220 of the low number of sites reported in the tropical and southern region with more than seven years of data, our understanding about the  $DOY_{GPPmax}$  variability in these regions is still limited. For that, increasing the data available for tropical and southern regions should be a fundamental task during the next decade to complement our knowledge about the physio-phenological ecosystem state.

The high values of the JS correlation coefficient for most of the sites demonstrate that the interannual variability of  $DOY_{GPPmax}$   
225 can be explained as the cumulative effect of the climate variables during the growing season. Sites where it was not possible to explain the variations of  $DOY_{GPPmax}$  with enough confidence level (JS correlation  $< 0.8$ ) might need an incorporation of biotic variables (e.g. species composition (Peichl et al., 2018)) that can improve the power prediction of the model.

Our results suggest that there is no pattern between the  $DOY_{GPPmax}$  sensitivity across vegetation type or climate classes. In other words, the  $DOY_{GPPmax}$  sensitivity is site-specific, probably produced by the unique combination of biotic (e.g. species  
230 composition, species dominance, species phenology, species interaction, and phenotypic plasticity) factors that are not evaluated in our study. Several studies that focussed on ecosystem phenology suggest that species composition play a fundamental role in ecosystem phenology of the  $CO_2$  uptake (Gonsamo et al., 2017; Peichl et al., 2018). Nevertheless, our results show that the interannual variability of  $DOY_{GPPmax}$  is still climatically driven.

235 While there is no clear relationship between the  $DOY_{GPPmax}$  sensitivity and the vegetation type, we find a predominant role of Shortwave incoming radiation (SWin) at the global scale on the  $DOY_{GPPmax}$  interannual variability, where for most of the sites SWin has a negative regression coefficient. This means, that if the SWin increases during the growing season the  $DOY_{GPPmax}$  will be reached earlier. This SWin effect can be a consequence of  $DOY_{GPPmax}$  being reached at the same time as SWin is maximum.

240 The second predominant factor at global scale is air temperature ( $T_{air}$ ). However, there is not a clear pattern in the sign of the regression coefficient (positive or negative) at global scale. Our hypothesis is that the sign of  $T_{air}$  is reflecting the speed consumption of the water available in the soil (water budget). In this way when the regression coefficient is positive and  $T_{air}$  increases during the growing season the  $DOY_{GPPmax}$  will be reached later reflecting a decrease in the speed of water consumption, and increasing the length of the growing season (Figure 8). Several studies demonstrated for different vegetation  
245 types that when temperature increases, spring onset is earlier and autumn senescence is later (Christensen et al., 2007; Linkosalo et al., 2009; Migliavacca et al., 2012; Morin et al., 2010; Post and Forchhammer, 2008), increasing the length of the growing season and the amount of  $CO_2$  that is uptake by ecosystems (Richardson et al., 2013). On the other hand, where the  $T_{air}$  regression coefficient is negative and the temperature increase during the first part of the growing season the speed of the water consumption will increase producing an earlier  $DOY_{GPPmax}$  (Figure 8).



**Figure 8.** Theoretical relationship between the sign of air temperature ( $T_{air}$ ) in the circular regression model and the water budget in an ecosystem. When the sign of the regression coefficient is negative and temperature increase the  $DOY_{GPP_{max}}$  is reached earlier (Red), on the other hand if the sign is positive and temperature increase the  $DOY_{GPP_{max}}$  is reach later (Green).





250 Ecosystems with two growing seasons per year represent a very interesting case of the effect of climate drivers on  $DOY_{GPPmax}$   
across different growing seasons. In Llano de los Juanes, Spain (ES-LJu, Figure 6)  $DOY_{GPPmax}$  is reached in the first growing  
season when the rainy season is finishing, while in the second growing season  $DOY_{GPPmax}$  is reached in the middle of the rainy  
season (Data not shown). The effect of temperature for the first growing season is positive suggesting that if we increase the  
temperature during the period before, the  $DOY_{GPPmax}$  will happen later. Following our hypothesis mentioned above this will  
255 happen because the speed of the water consumption is reduced, probably because the precipitation is also increase during the  
spring. However, as VPD has a negative effect and given the covariance between the  $T_{air}$  and VPD the effect of the increase  
of temperature is in part countered by the increase of VPD. During the second growing season the effect of  $T_{air}$  is negative  
meaning in this case that the water budget is lower, then if  $T_{air}$  increase the  $DOY_{GPPmax}$  will be reached earlier.

Phenology in Mediterranean ecosystems is mainly controlled by water availability (Kramer et al., 2000; Luo et al., 2018;  
260 Peñuelas et al., 2009). However, our results suggest that  $DOY_{GPPmax}$  is mainly sensitive to temperature. This result agrees with  
the analysis performed by (Gordo and Sanz, 2005) where the authors evaluated the phenological sensitivity of Mediterranean  
ecosystem to temperature and precipitation, and they concluded that temperature was the most important driver. Although water  
is a limiting factor in Mediterranean ecosystems, its influence on plant physiology and plant phenology can be completely  
different. In terms of physiology the  $GPP_{max}$  value can decrease but in terms of phenology  $DOY_{GPPmax}$  can be still being the  
265 same.

Complex interactions between climate variables and phenological response and the interspecificity of the sensitivity at  
site level explain in part the poor power prediction of the model for grasslands, Evergreen Broadleaf Forest, and Deciduous  
Broadleaf Forests in the cross validation analysis (Figure 7). However, the power prediction for Mixed Forest and Evergreen  
Needleleaf Forests is good, also when the distribution of the latitudinal gradient is not the same for all the sites. These results  
270 reflect that circular regression model can be extrapolated from different sites, to predict the  $DOY_{GPPmax}$  interannual variability.  
This advantage could be a way to solve the common critic that phenological models can not be extrapolated generating only  
ad hoc hypothesis (Richardson et al., 2013).

## 5 Conclusions

In this study we explore the potential of “circular regressions” to explain the phenology of maximal  $CO_2$  uptake rates. We  
275 conclude that 1) shortwave incoming radiation, and temperature are the main drivers of the timing of maximal  $CO_2$  uptake at  
global scale; precipitation and VPD only play a secondary role. 2) Although the sensitivity of the  $DOY_{GPPmax}$  to the climate  
drivers is site specific, it is possible to extrapolate the circular regression model for different sites with the same vegetation  
type and similar latitudes. Finally, we demonstrated using simulated and empirical data, that circular regression produces more  
accurate results than linear regression, in particular in cases when data needs to be explored across hemispheres.



