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The circular nature of recurrent life cycle events: a test comparing tropical and temperate phenology

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Abstract

1. The high diversity of plant species in the tropics has revealed complex phenological patterns and reproductive strategies occurring throughout the year. Describing and analysing tropical plant phenology, and detecting triggers, demands to consider the circular nature of recurrent life cycle events and the use of appropriated statistical metrics.
2. Here, we explore analytical pitfalls potentially affecting results of studies that do not consider the circular nature of phenology data when comparing resting and non-resting systems, especially when accounting for phylogeny. We discuss definitions of the widely used first flowering date and revisit the literature on phylogenetic signal in plant phenology. We compare statistical analyses for tropical and temperate phenology by simulating communities with known phenological and phylogenetic structures.
3. We demonstrate that ignoring the circular nature of phenological data underestimates the phylogenetic signal in plant phenology. Using the proposed circular transformation for non-resting tropical ecosystems and resting temperate systems prevented errors, yielding precise comparisons.
4. *Synthesis.* The analysis of both non-resting and resting systems must consider the circularity of phenological events. Circular statistics is the appropriate approach to calculate phenological parameters, identify phylogenetic signal and assess drivers, allowing accurate cross-comparisons of phenology across environments at large spatial scales.

KEYWORDS

circular statistics, climate seasonality, first flowering date, K-statistic, Mantel correlation, Pagel's lambda, phylogenetic eigenvector regression, phylogenetic signal

"It is beneath the glowing rays of tropical sun, that the noblest forms of vegetation are developed. In the cold North the bark of trees is covered only with dry lichens and mosses, while beneath the tropics the Cymbidium and the fragrant Vanilla adorn the trunks of the Anacardias and the gigantic Fig-tree. The fresh green of the Pothos leaves and of the Dracontias contrast with the many coloured blossoms of the Orchideae; climbing Bauhinias, Passion-flowers and golden flowered Banisterias encircle every tree of the forest. Delicate blossoms unfold themselves from the roots of *Theobroma*, and from the thick and rough bark of the *Crescentia* and *Gustavia*. ... The extraordinary height to which not only individual mountains but even whole districts rise in tropical regions, and the consequent cold of such elevations, affords the inhabitant of the tropics a singular spectacle."

Alexander von Humboldt (from an 1850 translation, pp. 230–231)

1 | INTRODUCTION

The high species diversity of the tropics generates a huge variation in life-forms and reproductive strategies (Newstrom, Frankie,

& Baker, 1994). This diversity has long been recognized, attracting the attention of early naturalists who were struck by the contrasts between temperate and tropical zones (Richards, 1952; Von Humboldt, 1850).

In temperate regions where seasonal weather predominates, there is a marked annual resting season (Figure 1a,b) followed by the reproductive and growing season (Figure 1c,d). The sharp transition from resting to growing seasons (winter to spring) leads to measurable onset dates of phenological events, such as first flowering date (FFD), first bird arrival, first leaf bud, among others.

Historical phenological databases hold information on FFD, defined as the emergence time of the first opened flower observed in a given species at a specific location (Fitter, Fitter, Harris, & Williamson, 2002; Marsham, 1789; Tooke & Battey, 2010). Scientists and citizens-scientists have registered the first reproductive event observed for common species, marking the beginning of the spring in temperate regions (Fitter et al., 2002; Miller-Rushing, Inouye, & Primack, 2008; Roberts, Tansey, Smithers, & Phillimore, 2015; Sparks & Carey, 1995; Tooke & Battey, 2010). The relatively low diversity of species and phenological patterns in temperate zones, compared to tropical areas (e.g. Newstrom et al., 1994), facilitates the recognition and long-term monitoring of the most common plants.

The phenology of tropical plant communities is more complex. Multiple flowering strategies may occur throughout the year, and

