Ecosystem physio-phenology revealed using circular statistics

Changes in the manuscript

06-04-2020

Dear Editors,

Please find below our responses to the reviewers, a description of the major changes, and a detailed version of the manuscript with all the changes.

The comments by the reviewers are very relevant and will certainly help us to improve the quality of the manuscript. In the following we repeat the comments by the reviewers in bold and our response (RS) to each one in normal font.

Responses to Reviewer 1

Reviewer 1: In "Ecosystem physio-phenology revealed using circular statistics", Pabon-Moreno et al. have analyzed how the timing of maximum gross primary productivity is related to climate variables such as air temperature, solar radiation, precipitation, and VPD. They have analyzed 52 FLUXNET sites with more than 7 years of data and applied a circular regression method to (a) understand which environmental variable best predicts the timing of GPPmax and (2) measure the sensitivity of the response to each variable and (c) evaluate the method for different plant functional types. The topics is interesting, and the questions are relevant. The authors have also performed a simulation analysis to compare linear and circular regression methods, in particular given that some of the sites are in the southern hemisphere and hence may not be on the same calendar year as the northern hemisphere sites, the authors have justified circular regression methods are more appropriate than linear regression methods. The manuscript is generally well written

and presented, however I have a couple major concerns related to the methods and conclusion that I strongly recommend being addressed by the authors.

We thank the reviewer for the accurate summary of our paper.

I am not sure how finding shortwave radiation is related to the annual trend of GPP is surprising. Especially with the not particularly high correlation values from the model outputs. My concern is that what the model predicts may be actually the average seasonality of the site, which is generally represented/regulated by the annual variation of solar radiation. I think it would have been more convincing if the model could predict "weird years" rather than normal years. So, one might argue that the model is tuned to track the seasonality of the sites with an average predictability power. See my next comment which is related.

The reviewer is right that shortwave incoming radiation (SWin) driving GPP - confirming this would be indeed no surprise. But please note that this paper does not analyze GPP: we are predicting the timing when GPP is maximized (the units we predict are "day of year" and not "g C /(m2 day)"). GPPmax represents the "optimum" ecosystem state when ecosystems are maximizing the uptake of CO₂ per year. We would also clarify that maximizing "predictability" is not our main aim as we are primarily interested in understanding the sensitivity of this state of ecosystem physio-phenology to climate variability. Given that radiation typically has a very low interannual variability we expect that the timing of GPPmax should be sensitive to other factors.

My other concern is that DOY values were directly used in the model as response variables. However, to analyze the inter-annual variability of the response, the anomalies should be used in the model. This is somehow related to the previous comment, as using site-specific model and absolute response values may result in obtaining the average annual trend and not the year-to-year variabilities. I think it would be best if the authors could use anomalies for each site as "y" in equation 2.

Equation 2 describes the circular linear regression where μ is the mean angular direction of a Von Mises distribution. As we mentioned in line 108 the mean angular direction is estimated via maximum likelihood. All interannual observations of DOY_{GPPmax} are used on the model, and the final result is constrained to a Von Mises distribution. The μ parameter cannot be removed from

the equation, on the other hand the anomalies are considered into the amplitude of the Von Mises distribution (β) that is estimated internally.

Note that using absolute values in a consolidated model (all sites together) is another potentially good idea but that would detect the spatial (or site-by-site) patterns in the data rather than the temporal trends (which is the main question here).

The use of DOY values is necessary to quantify the sensitivity to the climate variables. On the other hand, if we only consider $DOY_{GPP_{max}}$ anomalies (outliers) the main research question regarding climate sensitivity can not be solved given that we will not analyze a representative sample of the observations. Considering only $DOY_{GPP_{max}}$ outliers the research question should be more related to extreme events or temporal anomalies that as we mentioned in the previous comment are not the main topic in our study.

Minor comments:

There are also a few minor comments that I came across:

1- There is extensive use of parentheses in the paper that sometimes make the narrative hard to follow. I suggest avoiding unnecessary parentheses in the manuscript.

The manuscript was modified following the recommendation.

2- The authors have used present tense throughout the manuscript at many places where past tense verbs are recommended.

This is a matter of "style" and we would like to keep the writing in present as we feel it is better to read.

3- line 141, "closed parenthesis" that was never opened

Solved. The parenthesis was removed

4- the narrative of the Results section can be improved, especially because the reader has to go back to the method to remember the terminologies and acronyms related to the method.

We improved the section following the recommendation.

5- line 277: "Although the sensitivity of the DOYGPPmax 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." That's a big claim. I'm not sure if the manuscript has provided convincing evidence with only 52 sites to support this.

Given that we used cross-validation to measure the performance of the model per vegetation type. We consider 52 sites should be enough to provide a robust analysis. On the other hand, 52 sites are the data available globally with at least 7 years of records.

6- What are the temporal windows for each predictor variable?

In our study the temporal window for the predictors is given by the half-time parameter of the half-life decay function (See Supplement 1. Half-time sensitivity analysis (System memory to explain DOY_{GPPmax})). In this section we run a sensitivity analysis to quantify how the change of the half-time parameter affects the correlation coefficient between the observed and predicted DOY_{GPPmax} .

Reviewer 2

General comments: In the manuscript "Ecosystem physio-phenology revealed using circular statistics", Pabon-Moreno et al. used a new method – the circular linear regression to estimate the timing of the maximum gross primary productivity (DOYgppmax) at 52 eddy covariance towers, and further quantified the sensitivity of DOYgppmax to a range of climate variables based on the results from this new regression. The manuscript is relevant to the topics of the journal. While I agree with the authors that circular linear regression has the potential to be a framework of future generalized phenology models, I have some doubts about the advantages of circular regression over the conventional linear regression approach, as well as the interpretation of results. It may need some substantial revisions. I apologize that I cannot be more supportive at this stage. I hope the authors can find this review helpful (please see below)

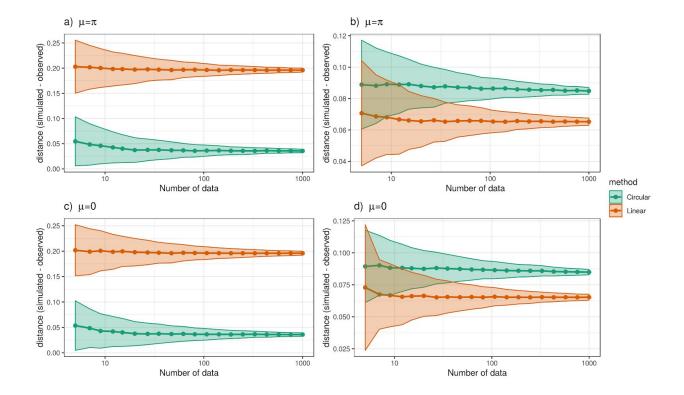
We thank the reviewer for sharing her considerations. The comments provided below are indeed very helpful.

The authors introduced two advantages of circular regression 1) it is more accurate than linear regression 2) it can analyze the phenological event regardless of the locations of events, esp. for the southern hemisphere. For 1), I am concerned about circular reasoning, as the authors used two phenological events pre-defined by circular regression to compare the performance of circular regression and linear regression, it is very likely the circular regression can outperform linear regression in this case. In addition, the author used the distance between observed beta and estimated beta to assess the efficiency of two models, and suggested that because the magnitude of distance for beta1 is larger than the distance for beta2, and the results on distance for beta1 favored circular regression, so circular regression is better. But the magnitude of distance for beta is also dependent on beta itself. Beta2 (0.3) is larger than beta1 (0.1), after normalize the distance of beta by beta, the result based on beta1 does not carry more weight than beta2, and the results on the distance of beta2 in fact favored linear regression.