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## Appendix A: FLUXNET Sites

Table A1: FLUXNET sites used in our study. We report the name of the sites, time period used for the analysis, the climate class of each site following the Köppen-Geiger classification: Tropical monsoon climate (Am), Tropical savanna climate (Aw), Cold semi-arid climates (BSk), Humid subtropical climate (Cfa), Oceanic climate (Cfb), Hot-summer mediterranean climate (Csa), Warm-summer mediterranean climate (Csb), Humid subtropical climate (Cwa), humid continental climate (Dfb), Subarctic climate (Dfc, Dsc), and Tundra climate (ET). We also report the Vegetation type of the sites: Closed Shrublands (CSH), Deciduous Broadleaf Forests (DBF), Evergreen Broadleaf Forest (EBF), Evergreen Needleleaf Forests (ENF), Grasslands (GRA), Mixed Forests (MF), Open Shrublands (OSH), Savannas (SAV), Permanent Wetlands (WET), Woody Savannas (WSA).

Site name	Köppen-Geiger class	Vegetation type	Period	N. years analyzed	Citation	Data DOI
US-Ha1	Dfb	DBF	1992:2012	21	(Urbanski et al., 2007)	10.18140/FLX/1440071
US-PFa	Dfb	MF	1996:2014	19	(Berger et al., 2001)	10.18140/FLX/1440089
BE-Bra	Cfb	MF	1999:2002, 2004:2014	15	(Carrara et al., 2004)	10.18140/FLX/1440128
BE-Vie	Cfb	MF	1997:2014	18	(Aubinet et al., 2001)	10.18140/FLX/1440130
DE-Tha	Cfb	ENF	1996:2014	19	(GrüNwald and Bernhofer, 2007)	10.18140/FLX/1440152
DK-Sor	Cfb	DBF	1996:2014	19	(Pilegaard et al., 2011)	10.18140/FLX/1440155
FI-Hyy	Dfc	ENF	1996:2014	19	(Sun et al., 2003)	10.18140/FLX/1440158
IT-Col	Csa	DBF	1996:2014	19	(Valentini et al., 1996)	10.18140/FLX/1440167
NL-Loo	Cfb	ENF	1996:2014	18	(Moors, 2012)	10.18140/FLX/1440178
CH-Dav	ET	ENF	1997:2014	18	(Zielis et al., 2014)	10.18140/FLX/1440178
RU-Fyo	Dfb	ENF	1998:2014	17	(Kurbatova et al., 2008)	10.18140/FLX/1440183
US-NR1	Dfc	ENF	1999:2014	16	(Monson et al., 2002)	10.18140/FLX/1440087
IT-Ren	Dfc	ENF	1999, 2002:2003, 2005:2013	12	(Montagnani et al., 2009)	10.18140/FLX/1440173
US-MMS	Cfa	DBF	1999:2014	16	(Schmid et al., 2000)	10.18140/FLX/1440083



US-WCr	Dfb	DBF	1999:2006, 2011:2014	12	(Curtis et al., 2002)	10.18140/FLX/1440095
CA-Man	Dfc	ENF	1994:1996, 1998:2003	12	(Brooks et al., 1997)	10.18140/FLX/1440035
DK-ZaH	ET	GRA	2000:2010, 2012:2014	14	(Lund et al., 2012)	10.18140/FLX/1440224
FR-Pue	Csa	EBF	2000:2015	15	(Rambal et al., 2004)	10.18140/FLX/1440164
US-Los	Dfb	WET	2001:2008, 2010, 2014	10	(Davis et al., 2003)	10.18140/FLX/1440076
US-UMB	Dfb	DBF	2000:2014	15	(Curtis et al., 2002)	10.18140/FLX/1440093
US-Var	Csa	GRA	2001:2014	14	(Xu and Baldocchi, 2004)	10.18140/FLX/1440094
AU-How	Aw	WSA	2002:2014	13	(Berlinger et al., 2007)	10.18140/FLX/1440125
AU-Tum	Cfb	EBF	2001:2014	14	(Leuning et al., 2005)	10.18140/FLX/1440126
FI-Sod	Dfc	ENF	2001:2014	14	(Thum et al., 2007)	10.18140/FLX/1440160
IT-SRo	Csa	ENF	1999:2012	14	(Chiesi et al., 2005)	10.18140/FLX/1440176
US-Syv	Dfb	MF	2001:2007, 2012:2014	10	(Desai et al., 2005)	10.18140/FLX/1440091
US-Ton	Csa	WSA	2001:2014	14	(Xu and Baldocchi, 2003)	10.18140/FLX/1440092
ZA-Kru	Cwa	SAV	2000:2005, 2007:2013	13	(Archibald et al., 2009)	10.18140/FLX/1440188
DE-Hai	Cfb	DBF	2000:2012	13	(Knobl et al., 2003)	10.18140/FLX/1440148
FR-LBr	Cfb	ENF	1996:2008	13	(Berbigier et al., 2001)	10.18140/FLX/1440163
IT-Cpz	Csa	EBF	2000:2008	9	(Garbulsky et al., 2008)	10.18140/FLX/1440168
US-Me2	Csb	ENF	2002:2014	13	(Treuhaft et al., 2004)	10.18140/FLX/1440079
IT-Lav	Cfb	ENF	2003:2014	12	(Marcolla et al., 2003)	10.18140/FLX/1440169