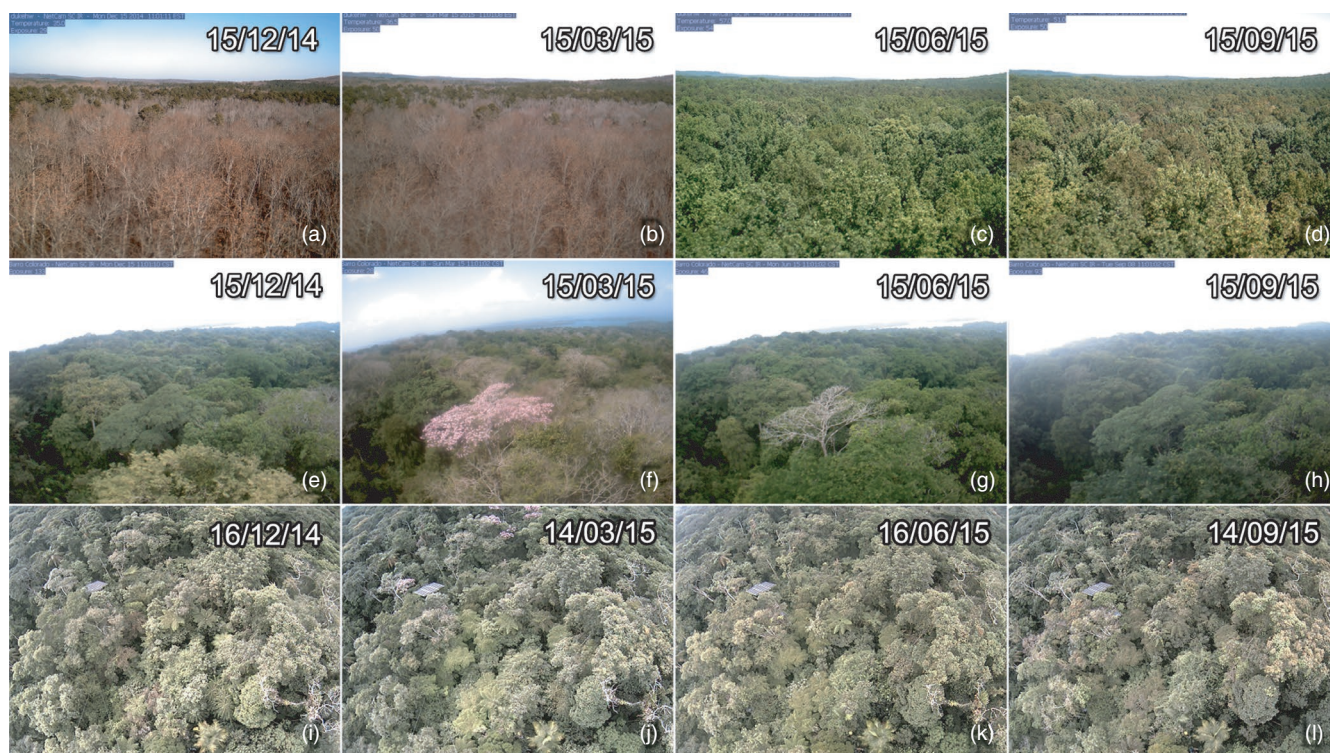


FIGURE 1 Phenology of a temperate forest in North Carolina, USA (a–d), a tropical seasonal forest in Barro Colorado Island, Panamá (e–h) and a tropical evergreen forest in Santa Virginia Station, São Paulo, Brazil (i–l), as illustrated by digital images. The selected images represent four seasons at the same day of the year for each vegetation. Note the remarkably seasonality and resting season (a–b) in temperate forest; the year-round phenological activity of tropical forests differing by the short dry season leaf fall (f) of the seasonal forest and the evergreen tree crowns throughout the year (i–l) in the tropical rainforest. Source: (a–h): <http://phenocam.sr.unh.edu/webcam/gallery/>; (i–l): <http://www.recod.ic.unicamp.br/ephenology/client/index.html#>

this complexity has challenged researchers' attempts to understand their drivers and constraints (Longman & Jeník, 1974; Richards, 1952). In the tropics, several phenological strategies may coexist at any period (Hilty, 1980; Morellato et al., 2000) because plants typically have year-round access to water, sunlight and warm temperatures (Figure 1e–l), without the marked and regular community-level resting season of temperate systems. However, a restrictive dry season is common for some tropical seasonal vegetations (Figure 1e–h). Interannually, the start of the dry season in the tropics is less predictable and less restrictive than the resting winter season in temperate environments. Tropical systems comprise a wide diversity of climates—from seasonal (e.g. tropical seasonally dry forests and savannas) to non-seasonal vegetation (e.g. tropical rainforests), according to rainfall, altitude and a wide temperature range—yet they always show reproductive activity year-round (Mendoza, Peres, & Morellato, 2017; Morellato, Camargo, & Gressler, 2013). Therefore, the absence of a marked annual resting season across the tropics requires that we consider the year as a circular continuum to interpret plant phenology (Morellato, Alberti, & Hudson, 2010).