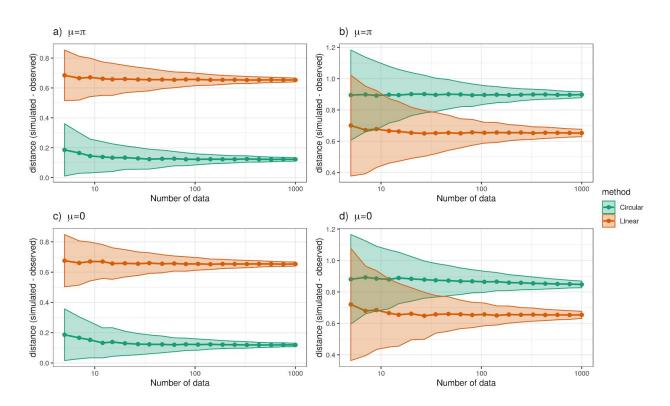
Regarding the first point. We used equation 2 to simulated the data. Nevertheless we are analyzing the performance to recover the original beta values of the equation and not the predictive power of the model. We used equation 2 given that linear regression does not allow to define the mean timing of phenological events. This is problematic especially when we want to analyze phenological events at the beginning and the end of the year.

Regarding the second point there is a misunderstanding related to the beta values. In our study beta₁ = 0.3 and beta₂ = 0.1 (Line 124). For this reason if we divide the distance by the beta values as suggested by the reviewer, the tendency of the results does not change (Please see the plots below). In both plots, circular regression has a better performance recovering beta₁, while linear regression has a better performance recovering beta₂ when the number of data is greater than 100. We will include the plot with the distances divided by the beta value to show that there is not a strong effect in the results. We will modify the line 135 of the methods by: "We estimate the difference between the recovered and the original coefficient divided by the beta value as the efficiency of the model (i.e. lower values mean higher efficiency)." And we will modify the line 166 of the results by: "Nevertheless, the differences between both regressions for beta₂ are of the order of 0.2 while the differences for beta₁ are of the order of 0.5."

Original Plot:



Plot normalizing the values per beta (distance / beta):



For 2), I am not sure why conventional phenology models cannot be used in the Southern Hemisphere (e.g. L208-209), say the degree-day model can be easily deployed if we know the temperature preceding budburst in Australia (e.g. Webb et al., 2008) and we can also get meaningful climate sensitivity of the event. Overall, I am not sure the circular model is superior to conventional models based on the evidence available in the manuscript.

Please note that the only claim we make is that circular regression is more suitable than conventional linear models for analyzing phenological data - of course, process-based phenological models should outperform such statistical approaches. But our analysis reveals that we can learn the sensitivity to climate drivers in a purely empirical manner. In general, in any degree-day model there is a parameter to set an initial time to start accumulating warming. This will require again to define a t0 and in our view circular statistics could potentially avoid manual tunings of this kind.

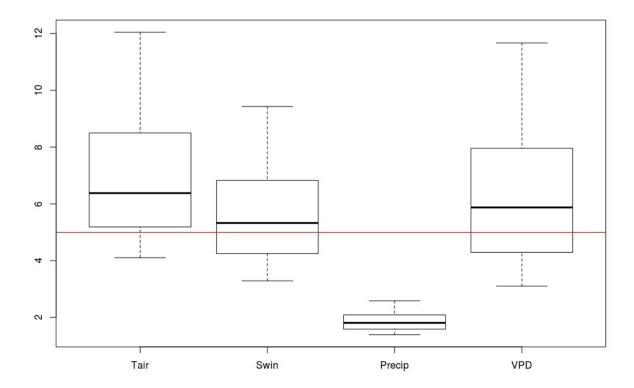
Some questions over the interpretation of the results. First, I am a bit worried about overfitting of the model, as the leave-one-out validation suggest much less robust performance ($r = -0.3 \sim 0.7$) for PFTs compared to the r ($r = 0.7 \sim 0.9$ according to Table S1) we obtained using the training dataset.

As we mentioned in previous comments the main objective of the study was to analyze the sensitivity of DOY_{GPPmax} to different climate drivers. For this reason, each site has a unique "r" we consider that high r values are not an argument for dismissing the sensitivities of the climate variables. After cross-validation is expected that the predictive power of the model decreases, but the performance is not so bad considering it is estimated across vegetation types.

Second, at seasonal time scale, air temperature, radiation and VPD are all highly correlated with each other, how much can we trust their respective sensitivities estimated by circular regression. Wouldn't the sensitivity of air temperature be account for by the sensitivity of radiation if there is co-linearity between the two?

We performed a variance inflation factor analysis (VIF) for all sites-variables. The analysis shows (see plot below) that the colinearity of Air temperature, Shortwave Incoming Radiation, and VPD increases the variance of the regression coefficient. (VIF > 5). To solve this problem it is necessary to implement a PCA with these variables and run again all the analysis using the first axis of the PCA and precipitation as predictors of DOY_{GPPmax}. This means a major change in

the manuscript given that the results of the sensitivity of DOY_{GPPmax} to climate variables will change. The respective discussion, and the conclusion need to be re-written. The revised version of the manuscript will contain these changes.



Third, I guess the so-called "memory effect" or "accumulated effect" of past climate is considered in circular regression through equation (1). Is this potentially one of the key differences between circular model and linear model? Does it mean the climate conditions closer to the event is more important than the climate conditions further back, and different climate variables are prescribed with different half-life here? I hope this part of the method is clearer.

We will add a better explanation:

"The idea of the decay function is that events in the present (DOY_{GPPmax}) are affected by past conditions (past climatic conditions). In this sense, the climatic conditions when DOY_{GPPmax} happens will have a weight of 1 to explain it. The day before will be less than the first day (e.g. weight of 0.8) and so on."

Fourth, the authors delegated the complex temperature sensitivity to consumption of available water (L240-). I am not sure there is a clear mechanistic underlying this link as there is no evidence supporting plant water uptake is related to temperature here. Soil water content may directly impact GPP (Stocker et al., 2018), it is not necessarily related to temperature, maybe VPD though. My major concern is about the robustness of the climate sensitivity identified in the manuscript.

The relationship temperature \sim water consumption is a hypothesis that we put forward to explain the non-predominant sign for the temperature coefficient. It is important to mention that GPPmax is different to DOY_{GPPmax} . The last one is the timing when GPP is maximized during the growing season. In this sense, the magnitude of GPP can decrease when soil water content decreases but this will not necessarily affect DOY_{GPPmax} . To clarify this point we will modify the legend of figure 8 from "theoretical" to "hypothetical"

Minor specific comments:

1. it is not accurate to say "(DOYgppmax). . . is the time the plants reach their maximum potential for CO2 absorption". GPP is the product of vegetation density (i.e. LAI) and the photosynthesis of individual leaves. When leaves have the maximum photosynthetic capacity/potential, it does not mean the whole canopy would be the most productive, as leaf photosynthesis can be downregulated by environment, and it also depends on how many leaves are there in the ecosystem.

The reviewer is right that our wording is not very accurate here. We will clarify that we are analyzing a metric at the canopy scale. We will write "the time when the ecosystem reaches its maximum potential for CO2 absorption".

2. Figure 1. In figure caption and in the text (L64), you mentioned each line represents the interannual variability. I feel it needs further clarification on how to read the figure. From what I understand, the distance between the line and the circle indicate the frequency of DOYgppmax, and the spread of linear may imply the variability of DOYgppmax.

We will modify the legend to "The distance between the color line and the circle represents the frequency of the $\mathrm{DOY}_{\mathrm{GPP_{max}}}$ observations. The distance between the end and the beginning of the distribution represent the $\mathrm{DOY}_{\mathrm{GPP_{max}}}$ interannual variability"

3. Method. Need more explanation about equation (1), as it not clear the meaning of x, N, N0, and the reason to include this half-life process here.