RU-Cok	Dsc	OSH	2003:2013	11	(Molen et al., 2007)	10.18140/FLX/1440182
AT-Neu	Dfc	GRA	2002:2012	11	(Wohlfahrt et al., 2008)	10.18140/FLX/1440121
CH-Lae	Cfb	MF	2004:2014	11	(Etzold et al., 2011)	10.18140/FLX/1440134
DE-Gri	Cfb	GRA	2004:2014	11	(Prescher et al., 2010)	10.18140/FLX/1440147
GF-Guy	Am	EBF	2004:2014	11	(Bonal et al., 2008)	10.18140/FLX/1440165
IT-MBo	Dfb	GRA	2003:2013	11	(Marcolla et al., 2011)	10.18140/FLX/1440170
IT-Noe	Csa	CSH	2004:2014	11	(Marras et al., 2011)	10.18140/FLX/1440171
IT-Ro2	Csa	DBF	2002:2008, 2010:2012	10	(Tedeschi et al., 2006)	10.18140/FLX/1440175
US-Blo	Csa	ENF	1997:2007	11	(Baker et al., 1999)	10.18140/FLX/1440068
US-GLE	Dfc	ENF	2005:2014	10	(McDowell et al., 2000)	10.18140/FLX/1440069
US-SRM	BSk	WSA	2004:2014	11	(Scott et al., 2008)	10.18140/FLX/1440090
US-Wkg	BSk	GRA	2004:2014	11	(Emmerich, 2003)	10.18140/FLX/1440096
BR-Sa1	Am	EBF	2002:2005, 2009:2011	7	(Saleska et al., 2003)	10.18140/FLX/1440032
CH-Cha	Cfb	GRA	2005:2014	10	(Merbold et al., 2014)	10.18140/FLX/1440131
CH-Fru	Cfb	GRA	2005:2014	10	(Imer et al., 2013)	10.18140/FLX/1440133
ES-LJu	Csa	OSH	2005:2013	9	(Serrano-Ortiz et al., 2009)	10.18140/FLX/1440226
FR-Fon	Cfb	DBF	2005:2014	10	(Delpierre et al., 2016)	10.18140/FLX/1440161
CZ-wet	Cfb	WET	2006:2014	9	(Dušek et al., 2012)	10.18140/FLX/1440145
IT-Ro1	Csa	DBF	2001:2008	8	(Rey et al., 2002)	10.18140/FLX/1440174



## References

- Agostinelli, C. and Lund, U.: R package circular: Circular Statistics (version 0.4-93), CA: Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA, <https://r-forge.r-project.org/projects/circular/>, 2017.
- Archibald, S. A., Kirton, A., Merwe, M. R. v. d., Scholes, R. J., Williams, C. A., and Hanan, N.: Drivers of inter-annual variability in Net Ecosystem Exchange in a semi-arid savanna ecosystem, South Africa, *Biogeosciences*, 6, 251–266, <https://doi.org/https://doi.org/10.5194/bg-6-251-2009>, <https://www.biogeosciences.net/6/251/2009/>, 2009.
- Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., and Laitat, E.: Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes, *Agricultural and Forest Meteorology*, 108, 293–315, [https://doi.org/https://doi.org/10.1016/S0168-1923\(01\)00244-1](https://doi.org/https://doi.org/10.1016/S0168-1923(01)00244-1), <http://www.sciencedirect.com/science/article/pii/S0168192301002441>, 2001.
- Aubinet, M., Vesala, T., and Papale, D., eds.: *Eddy Covariance: A Practical Guide to Measurement and Data Analysis*, Springer Atmospheric Sciences, Springer Netherlands, <https://www.springer.com/de/book/9789400723504>, 2012.
- Baker, B., Guenther, A., Greenberg, J., Goldstein, A., and Fall, R.: Canopy fluxes of 2-methyl-3-buten-2-ol over a ponderosa pine forest by relaxed eddy accumulation: Field data and model comparison, *Journal of Geophysical Research: Atmospheres*, 104, 26 107–26 114, <https://doi.org/10.1029/1999JD900749>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/1999JD900749>, 1999.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K. T., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: A New Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon Dioxide, Water Vapor, and Energy Flux Densities, *Bulletin of the American Meteorological Society*, 82, 2415–2434, [https://doi.org/10.1175/1520-0477\(2001\)082<2415:FANTTS>2.3.CO;2](https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2), <https://journals.ametsoc.org/doi/abs/10.1175/1520-0477%282001%29082%3C2415%3AFANTTS%3E2.3.CO%3B2>, 2001.
- Bauerle, W. L., Oren, R., Way, D. A., Qian, S. S., Stoy, P. C., Thornton, P. E., Bowden, J. D., Hoffman, F. M., and Reynolds, R. F.: Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling, *Proceedings of the National Academy of Sciences*, 109, 8612–8617, <https://doi.org/10.1073/pnas.1119131109>, <https://www.pnas.org/content/109/22/8612>, 2012.
- Berbigier, P., Bonnefond, J.-M., and Mellmann, P.: CO<sub>2</sub> and water vapour fluxes for 2 years above Euroflux forest site, *Agricultural and Forest Meteorology*, 108, 183–197, [https://doi.org/10.1016/S0168-1923\(01\)00240-4](https://doi.org/10.1016/S0168-1923(01)00240-4), <http://www.sciencedirect.com/science/article/pii/S0168192301002404>, 2001.
- Berger, B. W., Davis, K. J., Yi, C., Bakwin, P. S., and Zhao, C. L.: Long-Term Carbon Dioxide Fluxes from a Very Tall Tower in a Northern Forest: Flux Measurement Methodology, *Journal of Atmospheric and Oceanic Technology*, 18, 529–542, [https://doi.org/10.1175/1520-0426\(2001\)018<0529:LTCDFF>2.0.CO;2](https://doi.org/10.1175/1520-0426(2001)018<0529:LTCDFF>2.0.CO;2), <https://journals.ametsoc.org/doi/full/10.1175/1520-0426%282001%29018%3C0529%3ALTCDFF%3E2.0.CO%3B2>, 2001.
- Beringer, J., Hutley, L. B., Tapper, N. J., and Cernusak, L. A.: Savanna fires and their impact on net ecosystem productivity in North Australia, *Global Change Biology*, 13, 990–1004, <https://doi.org/10.1111/j.1365-2486.2007.01334.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2007.01334.x>, 2007.
- Beyene, M. T., Jain, S., and Gupta, R. C.: Linear-Circular Statistical Modeling of Lake Ice-Out Dates, *Water Resources Research*, 54, 7841–7858, <https://doi.org/10.1029/2017WR021731>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2017WR021731>, 2018.