The manuscript was modified following the recommendation.

4. I think the title of the paper might overshoot what in fact was done in the paper, since only one type of phenological event was studied, and I am not sure there is a pattern that really is "revealed" here that we can easily extrapolate for us to understand DOYgppmax due to the reported site-specific sensitivities. The concept of physiphenology is new to me, maybe the authors can provide a reference? I feel most conventional phenological events (e.g. budburst, leafout, leaf coloring, leaf senescence) are physiological changes of plants, so why they are not qualified as physi-phenology or do we really need this definition here. DOYgppmax sounds like a carbon uptake phenological phase.

We defined ecosystem physio-phenology as the temporal variability of optimum and basal ecosystem states in terms of the exchange of energy and matter between the ecosystem and the atmosphere. We defined DOY_{GPPmax} as a physio-phenological event because data is derived from the fluxes of the exchange of energy and matter between the ecosystems and the atmosphere and represents in a very accurate way the plants' photosynthesis. Budburst, leaf coloring etc. are phenological state of plants that in specific cases not necessarily represent the physiological state of the plants (e.g. A green canopy does not necessarily mean that plants are photosynthetically active during winter). This limit between how much we can extrapolate between physiology and the light reflectance of the leaves is surpassed by the eddy covariance technique allowing us to quantify the ecosystem fluxes.

Although we only analyze one physio-phenological event (DOY_{GPPmax}), given that this study introduced the conceptual and methodological framework to analyze physio-phenological events we consider that the title is according to the research presented in the paper.

Regarding the comment: "I am not sure there is a pattern that really is "revealed" here that we can easily extrapolate for us to understand DOYgppmax due to the reported site-specific

sensitivities". In section 4.2 "Sensitivity of DOY_{GPPmax} to climate variables," we summarized the effect of each climate variable at global scale.

Technical comments:

1. "2" in "CO2" is subscript

Fixed

2. please define "GPPmax" at its first appearance.

Fixed Line 46

3. L201, according to Figure 7, GRA is -0.3 rather than 0?

Fixed

4. How to interpret the tendency in Figure 7?

In Figure 7 the tendency (blue line) represents the overestimation or underestimation of the model for specific DOY_{GPPmax} values.

5. L150, "leaf" to "leave"

Fixed

6. Table A1, maybe list the site according to their names or vegetation types. Now it is based on doi and not easy for readers to search sites.

We modified the table showing the sites names by alphabetical order.

7. It would be helpful to condense figures in supplementary material 2 into a table, showing the sensitivity of each climate variable and significant level indicated by *. And please consider merging two supplementary materials into one.

Given that $DOY_{GPP_{max}}$ sensitivity to the climate variables was estimated implementing bootstrapping, we consider that it is more important to show the distribution of the data than just the mean, also for the p-values. Regarding the second comment, we would like to keep the supplementary materials as separate.

Major changes

In the new version of our study we performed a principal component analysis (PCA) for air temperature, short-wave incoming radiation and vapor pressure deficit. As explanatory variables of DOY_{GPPmax} we used the first component of the PCA and precipitation. The methods, results, discussion and conclusion sections were re-written accordly.

The entire document was improved in terms of wording and structure.

Ecosystem physio-phenology revealed using circular statistics

Daniel E. Pabon-Moreno¹, Talie Musavi¹, Mirco Migliavacca¹, Markus Reichstein^{1,2}, Christine Römermann^{2,3}, and Miguel D. Mahecha^{1,2,4}

Correspondence: Daniel E. Pabon-Moreno (dpabon@bgc-jena.mpg.de)

Abstract.

Quantifying responses of vegetation phenology Quantifying how vegetation phenology responds to climate variability is a key prerequisite to predict shifts in how ecosystem dynamics due to will shift with 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 the dynamics of physio-phenological events such as the timing of the maximum gross primary production (DOY_{GPPmax}). However, understanding this type of physio-phenological phenomena is an essential element in predicting the response of the, i.e. quantities that are relevant for understanding terrestrial carbon cycle responses to climate variability and change. In this study, we aim to understand how DOY_{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 One solution could be a new class of circular-linear (here called circular) regression approach that may show a path aheadapproaches, Circular regression allows relating circular variables (in our case phenological events) to linear predictor variables (e.g. climate conditions) as 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 DOY_{GPPmax} across FLUXNET sites to air temperature, shortwave incoming radiation, precipitation and vapor pressure deficitusing circular regressions. Finally, we evaluate the predictive power of the regression models for different vegetation types. Our results show that the DOYGPPMAX of each FLUXNET site has a unique signature of climatic sensitivities. Overall radiationand temperature are circular regression model joint effects of radiation, temperature and vapor pressure deficit is the most relevant controlling factors factor of DOY_{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 Woody savannas are an exception where the most important factor is precipitation. Although the sensitivity of the DOY_{GPPmax} to the climate drivers is very site specific, it is possible to extrapolate generalize the circular regression model across models across specific 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

¹Max Planck Institute for Biogeochemistry, 07745 Jena, Germany

²German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5e, 04103 Leipzig, Germany

³Friedrich Schiller University, Institute of Ecology and Evolution, Philosophenweg 16, D-07743 Jena, Germany

⁴Remote Sensing Center For Earth System Research, Leipzig University, 04103 Leipzig, Germany

global analyses can benefit , where from this approach i.e. when phase shifts play a role or double peaked growing seasons may occur.

have to be considered.

1 Introduction

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Phenology is the study of the timing of biological events that can be observed either at the organismic level or at the ecosystem scale (?)(Lieth, 1974). For the latter, phenology is the study of some integral behavior across phenological states of e.g. the integrated canopy reflectance captured by remote sensing (Richardson et al., 2009; Zhang et al., 2003), or vegetation-driven ecosystem-atmosphere CO₂-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 CO2 by photosynthesis and the timing when 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 Ecosystem scale physio-phenological processes of this kind are relevant quantities in global biogeochemical cycles and integrates both, the seasonal dynamics of biophysical states (e.g. reflected in the canopy development), and the observed photosynthesis at the stand level (i.e. gross primary production). Here we are particularly interested in the timing when ecosystems reach their maximum CO₂-uptake potential within a growing season. Note that the maximum CO₂-uptake potential does not necessarily coincide with the realized maximum GPP which is essentially driven by actual meteorological conditions (Musavi et al., 2016). Ecosystem-physiophenology is influenced by climate conditions but simultaneously contributes to the regulation of different micro and macro meteorological conditions. Then, phenology influences Physio-phenological cycles determine the temporal dynamics of land-atmosphere water and energy exchange fluxes. Likewise, the terrestrial carbon cycle is affected by phenological controls on CO2 CO₂ uptake and release (Peñuelas et al., 2009).

The eddy covariance technique allows for (EC) allows to continuously measuring the exchange of energy and matter between ecosystems 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 CO2 between ecosystems and the atmosphere in relationship with meteorological variables (The FLUXNET network collects EC data for most ecosystems of the world along with other meteorological variables, i.e. radiation, temperature, precipitation, as well as with atmospheric humidity) and soil moisture (Migliavacca et al., 2015; Richardson et al., 2010). Specifically, one can monitor the and often soil moisture (Baldocchi et al., 2001; Baldocchi, 2020). Particularly relevant to pheneological studies is the seasonal trajectory of gross primary production (GPP) along the growing season and can allowing to derive phenological transition dates such as start and end of the growing season (e.g. (Luo et al., 2018))(e.g., Luo et al., 2018), as well as the timing of the maximum gross primary production, hereafter as referred to as DOY_{GPPmax} (Zhou et al., 2016; Peichl et al., 2018; Wang and Wu, 2019). Understanding In this study we focus on understanding how climate variability affects DOY_{GPPmax} is fundamental given that it is the time when plants ecosystems reach their maximum potential for CO2 absorption. This optimum staterequire that several

preconditions be achieved during the growing season and the preceding starvation phaseCO₂ absorption. In order to reach this "optimum state" several preconditions must be met during the preceding part of the growing season. 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, CO2 fertilization and Nitrogen deposition. maximum GPP during the growing season (GPPmax). For instance, 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 The authors found that GPPmax better explains the is a better explanatory parameter for the inter-annual variability of annual GPP than the days of the beginning and end start and end days of the growing season. Bauerle et al. (2012) studied how photoperiod and temperature influence plants photosynthetic capacity. They found that photoperiod explains better, reporting that the photoperiod explains the variability of photosynthetic capacity better 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 remote sensing, and eddy-covariance data to explore how DOY_{GPPmax} is controlled by climatic conditions. The authors reported that higher temperature temperatures advance DOY_{GPPmax}, while the influence of precipitation and radiation were biome-dependent. Nevertheless, this study was geographically located in Chinatherefore, This study had a geographical focus on China; a global approach considering several ecosystems across the whole latitudinal gradient is still missing. lacking.

The challenge of understanding phenology is generally to characterize a discrete event recurring with certain that repeats with

characteristic periodicity. Classically, phenological analyses have been performed using linear regression models (Morente-López et al., 20)

Most of these studies analyze ecosystems with only characterized by one growing season (e.g. temperate or boreal forests), and when the summer is in-centered around the middle of the calendar year. However, the The existing methods are, however, not sufficiently generic to describe i) ecosystems in the Southern Hemisphere, and ii) ecosystems with multiple growing seasons per year as it is often observed in e.g. semi-arid regions.

Figure 1 illustrates the first problem of Northern vs. Southern Hemispheric summers 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 need to find a predictive model explaining the inter-annual variability of phenology which essentially reflects i.e. the probability of this recurrent event in the course of the annual cycle.

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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.

Figure The Fig. 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 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 eircular statistics, as shown in 1) with the circular statistics. The von-Mises distribution is described

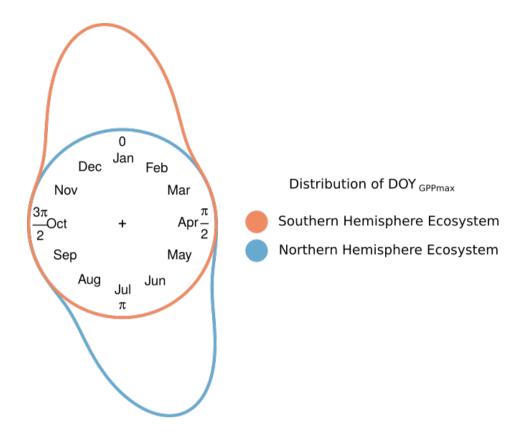


Figure 1. Conceptual distribution of GPPmax timing (DOY_{GPPmax}) for two hypothetical ecosystems one in the Northern (Blue), and one in the Southern Hemisphere (Red). The distance between the color line and the circle represent the frequency of the DOY_{GPPmax} observations. The distance between the end and the beginning of the distribution represent the DOY_{GPPmax} inter-annual variability.

by two parameters: The mean angular direction (μ) and the concentration parameter (κ). Circular-linear (here called circular regressions) regressiontechnique allows to predict such regressions (in the following simply named circular regression) allow to predict circular responses (e.g. the timing of phenological events) from other linear variables (Morellato et al., 2010). Given that any phenological event can be interpreted as an angular direction and and should be 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 timing of the maximal seasonal GPP (GPPmax). Specifically, we want to understand what are the climate controls of the timing of GPPmax (DOY_{GPPmax}) and provide a predictive framework 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_{GPPmax} per vegetation typestype? Can DOY_{GPPmax} be explained using the climate conditions a cumulative factors cumulative climate conditions? How is DOY_{GPPmax} 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.

2 Methods

2.1 Data

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We use 52 FLUXNET-EC 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, (Pastorello et al., 2017)) (Table A1, http://
Each FLUXNET site is identified with an abbreviation of the country and the name of the place e.g. the EC tower AUHowmeans tower, means that it is located 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*-threshold u*-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_{GPPmax} we use on the daily air temperature (Tair), shortwave incoming radiation (SWin), precipitation (Precip), and vapor pressure deficit (VPD).

Given that the past climate conditions affect the CO2 CO2 exchange between the atmosphere (ecological memory, (?Ryan et al., 2015)), we need to understand whether (ecological memory, Liu et al., 2019; Ryan et al., 2015), we assume that an aggregated form of these climatic variables would better predict needs to be considered in the prediction of the phenological responses. For this we We aggregate the original times-series of the Tair, SWin, Precip, and VPD for each DOY GPPmax using a half-life decay function (equation ??).

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

$$\langle x \rangle = \frac{\sum_{i=0}^{\tau} x_{t-i} w_i}{\sum_{i=0}^{\tau-1} w_i} \tag{1}$$

where $\langle x \rangle$ denotes the weighted mean of the vector of observations $x = (x_t, x_{t-1}, \dots, x_{t-\tau})^T$ with exponentially decaying weights

$$w_i = w_0 e^{-i\frac{\ln(2)}{t_{1/2}}} \tag{2}$$

This approach assigns a lower weight the further we go back in time to a maximum of τ days (τ = 365) before the time step t that is set to the DOY_{GPPmax}. We can then vary the half-time parameter ($t_{1/2}$) from 2 to 365 days. The decay function

give the instantaneous value a weight of 1 and, all preceding values an exponentially reduced weight as determined by the half-time-parameter $t_{1/2}$. We make these variables comparable via centering standardization to unit variance and identify the optimal $t_{1/2}$ (S1.1to increase the variance explained by the circular-regression model using the Jammalamadaka-Sarma (JS) correlation coefficient (Jammalamadaka and Sarma, 1988) (Supplement 1).

Due to the high co-linearity between the exponential weighted variables of Tair, SWin and VPD we perform a principal component analysis (PCA) on the matrix of variables and FLUXNET sites and retain the leading principal component of these variables, and precipitation as input for the circular statistics model (Hastie et al., 2009). The results of the PCA analysis are presented in the Supplement 2.

2.2 Circular statistics

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

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$$y = \mu + 2 * \operatorname{atan}(\beta_i x_i)$$
 (3)

where y is the target variable (i.e. DOY_{GPPmax}), μ is the mean angular direction of the target variable, x_i are the predictor variables values for the variable i, and β_i the regression coefficients the regression coefficient. The parameters μ and β_i are fitted via the maximum likelihood method using reweighted least squares algorithm as proposed by (?). Circular regression models allow to interpret Green (1984).

Relevant interpretations of fitted circular regression models are 1) the sign of the coefficient \$\beta\$-coefficients, 2) the statistical significance of the coefficient coefficients, and 3) the accuracy of the prediction. Regarding the first point: Consider a \$\text{A}\$ negative sign of the coefficient \$\text{, this}\$-would mean that an increasing value of the predictor would lead to an earlier DOY_{GPP_max} compared to the mean angular direction. Obviously the 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 distribution of \$\frac{p-values}{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 DOY_{GPP_max}.