- 325 Bonal, D., Bosc, A., Ponton, S., Goret, J.-Y., Burban, B., Gross, P., Bonnefond, J.-M., Elbers, J., Longdoz, B., Epron, D., Guehl, J.-M., and Granier, A.: Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana, *Global Change Biology*, 14, 1917–1933, <https://doi.org/10.1111/j.1365-2486.2008.01610.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2008.01610.x>, 2008.
- Brooks, J. R., Flanagan, L. B., Varney, G. T., and Ehleringer, J. R.: Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO<sub>2</sub> within boreal forest canopies, *Tree Physiology*, 17, 1–12, <https://doi.org/10.1093/treephys/17.1.1>, <https://academic.oup.com/treephys/article/17/1/1/1640508>, 1997.
- 330 Carrara, A., Janssens, I. A., Yuste, J. C., and Ceulemans, R.: Seasonal changes in photosynthesis, respiration and NEE of a mixed temperate forest, *Agricultural and Forest Meteorology*, 126, 15–31, <https://doi.org/https://doi.org/10.1016/j.agrformet.2004.05.002>, <http://www.sciencedirect.com/science/article/pii/S0168192304001145>, 2004.
- 335 Chiesi, M., Maselli, F., Bindi, M., Fibbi, L., Cherubini, P., Arlotta, E., Tirone, G., Matteucci, G., and Seufert, G.: Modelling carbon budget of Mediterranean forests using ground and remote sensing measurements, *Agricultural and Forest Meteorology*, 135, 22–34, <https://doi.org/10.1016/j.agrformet.2005.09.011>, <http://www.sciencedirect.com/science/article/pii/S0168192305002108>, 2005.
- Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, R., Jones, R., Kolli, R. K., Kwon, W. K., Laprise, R., Magana Rueda, V., Mearns, L., Menendez, C. G., Räisänen, J., Rinke, A., Sarr, A., Whetton, P., Arritt, R., Benestad, R., Beniston, M., Bromwich, D., 340 Caya, D., Comiso, J., de Elia, R., and Dethloff, K.: Regional climate projections, <https://epic.awi.de/id/eprint/17617/>, 2007.
- Cooley, J. W. and Tukey, J. W.: An Algorithm for the Machine Calculation of Complex Fourier Series, *Mathematics of Computation*, 19, 297–301, <https://doi.org/10.2307/2003354>, <https://www.jstor.org/stable/2003354>, 1965.
- Curtis, P. S., Hanson, P. J., Bolstad, P., Barford, C., Randolph, J. C., Schmid, H. P., and Wilson, K. B.: Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests, *Agricultural and Forest Meteorology*, 113, 3–19, 345 [https://doi.org/10.1016/S0168-1923\(02\)00099-0](https://doi.org/10.1016/S0168-1923(02)00099-0), <http://www.sciencedirect.com/science/article/pii/S0168192302000990>, 2002.
- Davis, K. J., Bakwin, P. S., Yi, C., Berger, B. W., Zhao, C., Teclaw, R. M., and Isebrands, J. G.: The annual cycles of CO<sub>2</sub> and H<sub>2</sub>O exchange over a northern mixed forest as observed from a very tall tower, *Global Change Biology*, 9, 1278–1293, <https://doi.org/10.1046/j.1365-2486.2003.00672.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2003.00672.x>, 2003.
- Delpierre, N., Berveiller, D., Granda, E., and Dufrière, E.: Wood phenology, not carbon input, controls the interannual variability of wood 350 growth in a temperate oak forest, *New Phytologist*, 210, 459–470, <https://doi.org/10.1111/nph.13771>, <https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/nph.13771>, 2016.
- Desai, A. R., Bolstad, P. V., Cook, B. D., Davis, K. J., and Carey, E. V.: Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA, *Agricultural and Forest Meteorology*, 128, 33–55, <https://doi.org/10.1016/j.agrformet.2004.09.005>, <http://www.sciencedirect.com/science/article/pii/S0168192304002369>, 2005.
- 355 Dušek, J., Čížková, H., Stellner, S., Czerný, R., and Květ, J.: Fluctuating water table affects gross ecosystem production and gross radiation use efficiency in a sedge-grass marsh, *Hydrobiologia*, 692, 57–66, <https://doi.org/10.1007/s10750-012-0998-z>, <https://doi.org/10.1007/s10750-012-0998-z>, 2012.
- Emmerich, W. E.: Carbon dioxide fluxes in a semiarid environment with high carbonate soils, *Agricultural and Forest Meteorology*, 116, 91–102, [https://doi.org/10.1016/S0168-1923\(02\)00231-9](https://doi.org/10.1016/S0168-1923(02)00231-9), <http://www.sciencedirect.com/science/article/pii/S0168192302002319>, 2003.
- 360 Etzold, S., Ruehr, N. K., Zweifel, R., Dobbertin, M., Zingg, A., Pluess, P., Häsler, R., Eugster, W., and Buchmann, N.: The Carbon Balance of Two Contrasting Mountain Forest Ecosystems in Switzerland: Similar Annual Trends, but Seasonal Differences, *Ecosystems*, 14, 1289–1309, <https://doi.org/10.1007/s10021-011-9481-3>, <https://doi.org/10.1007/s10021-011-9481-3>, 2011.