To estimate the relative sensitivity of DOY_{GPPmax} to the leading principal component representing Tair, SWin, Precip, and VPD and VPD, as well to Precip we use the implementation of equation 3 in the "circular" R package R package "circular" (Agostinelli and Lund, 2017). To increase assess the robustness of the method we implement implemented 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

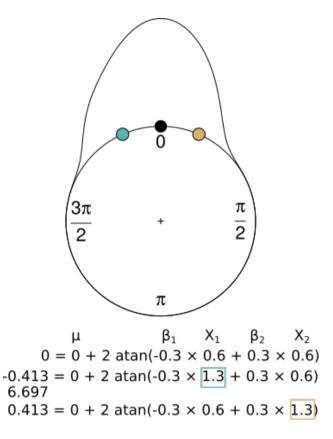


Figure 2. Interpretation of the coefficients in the circular regression. Consider a reference point (Black) generated with a circular-linear model with mean angular direction ($\mu = 0$), two coefficients (β_1, β_2) and two variables (X1x1, X2x2), where one of the coefficients is negative (β_1) and the other one is positive (β_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.

To assess the performance of linear versus circular regressions we performed a small experiment with artificial data: We use equation 3, where we predefined where we predefine two coefficient regressions ($\beta_1 = 0.3$, $\beta_2 = 0.1$). We generate two scenarios: 1) when 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 happens at mid-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, set them to unit variance. For each scenario the amount number of data is given by the equation 4 where N-n (rounded) is the amount of data for x_1 and x_2 and x_3 take arbitrary values from 5 to 1000.

$$\underline{Nn} = e^{\log(x)\log(d)} \tag{4}$$

We use the simulated data from equation $\frac{13}{2}$, and the original values of x_1 and x_2 to recover the original values of the regression coefficients β_1 and β_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 namount of data. We estimate the difference between the recovered and the original coefficient divided by the beta value as the efficiency of the model (i.e. lower values mean higher efficiency).

2.4 Analysis setup

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The target variable DOY_{GPPmax} 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 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, we reconstructed reconstruct the GPP time series taking the real numbers of the inverse FFT. We used use these reconstructed time series to calculate the expected mean timing of DOY_{GPPmax} and use this value as a template). To recover the real DOY_{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 To increase the robustness of the analysis we identify the days with the 10 greatest highest GPP values. Finally, given that These days are used in the block bootstrapping mentioned above. Finally, since most of the sites are located in the northern hemisphere Northern Hemisphere we expect that in most cases DOY_{GPPmax} will be reached at the by 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), calendar year.

To quantify the contribution of each climate variable, we count the number of sites per vegetation type where the regression coefficient is statistically significant. We perform a one-leaf-out cross-validation leave-one-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

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 DOY_{GPPmax} across vegetation types and climate classes. Finally, we show the results of the predictive power of circular regression per vegetation type.

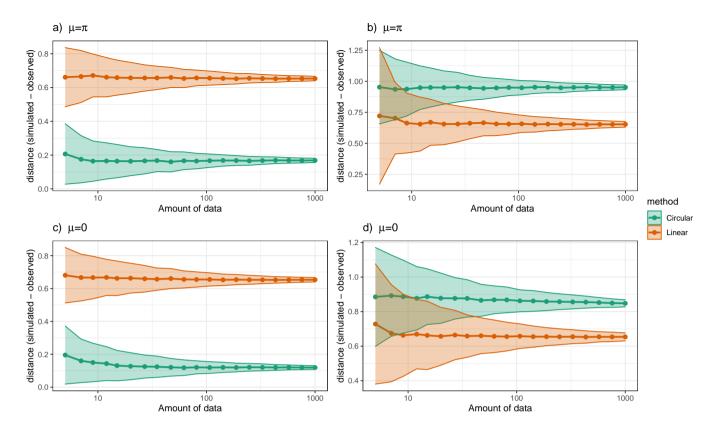


Figure 3. Efficiency of linear and circular regression models by recovering the original coefficients of a circular regression to the number for different numbers of data (lower values mean higher efficiency). Upper side: $\mu = \pi$ (Maximum at the middle of the yearmid-year). Bottom side $\mu = 0$ (Maximum at the beginning of the year). The effect is analyzed for each regression coefficient individually. a. and c. correspond to the regression coefficient β_1 and b. and d. correspond to the regression coefficient β_2 .

3.1 Circular vs. Linear Regression

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Figure 3 shows that for $\mu=0$ (DOY_{GPPmax} at the beginning of the year) and $\mu=\pi$ (DOY_{GPPmax} at the middle of the yearmid-year) the circular regression method is generally more efficient as it has a lower distance in case of β_1 . For β_2 linear regression performs better than circular regression when the number amount of data is higher than 100. Nevertheless, the differences between both regressions for β_2 are of in the order of 0.01-0.2 while the differences for β_1 are of in the order of 0.10.5. These results show that circular regression produces more accurate results than linear regression in terms of the coefficient estimation.

To illustrate the method in practice, we compare the circular and linear models using data from two sites: US-Ha1 (Northern Hemisphere deciduous Broadleaf, deciduous broadleaf forest), and AU-How (Southern Hemisphere, woody savanna). We relate the climate variables with DOY_{GPPmax} (See methods) and reconstructed the DOY_{GPPmax} using the linear and circular regression models. We compare observed and predicted DOY_{GPPmax} using JS correlation for circular model and Pearson-Product Moment for linear model. For US-Ha1 both methods shows similar performance predicting DOY_{GPPmax} (Figure 4), while for AU-

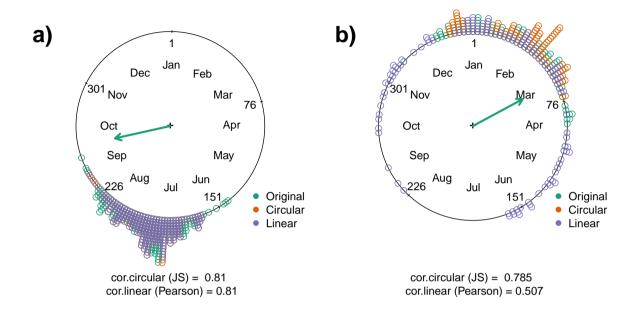


Figure 4. Correlation coefficient between the observed and predicted DOY_{GPPmax} using climatic variables. Two sites are presented: a. US-Ha1, and b. AU-How. Observed The observed DOY_{GPPmax} (Green) is compared with the data recovered retrieved using Circular (Orange) and Linear (Purple) regressions. 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 plotted every 75 days. The green arrow indicates the mean angular direction of the distribution.

Howeireular model recover better, the circular model retrieves the original data better than the linear model explaining 30 % more of the variance. In the case when the DOY_{GPPmax} is reached at the beginning of the year, linear methods produce a strong bias predicting that predicts the timing across all the entire year (Figure 4,b).

3.2 Sensitivity of DOY_{GPPmax} to climate variables

From 52 sites analyzed in this study, only one site (ES-LJu) shows a bimodal growing seasons (see \$1.2Supplement 1.2). As expected in most cases DOY_{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 DOY_{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 standard deviation is 46.9 [days] for AU-Tum site. A detailed table with the mean angular direction and standard deviation of DOY_{GPPmax} of each site is presented in Supplement 1.2 section \$1.2.

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For most half of the sites, the JS correlation coefficients are between 0.98 and 0.85 (0.70 and 0.97 (Supplement 1, Figure S5) showing that the interannual inter-annual variability of DOY_{GPPmax} is mainly explained by the cumulative effect of the climate variables. Only five Nineteen sites have a JS coefficient less than 0.8: 0.7 (DK-Sor, FI-Hyy, US-MMS, DK-ZaH, FR-Pue, US-UMB, AU-Tum, US-Ton, FR-LBr, US-Me2, IT-Lav, AT-Neu, DE-Gri, IT-MBo, IT-Ro2, US-Wkg, and BR-Sa1, FR-Fon, CZ-wet). For ES-LJu the JS coefficient for the first growing season is 0.94 and 0.93 0.77 and 0.78 for the second one (Table S2).