- Fisher, N. I.: Statistical Analysis of Circular Data, Cambridge University Press, google-Books-ID: wGPj3EoFdJwC, 1995.
- Fisher, N. I. and Lee, A. J.: Regression Models for an Angular Response, *Biometrics*, 48, 665–677, <https://doi.org/10.2307/2532334>, <http://www.jstor.org/stable/2532334>, 1992.
- Garbulsky, M. F., Peñuelas, J., Papale, D., and Filella, I.: Remote estimation of carbon dioxide uptake by a Mediterranean forest, *Global Change Biology*, 14, 2860–2867, <https://doi.org/10.1111/j.1365-2486.2008.01684.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2008.01684.x>, 2008.
- Gonsamo, A., D’Odorico, P., Chen, J. M., Wu, C., and Buchmann, N.: Changes in vegetation phenology are not reflected in atmospheric CO<sub>2</sub> and 13C/12C seasonality, *Global Change Biology*, 23, 4029–4044, <https://doi.org/10.1111/gcb.13646>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13646>, 2017.
- Gordo, O. and Sanz, J. J.: Phenology and climate change: a long-term study in a Mediterranean locality, *Oecologia*, 146, 484–495, <https://doi.org/10.1007/s00442-005-0240-z>, <https://doi.org/10.1007/s00442-005-0240-z>, 2005.
- Green, P. J.: Iteratively Reweighted Least Squares for Maximum Likelihood Estimation, and some Robust and Resistant Alternatives, *Journal of the Royal Statistical Society. Series B (Methodological)*, 46, 149–192, <https://www.jstor.org/stable/2345503>, 1984.
- GrüNwald, T. and Bernhofer, C.: A decade of carbon, water and energy flux measurements of an old spruce forest at the Anchor Station Tharandt, *Tellus B: Chemical and Physical Meteorology*, 59, 387–396, <https://doi.org/10.1111/j.1600-0889.2007.00259.x>, <https://doi.org/10.1111/j.1600-0889.2007.00259.x>, 2007.
- Huang, K., Xia, J., Wang, Y., Ahlström, A., Chen, J., Cook, R. B., Cui, E., Fang, Y., Fisher, J. B., Huntzinger, D. N., Li, Z., Michalak, A. M., Qiao, Y., Schaefer, K., Schwalm, C., Wang, J., Wei, Y., Xu, X., Yan, L., Bian, C., and Luo, Y.: Enhanced peak growth of global vegetation and its key mechanisms, *Nature Ecology & Evolution*, p. 1, <https://doi.org/10.1038/s41559-018-0714-0>, <https://www.nature.com/articles/s41559-018-0714-0>, 2018.
- Imer, D., Merbold, L., Eugster, W., and Buchmann, N.: Temporal and spatial variations of soil CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes at three differently managed grasslands, *Biogeosciences*, 10, 5931–5945, <https://doi.org/https://doi.org/10.5194/bg-10-5931-2013>, <https://www.biogeosciences.net/10/5931/2013/bg-10-5931-2013.html>, 2013.
- Jammalamadaka, S. R. and Sarma, Y.: A correlation coefficient for angular variables, *Statistical theory and data analysis II*, pp. 349–364, [bibtext\\*\[publisher=Amsterdam North-Holland\] Citation Key Alias: jammalamadaka\\_correlation\\_1988](https://doi.org/10.1016/S0168192303001151), 1988.
- Knohl, A., Schulze, E.-D., Kolle, O., and Buchmann, N.: Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany, *Agricultural and Forest Meteorology*, 118, 151–167, [https://doi.org/10.1016/S01681923\(03\)00115-1](https://doi.org/10.1016/S01681923(03)00115-1), <http://www.sciencedirect.com/science/article/pii/S0168192303001151>, 2003.
- Kraemer, G., Reichstein, M., and D, M. M.: dimRed and coRanking—Unifying Dimensionality Reduction in R, *The R Journal*, 10, 342–358, <https://journal.r-project.org/archive/2018/RJ-2018-039/index.html>, 2018.
- Kramer, K., Leinonen, I., and Loustau, D.: The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview, *International Journal of Biometeorology*, 44, 67–75, <https://doi.org/10.1007/s004840000066>, <https://doi.org/10.1007/s004840000066>, 2000.
- Kurbatova, J., Li, C., Varlagin, A., Xiao, X., and Vygodskaya, N.: Modeling carbon dynamics in two adjacent spruce forests with different soil conditions in Russia, *Biogeosciences*, 5, 969–980, <https://doi.org/https://doi.org/10.5194/bg-5-969-2008>, <https://www.biogeosciences.net/5/969/2008/>, 2008.
- Leuning, R., Cleugh, H. A., Zegelin, S. J., and Hughes, D.: Carbon and water fluxes over a temperate Eucalyptus forest and a tropical wet/dry savanna in Australia: measurements and comparison with MODIS remote sensing estimates, *Agricultural and Forest Mete-*



- orology, 129, 151–173, <https://doi.org/https://doi.org/10.1016/j.agrformet.2004.12.004>, <http://www.sciencedirect.com/science/article/pii/S0168192305000079>, 2005.
- Lieth, H., ed.: Phenology and Seasonality Modeling, Ecological Studies, Springer-Verlag, Berlin Heidelberg, <https://www.springer.com/gp/book/9783642518652>, citation Key Alias: lieth\_phenology\_1974, 1974.
- 405 Linkosalo, T., Häkkinen, R., Terhivuo, J., Tuomenvirta, H., and Hari, P.: The time series of flowering and leaf bud burst of boreal trees (1846–2005) support the direct temperature observations of climatic warming, *Agricultural and Forest Meteorology*, 149, 453–461, <https://doi.org/10.1016/j.agrformet.2008.09.006>, <http://www.sciencedirect.com/science/article/pii/S0168192308002530>, 2009.
- Liu, Y., Schwalm, C. R., Samuels-Crow, K. E., and Ogle, K.: Ecological memory of daily carbon exchange across the globe and its importance in drylands, *Ecology Letters*, 0, <https://doi.org/10.1111/ele.13363>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13363>, 2019.
- 410 Lund, M., Falk, J. M., Friborg, T., Mbufong, H. N., Sigsgaard, C., Soegaard, H., and Tamstorf, M. P.: Trends in CO<sub>2</sub> exchange in a high Arctic tundra heath, 2000–2010, *Journal of Geophysical Research: Biogeosciences*, 117, <https://doi.org/10.1029/2011JG001901>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2011JG001901>, 2012.
- Luo, Y., El-Madany, T. S., Filippa, G., Ma, X., Ahrens, B., Carrara, A., Gonzalez-Cascon, R., Cremonese, E., Galvagno, M., Hammer, T. W., Pacheco-Labrador, J., Martín, M. P., Moreno, G., Perez-Priego, O., Reichstein, M., Richardson, A. D., Römermann, C., and Migliavacca, M.: Using Near-Infrared-Enabled Digital Repeat Photography to Track Structural and Physiological Phenology in Mediterranean Tree–Grass Ecosystems, *Remote Sensing*, 10, 1293, <https://doi.org/10.3390/rs10081293>, <https://www.mdpi.com/2072-4292/10/8/1293>, 2018.
- 415 Maaten, L. v. d. and Hinton, G.: Visualizing Data using t-SNE, *Journal of Machine Learning Research*, 9, 2579–2605, <http://www.jmlr.org/papers/v9/vandermaaten08a.html>, 2008.
- 420 Marcolla, B., Pitacco, A., and Cescatti, A.: Canopy Architecture and Turbulence Structure in a Coniferous Forest, *Boundary-Layer Meteorology*, 108, 39–59, <https://doi.org/10.1023/A:1023027709805>, <https://doi.org/10.1023/A:1023027709805>, 2003.
- Marcolla, B., Cescatti, A., Manca, G., Zorer, R., Cavagna, M., Fiora, A., Gianelle, D., Rodeghiero, M., Sottocornola, M., and Zampedri, R.: Climatic controls and ecosystem responses drive the inter-annual variability of the net ecosystem exchange of an alpine meadow, *Agricultural and Forest Meteorology*, 151, 1233–1243, <https://doi.org/10.1016/j.agrformet.2011.04.015>, <http://www.sciencedirect.com/science/article/pii/S0168192311001444>, 2011.
- 425 Marras, S., Pyles, R. D., Sirca, C., Paw U, K. T., Snyder, R. L., Duce, P., and Spano, D.: Evaluation of the Advanced Canopy–Atmosphere–Soil Algorithm (ACASA) model performance over Mediterranean maquis ecosystem, *Agricultural and Forest Meteorology*, 151, 730–745, <https://doi.org/10.1016/j.agrformet.2011.02.004>, <http://www.sciencedirect.com/science/article/pii/S0168192311000566>, 2011.
- 430 McDowell, N. G., Marshall, J. D., Hooker, T. D., and Musselman, R.: Estimating CO<sub>2</sub> flux from snowpacks at three sites in the Rocky Mountains, *Tree Physiology*, 20, 745–753, <https://doi.org/10.1093/treephys/20.11.745>, <https://academic.oup.com/treephys/article/20/11/745/1690523>, 2000.
- Merbold, L., Eugster, W., Stieger, J., Zahniser, M., Nelson, D., and Buchmann, N.: Greenhouse gas budget (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) of intensively managed grassland following restoration, *Global Change Biology*, 20, 1913–1928, <https://doi.org/10.1111/gcb.12518>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12518>, 2014.
- 435 Migliavacca, M., Sonnentag, O., Keenan, T. F., Cescatti, A., O’Keefe, J., and Richardson, A. D.: On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model, *Biogeosciences*, 9, 2063–2083, <https://doi.org/https://doi.org/10.5194/bg-9-2063-2012>, <https://www.biogeosciences.net/9/2063/2012/>, 2012.



- Migliavacca, M., Reichstein, M., Richardson, A. D., Mahecha, M. D., Cremonese, E., Delpierre, N., Galvagno, M., Law, B. E., Wohlfahrt, G., Black, T. A., Carvalhais, N., Ceccherini, G., Chen, J., Gobron, N., Koffi, E., Munger, J. W., Perez-Priego, O., Robustelli, M., Tomelleri, E., and Cescatti, A.: Influence of physiological phenology on the seasonal pattern of ecosystem respiration in deciduous forests, *Global Change Biology*, 21, 363–376, <https://doi.org/10.1111/gcb.12671>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12671>, 2015.
- Molen, M. K. v. d., Huissteden, J. v., Parmentier, F. J. W., Petrescu, A. M. R., Dolman, A. J., Maximov, T. C., Kononov, A. V., Karsanaev, S. V., and Suzdalov, D. A.: The growing season greenhouse gas balance of a continental tundra site in the Indigirka lowlands, NE Siberia, *Biogeosciences*, 4, 985–1003, <https://doi.org/https://doi.org/10.5194/bg-4-985-2007>, <https://www.biogeosciences.net/4/985/2007/>, 2007.
- Monson, R. K., Turnipseed, A. A., Sparks, J. P., Harley, P. C., Scott-Denton, L. E., Sparks, K., and Huxman, T. E.: Carbon sequestration in a high-elevation, subalpine forest, *Global Change Biology*, 8, 459–478, <https://doi.org/10.1046/j.1365-2486.2002.00480.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2002.00480.x>, 2002.
- Montagnani, L., Manca, G., Canepa, E., Georgieva, E., Acosta, M., Feigenwinter, C., Janous, D., Kerschbaumer, G., Lindroth, A., Minach, L., Minerbi, S., Mölder, M., Pavelka, M., Seufert, G., Zeri, M., and Ziegler, W.: A new mass conservation approach to the study of CO<sub>2</sub> advection in an alpine forest, *Journal of Geophysical Research: Atmospheres*, 114, <https://doi.org/10.1029/2008JD010650>, <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2008JD010650>, 2009.
- Moors, E.: Water use of forests in the Netherlands, Tech. rep., Vrije Universiteit, Amsterdam, <http://edepot.wur.nl/213926>, 2012.
- Morellato, L. P. C., Alberti, L. F., and Hudson, I. L.: Applications of Circular Statistics in Plant Phenology: a Case Studies Approach, in: *Phenological Research*, pp. 339–359, Springer, Dordrecht, [https://doi.org/10.1007/978-90-481-3335-2\\_16](https://doi.org/10.1007/978-90-481-3335-2_16), [https://link.springer.com/chapter/10.1007/978-90-481-3335-2\\_16](https://link.springer.com/chapter/10.1007/978-90-481-3335-2_16), 2010.
- Morente-López, J., Lara-Romero, C., Ornos, C., and Iriondo, J. M.: Phenology drives species interactions and modularity in a plant - flower visitor network, *Scientific Reports*, 8, 9386, <https://doi.org/10.1038/s41598-018-27725-2>, <https://www.nature.com/articles/s41598-018-27725-2>, 2018.
- Morin, X., Roy, J., Sonié, L., and Chuine, I.: Changes in leaf phenology of three European oak species in response to experimental climate change, *New Phytologist*, 186, 900–910, <https://doi.org/10.1111/j.1469-8137.2010.03252.x>, <https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.2010.03252.x>, 2010.
- Pastorello, G., Papale, D., Chu, H., Trotta, C., Agarwal, D., Canfora, E., Baldocchi, D., and Torn, M.: A New Data Set to Keep a Sharper Eye on Land-Air Exchanges, *Eos*, <https://doi.org/10.1029/2017EO071597>, <https://eos.org/project-updates/a-new-data-set-to-keep-a-sharper-eye-on-land-air-exchanges>, 2017.
- Peichl, M., Gažovič, M., Vermeij, I., Goede, E. d., Sonnentag, O., Limpens, J., and Nilsson, M. B.: Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production, *Scientific Reports*, 8, 8012, <https://doi.org/10.1038/s41598-018-26147-4>, <https://www.nature.com/articles/s41598-018-26147-4>, 2018.
- Peñuelas, J., Rutishauser, T., and Filella, I.: Phenology Feedbacks on Climate Change, *Science*, 324, 887–888, <https://doi.org/10.1126/science.1173004>, <http://science.sciencemag.org/content/324/5929/887>, 2009.
- Pilegaard, K., Ibrom, A., Courtney, M. S., Hummelshøj, P., and Jensen, N. O.: Increasing net CO<sub>2</sub> uptake by a Danish beech forest during the period from 1996 to 2009, *Agricultural and Forest Meteorology*, 151, 934–946, <https://doi.org/10.1016/j.agrformet.2011.02.013>, <http://www.sciencedirect.com/science/article/pii/S0168192311000797>, 2011.
- Post, E. and Forchhammer, M. C.: Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 2367–2373, <https://doi.org/10.1098/rstb.2007.2207>, <http://www.royalsocietypublishing.org/doi/10.1098/rstb.2007.2207>, 2008.