Across all sites we find that air temperature, shortwave incoming radiationappears, and vapor pressure deficit appear as the dominant driver worldwide in 34 sites (66 %). Air temperature drivers worldwide in 43 sites (84 %, Supplement 3). Precipitation 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-So1for 5 sites (AU-How US-Ton ZA-Kru US-SRM US-Wkg, Supplement 3). Interestingly precipitation was the most important factor for all the woody savanna sites (Supplement 3). For three sites (DE-Gri, IT-Ro2, BRSa1) any climatic variable is significant. In terms of the sign of the coefficients, shortwave incoming radiation and precipitation all the variables are predominantly negative, while for VPD is predominantly positive (Table 1). This means that higher integrated values of radiation, air temperature, VPD and precipitation lead to an earlier DOY_{GPPmax}, while and 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 2.3.

Table 1. Number of FLUXNET sites where each regression coefficient is statistically significant to explain the phenology physio-phenology of GPPmax (DOY_{GPPmax}), and if the coefficient is positive or negative. We each category we present The table is divided by the number sign of sites the coefficient. SWin = Shortwave incoming radiation, Tair = The first column is coefficient for the dimensionality reduction between: Air temperature (Tair), Precip = PrecipitationShortwave incoming radiation (SWin), VPD = and Vapor pressure deficit (VPD), the second column is the coefficient for Precipitation (Precip).

	Climatic variable	
Sign	SWin Tair Tair, SWin, VPD	Precip VPD
(+)	121 <u>8</u>	2 17-
(-)	48-17-21-38	5 -14

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 elimate class where the ecosystem is located (Figure S7). Considering the frequency per vegetation type, The PCA between shortwave incoming radiation, air temperature and vapor pressure deficit has the highest frequency in Evergreen Needleleaf Forest, Deciduous Broadleaf Forest, Grassland, Mixed Forest (MF), and Evergreen Broadleaf Forest, of significant corrrelation

coefficients by number of sites for all the vegetation types with exception of Woody Savannas (WSA) where precipitation show to be more important for most sites than the dimensionality reduction between Tair, SWin, and VPD (Figure 5). VPD is not significant for Permanent Wetlands (WET) and Open Shrublands (OSH). While for For Closed Shrublands (CSH), and Savannas (SAV) all the climate variables both drivers have the same frequency number of sites where the coefficients are statistically significant.

A special case to understand the sensitivity of DOY_{GPPmax} to climate variables is the site: ""Llano de los Juanes", "an open shrubland ecosystem in Spain (ES-LJu). It is the only clearly bimodal ecosystem in our study (Figure 6). In this case nighter SWin nor Precip are precipitation is not statistically significant. While Tair and VPD are the combination of Tair, SWin and VPD is 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 oneboth growing seasons Tair, SWin and VPD have a negative coefficient.

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 and EBF is -0.3 and -0.31 respectively. For DBF and EBF is 0.49 and 0.19, respectively, while for MF and ENF is 0.46 and for ENF is 0.4. While for MF the power prediction of the model is 0.68 and 0.70.88, respectively (Figure 7).

4 Discussion

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4.1 Circular vs Linear regression

We show that explored whether 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 a set of simulations with higher accuracy than linear regression (in the order of 0.1 to 0.01), presenting an advantage when regressions. Hence, we would generally suggest that circular regressions may be advantageous when the aim is analyzing the effect of climatic variables on phenological events. In addition, circular regression is able. We did find, however, also cases where the classical linear regression may be either more robust or equally suitable e.g. when phenological events are reached close to the mid-year. In the overall view, however, we consider that circular regressions are to be preferred over linear regression for their conceptual capacity to analyze the phenology physio-phenology of ecosystems regardless of the day of the year when the event occurs, allowing an event of interest occurs. This allows us to analysing phenological studies at global scale regardless of geographic location or the distribution of the observations during the year.

Richardson et al. (2013) 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, for this aim. In fact the results on phenological sensitivity of DOY_{GPPmax} in this study indicate the complexity of ecosystem responses to climate variability. This should be considered Indeed we considered our approach as a first step to implement more complex statistical techniques like decision trees, Gaussian process, or artificial neural networks, targeting a circular response variable.

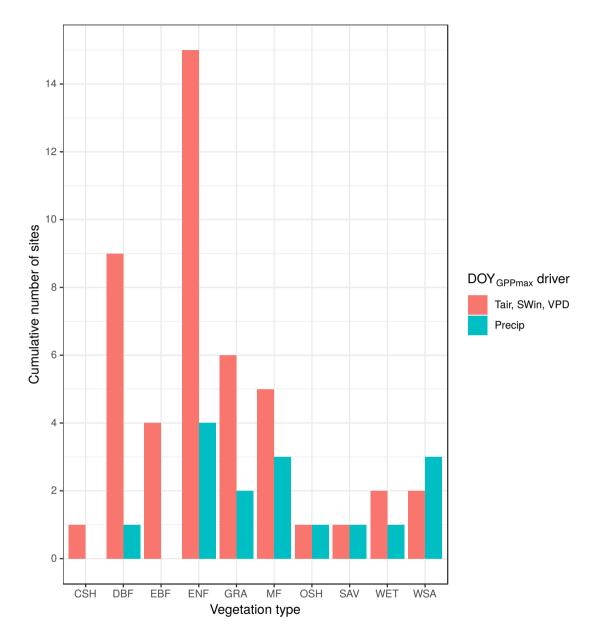


Figure 5. Contribution of each climate variable to explain the interannual inter-annual variation of DOY_{GPPmax} per vegetation type. CSH: Closed Shrublands (n = 1), DBF: Deciduous Broadleaf Forest (n = 10), EBF: Evergreen Broadleaf Forest (n = 5), ENF: Evergreen Needleleaf Forest (n = 15), GRA: Grassland (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.

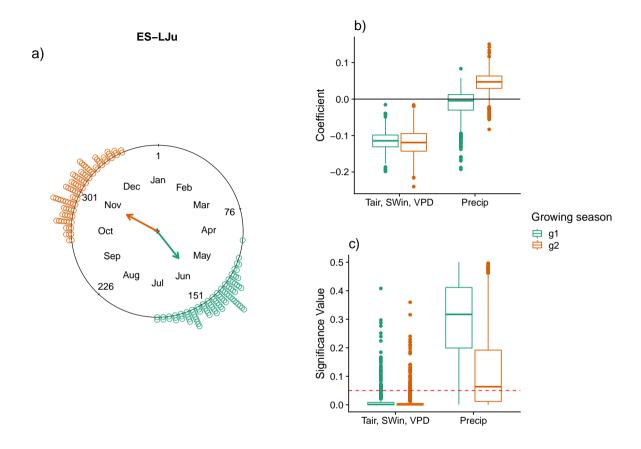


Figure 6. DOY_{GPPmax} sensitivity to different climate drivers in a Mediterranean ecosystem: "Llano de los Juanes", Spain (ES-Lju) with two growing seasons (green and orange). a) DOY_{GPPmax} distribution across the year. The arrows indicate the mean angular direction of the growing season. b) regression 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.

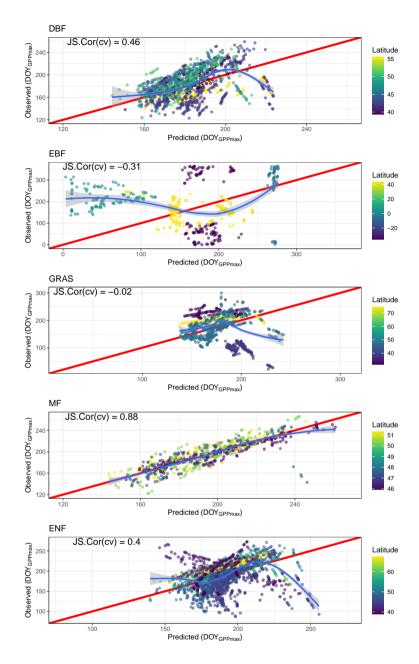


Figure 7. Cross validation of the circular regression model to predict DOY_{GPPmax} for different vegetation types using air temperature, Shortwave shortwave incoming radiation, precipitation and Vapor-vapor pressure deficit (see methods). Deciduous Broadleaf Forest (DBF). Evergreen Broadleaf Forest (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.