- Prescher, A.-K., Grünwald, T., and Bernhofer, C.: Land use regulates carbon budgets in eastern Germany: From NEE to NBP, *Agricultural and Forest Meteorology*, 150, 1016–1025, <https://doi.org/10.1016/j.agrformet.2010.03.008>, <http://www.sciencedirect.com/science/article/pii/S0168192310000961>, 2010.
- 480 Rambal, S., Joffre, R., Ourcival, J. M., Cavender-Bares, J., and Rocheteau, A.: The growth respiration component in eddy CO<sub>2</sub> flux from a *Quercus ilex* mediterranean forest, *Global Change Biology*, 10, 1460–1469, <https://doi.org/10.1111/j.1365-2486.2004.00819.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2004.00819.x>, 2004.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., 485 Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Global Change Biology*, 11, 1424–1439, <https://doi.org/10.1111/j.1365-2486.2005.001002.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2005.001002.x>, 2005.
- Rey, A., Pegoraro, E., Tedeschi, V., Parri, I. D., Jarvis, P. G., and Valentini, R.: Annual variation in soil respiration and its components 490 in a coppice oak forest in Central Italy, *Global Change Biology*, 8, 851–866, <https://doi.org/10.1046/j.1365-2486.2002.00521.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2002.00521.x>, 2002.
- Rezaei, E. E., Siebert, S., Hüging, H., and Ewert, F.: Climate change effect on wheat phenology depends on cultivar change, *Scientific Reports*, 8, 4891, <https://doi.org/10.1038/s41598-018-23101-2>, <https://www.nature.com/articles/s41598-018-23101-2>, 2018.
- Richardson, A. D., Braswell, B. H., Hollinger, D. Y., Jenkins, J. P., and Ollinger, S. V.: Near-surface remote sensing of spatial and temporal variation in canopy phenology, *Ecological Applications*, 19, 1417–1428, <https://doi.org/10.1890/08-2022.1>, <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/08-2022.1>, 2009.
- Richardson, A. D., Andy Black, T., Ciais, P., Delbart, N., Friedl, M. A., Gobron, N., Hollinger, D. Y., Kutsch, W. L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., William Munger, J., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., and Varlagin, A.: Influence of spring and autumn phenological transitions on forest ecosystem productivity, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3227–3246, <https://doi.org/10.1098/rstb.2010.0102>, <http://www.royalsocietypublishing.org/doi/10.1098/rstb.2010.0102>, 2010.
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., and Toomey, M.: Climate change, phenology, and phenological control of vegetation feedbacks to the climate system, *Agricultural and Forest Meteorology*, 169, 156–173, <https://doi.org/10.1016/j.agrformet.2012.09.012>, <http://www.sciencedirect.com/science/article/pii/S0168192312002869>[https://ac.els-cdn.com/S0168192312002869/1-s2.0-S0168192312002869-main.pdf?\\_tid=76d74384-1176-11e8-af6a-00000aacb35f&acdnt=1518606293\\_09713e0dfdf7faf8bd98f605a02a234f](https://ac.els-cdn.com/S0168192312002869/1-s2.0-S0168192312002869-main.pdf?_tid=76d74384-1176-11e8-af6a-00000aacb35f&acdnt=1518606293_09713e0dfdf7faf8bd98f605a02a234f)<https://www.sciencedirect.com/science/article/pii/S0168192312002869>, 2013.
- 505 Ryan, E. M., Ogle, K., Zelikova, T. J., LeCain, D. R., Williams, D. G., Morgan, J. A., and Pendall, E.: Antecedent moisture and temperature conditions modulate the response of ecosystem respiration to elevated CO<sub>2</sub> and warming, *Global Change Biology*, 21, 2588–2602, <https://doi.org/10.1111/gcb.12910>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12910>, 2015.
- 510 Saleska, S. R., Miller, S. D., Matross, D. M., Goulden, M. L., Wofsy, S. C., da Rocha, H. R., de Camargo, P. B., Crill, P., Daube, B. C., de Freitas, H. C., Hutrya, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J. W., Pyle, E. H., Rice, A. H., and Silva, H.: Carbon in Amazon Forests: Unexpected Seasonal Fluxes and Disturbance-Induced Losses, *Science*, 302, 1554–1557, <https://doi.org/10.1126/science.1091165>, <https://science.sciencemag.org/content/302/5650/1554>, bibtext\*[publisher=American Association for the Advancement of Science;eprint=<https://science.sciencemag.org/content/302/5650/1554.full.pdf>], 2003.



- 515 Schimel, D., Pavlick, R., Fisher, J. B., Asner, G. P., Saatchi, S., Townsend, P., Miller, C., Frankenberg, C., Hibbard, K., and Cox, P.: Observing terrestrial ecosystems and the carbon cycle from space, *Global Change Biology*, 21, 1762–1776, <https://doi.org/10.1111/gcb.12822>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12822>, 2015.
- Schmid, H. P., Grimonard, C. S. B., Cropley, F., Offerle, B., and Su, H.-B.: Measurements of CO<sub>2</sub> and energy fluxes over a mixed hardwood forest in the mid-western United States, *Agricultural and Forest Meteorology*, 103, 357–374, [https://doi.org/10.1016/S0168-1923\(00\)00140-4](https://doi.org/10.1016/S0168-1923(00)00140-4), <http://www.sciencedirect.com/science/article/pii/S0168192300001404>, 2000.
- 520 Scott, R. L., Cable, W. L., and Hultine, K. R.: The ecohydrologic significance of hydraulic redistribution in a semiarid savanna, *Water Resources Research*, 44, <https://doi.org/10.1029/2007WR006149>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2007WR006149>, 2008.
- Serrano-Ortiz, P., Domingo, F., Cazorla, A., Were, A., Cuezva, S., Villagarcía, L., Alados-Arboledas, L., and Kowalski, A. S.: Interannual CO<sub>2</sub> exchange of a sparse Mediterranean shrubland on a carbonaceous substrate, *Journal of Geophysical Research: Biogeosciences*, 114, <https://doi.org/10.1029/2009JG000983>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2009JG000983>, 2009.
- 525 Suni, T., Rinne, J., Reissell, A., Altimir, N., Keronen, P., Rannik, U., Dal Maso, M., Kulmala, M., and Vesala, T.: Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, southern Finland, 1996–2001, *BOREAL ENVIRONMENT RESEARCH*, 8, {287–301}, [bibtex\\*\[researcherid-numbers=Vesala, Timo/C-3795-2017 Kulmala, Markku/I-7671-2016 Rinne, Janne/A-6302-2008 Dal Maso, Miiikka/A-7980-2008 ;orcid-numbers=Vesala, Timo/0000-0002-4852-7464 Kulmala, Markku/0000-0003-3464-7825 Rinne, Janne/0000-0003-1168-7138 Dal Maso, Miiikka/0000-0003-3040-3612 Keronen, Petri/0000-0001-5019-0904;unique-id=ISI:000221372700003\]](https://doi.org/10.1029/2009JG000983), 2003.
- 530 Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P. G., and Borghetti, M.: Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing, *Global Change Biology*, 12, 110–121, <https://doi.org/10.1111/j.1365-2486.2005.01081.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2005.01081.x>, 2006.
- 535 Thum, T., Aalto, T., Laurila, T., Aurela, M., Kolari, P., and Hari, P.: Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest, *Tellus B*, 59, 874–890, <https://doi.org/10.1111/j.1600-0889.2007.00305.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0889.2007.00305.x>, 2007.
- Treuhaft, R. N., Law, B. E., and Asner, G. P.: Forest Attributes from Radar Interferometric Structure and Its Fusion with Optical Remote Sensing, *BioScience*, 54, 561–571, [https://doi.org/10.1641/0006-3568\(2004\)054\[0561:FAFRIS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0561:FAFRIS]2.0.CO;2), <https://academic.oup.com/bioscience/article/54/6/561/294539>, 2004.
- 540 Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald, D., Czikowsky, M., and Munger, J. W.: Factors controlling CO<sub>2</sub> exchange on timescales from hourly to decadal at Harvard Forest, *Journal of Geophysical Research: Biogeosciences*, 112, <https://doi.org/10.1029/2006JG000293>, <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2006JG000293>, 2007.
- 545 Valentini, R., Angelis, P. D., Matteucci, G., Monaco, R., Dore, S., and Mucnozza, G. E. S.: Seasonal net carbon dioxide exchange of a beech forest with the atmosphere, *Global Change Biology*, 2, 199–207, <https://doi.org/10.1111/j.1365-2486.1996.tb00072.x>, <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.1996.tb00072.x>, 1996.
- Von Mises, R.: Über die 'Ganzzahligkeit' der Atomgewichte und verwandte Fragen, *Physikalische Zeitschrift*, 19, 490–500, 1918.
- 550 Wang, X. and Wu, C.: Estimating the peak of growing season (POS) of China's terrestrial ecosystems, *Agricultural and Forest Meteorology*, 278, 107–139, <https://doi.org/10.1016/j.agrformet.2019.107639>, <http://www.sciencedirect.com/science/article/pii/S0168192319302473>, 2019.



- Wohlfahrt, G., Hammerle, A., Haslwanter, A., Bahn, M., Tappeiner, U., and Cernusca, A.: Seasonal and inter-annual variability of the net ecosystem CO<sub>2</sub> exchange of a temperate mountain grassland: Effects of weather and management, *Journal of Geophysical Research: Atmospheres*, 113, <https://doi.org/10.1029/2007JD009286>, <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2007JD009286>, 2008.
- 555 Xu, L. and Baldocchi, D. D.: Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature, *Tree Physiology*, 23, 865–877, <https://doi.org/10.1093/treephys/23.13.865>, <https://academic.oup.com/treephys/article/23/13/865/1650675>, 2003.
- Xu, L. and Baldocchi, D. D.: Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, *Agricultural and Forest Meteorology*, 123, 79–96, <https://doi.org/10.1016/j.agrformet.2003.10.004>, <http://www.sciencedirect.com/science/article/pii/S0168192303002533>, 2004.
- 560 Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., Hodges, J. C. F., Gao, F., Reed, B. C., and Huete, A.: Monitoring vegetation phenology using MODIS, *Remote Sensing of Environment*, 84, 471–475, [https://doi.org/10.1016/S0034-4257\(02\)00135-9](https://doi.org/10.1016/S0034-4257(02)00135-9), <http://www.sciencedirect.com/science/article/pii/S0034425702001359>, 2003.
- Zhou, S., Zhang, Y., Caylor, K. K., Luo, Y., Xiao, X., Ciais, P., Huang, Y., and Wang, G.: Explaining inter-annual variability of gross primary productivity from plant phenology and physiology, *Agricultural and Forest Meteorology*, 226–227, 246–256, <https://doi.org/10.1016/j.agrformet.2016.06.010>, <http://www.sciencedirect.com/science/article/pii/S0168192316303070>, 2016.
- Zhou, S., Zhang, Y., Ciais, P., Xiao, X., Luo, Y., Caylor, K. K., Huang, Y., and Wang, G.: Dominant role of plant physiology in trend and variability of gross primary productivity in North America, *Scientific Reports*, 7, 41 366, <https://doi.org/10.1038/srep41366>, <https://www.nature.com/articles/srep41366>, 2017.
- 570 Zielis, S., Etzold, S., Zweifel, R., Eugster, W., Haeni, M., and Buchmann, N.: NEP of a Swiss subalpine forest is significantly driven not only by current but also by previous year's weather, *Biogeosciences*, 11, 1627–1635, <https://doi.org/https://doi.org/10.5194/bg-11-1627-2014>, <https://www.biogeosciences.net/11/1627/2014/bg-11-1627-2014.html>, 2014.



*Code availability.* Code will be made available under GPL-3 license upon publication

*Data availability.* FLUXNET database is available in the web page: <https://fluxnet.fluxdata.org/>

575 *Author contributions.* DEPM, TM, MM, and MDM designed the study in collaboration with MR and CR. DEPM conducted the analysis and wrote the manuscript with substantial contributions from all co-authors

*Competing interests.* The authors declare that they have no conflict of interest