275 4.2 Sensitivity of DOY_{GPPmax} to climate variables

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The geographical location of the FLUXNET 2015 sites represent an advantage to capture the DOY_{GPPmax} variability at global scale (Supplement 1, 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 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 Increasing the number of tropical and Southern Hemisphere sites should be considered a high-priority in the near future to complement our knowledge about the physio-phenological ecosystem state.

The high values of the JS correlation coefficient coefficients for most of the sites demonstrate that the interannual inter-annual variability of DOY_{GPPmax} 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 0.7) might require incorporating biotic variables (e.g. species composition (Peichl et al., 2018)) or soil properties information 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 (Sect. Figure S1.7). In other words, the DOY_{GPPmax} sensitivity is site-specific, probably produced by the unique combination of biotic (e.g. species composition, species dominance, species phenology, species interaction, and phenotypic plasticity) factors that are not evaluated in our study. Several studies that focussed focused on ecosystem phenology suggest that species composition play a fundamental role in ecosystem phenology of the CO₂ physio-phenology of the CO₂ uptake (Gonsamo et al., 2017; Peichl et al., 2018). Nevertheless, our results show that the interannual variability of DOY_{GPPmax} is still climatically driven.

While there is no clear relationship between the DOY_{GPPmax} sensitivity and the vegetation type, we find a predominant role of Shortwave the combined effects of shortwave incoming radiation (SWin), air temperature (Tair) and vapor pressure deficit (VPD) at the global scale on the DOY_{GPPmax} interannual inter-annual variability, where for most of the sites SWin has these variables have a negative regression coefficient. This means, that if the SWininereases, Tair, and VPD increase 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. The second predominant factor at global scale is air temperature(Tair). 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 Tair is reflecting the speed consumption of the water available in the soil (water budget). In this way when the regression coefficient is positive and Tair increases and Tair are maximum.

On a global scale our analysis shows that the combination of air temperature, short-wave incoming radiation and vapour pressure deficit has a negative sign as well as precipitation. This means that if these variables increase during the growing seasonthe DOY_{GPPmax}, the GPPmax will be reached later reflecting a decrease in the speed of water consumption, and increasing the length of earlier. Our results are similar to those obtained by Wang and Wu (2019) were the authors conclude that an increase in the temperature produces an earlier DOY_{GPPmax}. This phenomenon is likely explained by the leaf-out advancing

during spring. Nevertheless, there is still no consensus on whether the increase in temperature will produce an earlier end to the growing season(Figure ??). Several studies demonstrated for different vegetation 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 CO2-CO2 that is uptake by ecosystems (Richardson et al., 2013). On the other hand, where the Tair 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 (pppmax (Figure ??)).

Theoretical relationship between the sign of air temperature (Tair) 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_{GPPmax} is reached earlier (Red), on the other hand if the sign is positive and temperature increase the DOY_{GPPmax} is reach later (Green).

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 short-wave incoming radiation, temperature and vapor pressure deficit for both growing seasons is negative suggesting that if we increase the temperature these variables during the period before, the DOY_{GPPmax} will happen later. Following our hypothesis mentioned above this will 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 Tair 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 Tair is negative meaning in this case that the water budget is lower, then if Tair 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; Peñuelas et al., However, our results suggest that DOY_{GPPmax} is mainly sensitive to temperature SWin, Tair, and VPD. This result agrees with the analysis performed by (Gordo and Sanz, 2005) Gordo and Sanz (2005) were 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 GPPmax value can decrease but in terms of phenology DOY_{GPPmax} can be still being the 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, Evergreen Needleleaf 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 is high, also when the distribution of the latitudinal gradient is not the same for all the sites. These results 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 hoe ad-hoc hypothesis (Richardson et al., 2013).

5 Conclusions

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In this study we explore the potential of "circular regressions" to explain the phenology of maximal CO2 physio-phenology of maximal CO2 uptake rates. We conclude that 1) shortwave incoming radiation, and temperature temperature and vapor pressure deficit are the main drivers of the timing of maximal CO2 CO2 uptake at global scale; precipitation and VPD only play a secondary role with the exception of woody savannas where the most important variable is precipitation. 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 AT-Neu	Dfb- Dfc	DBF <u>GRA</u>	1992 2002:2	0 22 − <u>11</u>	(Urbanski et al., 2007) (VO.118140/ELX/12408121
US-PFa AU-How	Dfb- Aw	MF-WSA	1996 2002:2	01149-13	(Berger et al., 2001) (Berioud&1400FL20074)40125
AU-Tum	<u>Cfb</u> _	EBF	2001:2014	14~	(Leuning et al., 2005) 10.18140/FLX/1440126
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 -Am €	DBF_EBF	1996:2014	19-7	(Pilegaard et al., 2011) (\$0148440/ELX70040032
Cfb ENF 1996:2014			2002:2005, 2009:2011		
	and Bernho	o fer, 2007) DK	(-Sor		
FI-Hyy	Dfc	ENF	1996 1994:2	01149 -1 <u>2</u>	(Suni et al., 2003) (Brooto d&140/FDX/1440035
CA-Man			1996, 1998:2003		
IT-Col CH-Cha	Csa Cfb	DBF GRA	1996 2005:2	01149-100	(Valentini et al., 1996) (NQ:18:140/F11X20440131

NL-Loo	Cfb-ET	ENF	1996 1997:20148	(?) (Zielis et al., 2014) 10.18140/FLX/1440178
CH-Dav				
CH-Dav	ET-Cfb	ENF-GRA	1997 2005:20 14 -10	(Zielis et al., 2014) (Ime#@tl&1.40/JFEX/1440133
<u>CH-Fru</u>				
RU-Fyo	Dfb-Cfb	ENF-MF	1998 2004:20 114 -11	(Kurbatova et al., 2008) (Dt18ll40/FLX/0440134
<u>CH-Lae</u>				
US-NR1	Dfe Cfb	ENF-WET	1999 2006:20 146 9	(Monson et al., 2002) (DIOdl8 \$407FDX71440145
<u>CZ-wet</u>				
IT-Ren	Dfe Cfb	ENF-GRA	1999, 12- 11	(Montagnani et al., 2009) 0 H&140/FEX/II 440147
DE-Gri			2002:2003,	
			2005:2013	
			2004:2014	
US-MMS	$\underbrace{Cfa}\underbrace{Cfb}$	DBF	1999:2014 16-13	(Schmid et al., 2000) (K110h118:140/F100/I)440148
DE-Hai			2000:2012	
US-WCr	Dfb-Cfb	DBF-ENF	1999:2006, 12-19	(Curtis et al., 2002) (Grüllowlal140/FIBX/h4404522007)
DE-Tha			2011 1996:2014	
CA-Man	Dfe Cfb	ENF_DBF	1994: 1996 , 12 - <u>19</u>	(Brooks et al., 1997) (Pill@:18:140/FLXVI440155
DK-Sor			1998:2003	
			:2014	
DK-ZaH	ET	GRA	2000:2010, 14	(Lund et al., 2012) 10.18140/FLX/1440224
			2012:2014	
FR-Pue	Csa	EBF-OSH	2000:2015 15-9	(Rambal et al., 2004) (Schoal & 140/FLX/41440226)
$\underbrace{ES\text{-}LJu}_{\sim}$			2005:2013	
US-Los	Dfb - <u>Dfc</u>	WET-ENF	2001:2008, 10-19	(Davis et al., 2003) (Sun10t18140/FLX/1440158
FI-Hyy			2010,	
			1996:2014	
US-UMB	Dfb - <u>Dfc</u>	DBF ENF	2000 2001:20 145-14	(Curtis et al., 2002) (Thulio. 48140 2FIDX) 1440160
FI-Sod				
US-Var	Csa <u>Cfb</u>	$\frac{GRA\text{-}\!DBF}{DBF}$	2001 2005:2014-10	(Xu and Baldocchi, 2004)XI&140MFLX(11140066)
FR-Fon				

AU-How	Aw -Cfb €	WSA	2002:2014 13	(Beringer et al., 2007) (Boli&140/FbX/1440163
FR-LBr		ENF	1996:2008	
AU-Tum	Cfb-Csa	EBF	2001:2014 14-15	(Leuning et al., 2005) (Rt0al8140/HLX0D440164
FR-Pue			2000:2015	
FI-Sod	Dfc -Am	ENF-EBF	2001 2004:2014-11	(?) (Bonal et al., 2008) 10.18140/FLX/1440165
GF-Guy				
IT-SRo	Csa	ENF-DBF	1999:2012 14-19	(Chiesi et al., 2005) (Valborli&lat0/FLX994)40167
IT-Col			1996:2014	
US-Syv	Dfb-Csa	MF-EBF	2001:2007, 10-9	(Desai et al., 2005) (Garb0ld8140ÆLX00\$40168
IT-Cpz	~~~	~~~	2012:2014	
			2000:2008	
US-Ton	Csa Cfb	WSA	2001 2003:2014-12	(Xu and Baldocchi, 2003)(1&1/40/FLX/1/440169)
IT-Lav		ENF		
ZA-Kru	Cwa	SAV-GRA	2000:2005, 13-11	(?) (Marcolla et al., 201 II) 0.18140/FLX/1440170
IT-MBo	$\underbrace{Dfb}_{}$		2007 2003:2013	
DE-Hai	Cfb-Csa	DBF-CSH	2000:2012 13-11	(Knohl et al., 2003) (Mattod 814D/EDX/1440171
IT-Noe			2004:2014	
FR-LBr	Cfb-Dfc	ENF	1996 1999, 12	(Montagnani et al., 2009)0.18140/FLX/1440173
IT-Ren	~~~		2002:2003,	A
~~~~			2005:2013	
IT-Ro1	Csa	<u>DBF</u>	<u>2001</u> :2008 <u>13-8</u>	(Berbigier et al., 2001) (Royl 81 40/FIONZ) 440174
<del>IT-Cpz</del>	Csa	EBF DBF	<del>2000</del> 2002:20 <b>9</b> 810	(Garbulsky et al., 2008) (Toell81410/FLX/,124401)75
IT-Ro2			2010:2012	
	Csb-Csa	ENF	<del>2002:2014</del> <del>13-</del> 14	(Treuhaft et al., 2004) (ClOcks 140//FI2XI/05440176
<del>US-Me2</del>	CSU CSa			

<del>IT-Lav</del>	Cfb	ENF	<del>2003</del> 1996:2011 <del>4</del> -18	(Marcolla et al., 2003) (NO 48140/FL)X/1440178
NL-Loo				
RU-Cok	Dsc	OSH	2003:2013 11	(Molen et al., 2007) 10.18140/FLX/1440182
AT-Neu	<del>Dfe-</del> Dfb	GRA ENF	2002:2012 11-17	(Wohlfahrt et al., 2008) (IOul 8140/FEIX/1,42018)
RU-Fyo			1998:2014	
<del>CH-Lae</del>	Cfb-Csa	MF-ENF	<del>2004:2014</del> 11	(Etzold et al., 2011) (Ball@: 18 140/F19X)/1440068
<u>US-Blo</u>			1997:2007	
<del>DE-Gri</del>	Cfb.Dfc	GRA-ENF	<del>2004</del> 2005:2014-10	(Prescher et al., 2010) (M0D8140/FLX/12400069
<u>US-GLE</u>				
GF-Guy	Am-Dfb	EBF-DBF	<del>2004:2014</del> <del>11-21</del>	(Bonal et al., 2008) (Urbholds k40/JFLXXXII)
<u>US-Ha1</u>			1992:2012	
IT-MBo	Dfb	GRA	2003:2013 11-10	(Marcolla et al., 2011) (D0v18 b40/F12N0B440076
<u>US-Los</u>		WET	2001:2008,	
			2010,	
			2014	
<del>IT-Noe</del>	<del>Csa</del> Csb	<del>CSH</del> ENF	<del>2004</del> 2002:201141-13	(Marras et al., 2011) (Trd@hl&tl40/AFLXX/0440079
US-Me2				
<del>IT-Ro2</del>	<del>Csa</del> Cfa	DBF	<del>2002:2008,</del> <del>10-16</del>	(Tedeschi et al., 2006) (Stont 8 d 40/FL, X/1044) 0083
<u>US-MMS</u>			<del>2010:2012</del>	
			1999:2014	
<del>US-Blo</del>	<del>Csa</del> Dfc	ENF	<del>1997:2007</del> <del>11-16</del>	(Baker et al., 1999) (Mont Ooth 8 dt 4 0 / FLXX 1) 440087
US-NR1			1999:2014	
US-GLE	Dfe-Dfb	ENF-MF	<del>2005</del> 1996:20140-19	(McDowell et al., 2000) [Bd: &b40/Fil.X2D440089
TIC DE				
<u>US-PFa</u>				

<del>US-Wkg</del>	BSk	GRA-MF	<del>2004:</del> 2001:2	20 <del>07</del> ,	(Saleska et al., 2003) (Dd Oni 81 4D/FDX71440091
<u>US-Syv</u>	$ \underbrace{Dfb}_{} $		2012:2014	(Emmerich,	-2003) BR-Sa1
				Am EBF	
				2002:2005,	
				2009:2011	
				<del>7</del> -1 <u>0</u>	
CH-Cha	Cfb-Csa	GRA	<del>2005</del> 2001:2	20140-14	(Merbold et al., 2014) (X10 al 81 44) (FID X/11440092)
<u>US-Ton</u>		WSA			
CH-Fru	Cfb-Dfb	GRA-DBF	<del>2005</del> 2000:2	20 <del>1140</del> -1 <u>5</u>	(Imer et al., 2013) (Curtis@18140/FDX/1440093
<u>US-UMB</u>					
ES-LJu	Csa	<del>OSH</del>	2005:2013	<del>9</del> -1 <u>4</u>	(Serrano-Ortiz et al., 2009). [X140/HEX/1944009/2004)
<u>US-Var</u>		<u>GRA</u>	2001:2014		
FR-Fon	$\frac{\textbf{Cfb-} \underbrace{\textbf{Dfb}}}{\textbf{Cfb}}$	DBF	<del>2005</del> 1999:2	2000-12	(Delpierre et al., 2016) (Out 8140/JFLX/02)10095
<u>US-WCr</u>			<u>2011</u> :2014		
CZ-wet	$\frac{\text{Cfb-}BSk}{}$	WET	<del>2006</del> 2004:2	20 <del>124</del> 11	(Dušek et al., 2012) (Emt0et8:h40/00023X/1440096
<u>US-Wkg</u>		<u>GRA</u>			
<del>IT-Ro1</del>	<del>Csa</del>	DBF-SAV	2001:2008	<del>8</del> -1 <u>3</u>	(Rey et al., 2002) (Archib@ld8:h40/FLXVI)440188
ZA-Kru	$\underbrace{Cwa}$		2000:2005,		
			2007:2013		

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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/

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