Although some studies recognize the necessity of analysing the year as a circular continuum (Table 1), this point has been neglected in the literature. One way to deal with this issue is by using circular statistics, in which the year is considered as a circle with no single starting point or date and all metrics are estimated based on directional data, angles or radians (Morellato et al., 2010). Circular statistics has been applied in many fields of research (Fisher, 1995; Jammalamadaka & SenGupta, 2001). Examples of its application include measuring flight directions of animals (van Dame, Meled, Colin, & Belzunces, 1995), feeding time and niche overlap (Galetti et al., 2015), plant niche preferences (Tremblay & Castro, 2009), plant root distribution (Geisler-Lee et al., 2017), dynamics of flooding (Villarini, 2016). There is an important distinction between using angles or ordinal numbers to represent the time of species activity (Figure 2). Standard linear scales and statistics, which work with day of the year (DOY) as response variable, represent the flowering dates as occurring sequentially along the linear year (Figure 2a). This representation is problematic for the analysis of phenological data because December and January are actually close on the circular temporal scale (Figure 2b). Phenological information consists of recurrent life cycle events throughout the lifetime of the plant, and circular statistics works with this temporal structure by using angles as response variable (Morellato et al., 2010). Further statistics (mean, median, standard deviation) are based on trigonometric functions, using the cartesian coordinates (cosines and sines of the angles) to represent the direction of the angle as a point in the unitary circle (for details please see Fisher, 1995; Jammalamadaka & SenGupta, 2001; Mardia & Jupp, 2000).

Here, we address the analytical pitfalls and implications of neglecting the circular nature of phenology data when analysing phenological parameters (e.g. first, mean or peak dates and phenological seasonality), comparing tropical (non-resting) and temperate (resting) phenologies. We specifically discuss the consequences when estimating phylogenetic signal in plant phenology, which

uses quantitative metrics based on linear distances or covariances (Münkemüller et al., 2012; Revell, Harmon, & Collar, 2008). To achieve that, we discuss the definitions of the widely used 'FFD' and revisit the literature on phylogenetic signal in plant phenology.

We aim to demonstrate (a) how the diversity of phenological patterns in the tropics limits the applicability of the typical linear FFD, with implications for calculating average parameters to represent species and community phenologies; and (b) how using the linear DOY to measure FFD or other phenological parameters for tropical species leads to biased conclusions, especially when used to calculate the phenological distance between a pair of species for phylogenetic signal metrics. Finally, we recommend the use of directional statistics, transforming FFDs (or any date) into angles to represent their cyclic occurrence, calculating the angular distance between pairs of FFDs and then converting the matrix of angular distances back to a linear scale. The linearized distance is then applicable in linear statistical analyses, allowing comparisons between tropical and temperate, resting and non-resting phenologies. We provide R code and examples (in Dryad; <https://doi.org/10.5061/dryad.64r8fc0>) for basic circular descriptive analysis and phylogenetic comparative analyses of plant phenology, taking into account the circular nature of the temporal structure of phenological datasets.

2 | FIRST FLOWERING DATES

A number of phenological studies, mostly from the 90s onwards, have used FFD as a key phenological parameter to analyse changes and triggers in temperate species' phenology, especially for tracking climate change effects on plant life cycles (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Fitter et al., 2002; Miller-Rushing et al., 2008; Roberts et al., 2015; Sparks & Carey, 1995; Tooke & Battey, 2010). Consequently, FFD has enabled detection, comparison and synthesis of trends and shifts in flowering phenology, as well as tracking the effects of climate change on reproduction of temperate vegetation (Chambers et al., 2013; Menzel et al., 2006; Primack & Miller-Rushing, 2011). However, the use of FFD to represent phenological patterns across an entire plant population or community has recently been challenged. Some authors advocate using the entire flowering season or combining phenological parameters, such as flowering peak date, phenological variance and synchrony, to describe plant phenology (e.g. Herrera, 1988; Miller-Rushing et al., 2008; Morellato et al., 2000). Others have criticized FFD, based on simulated datasets (e.g. Moussus, Julliard, & Jiguet, 2010). Nevertheless, FFD has been collected extensively for many years to describe flowering phenology over temperate areas, and no similar long-term information exists (Chambers et al., 2013).

To examine the differences between linear and circular statistics in estimating phenological parameters (peak date and seasonality) using FFD, we simulated 1,000 phylogenies with phenological traits for 100 species in resting and non-resting systems (Figure 3; description of analyses in Supporting Information). For resting systems, the first and last records of flowering were set to DOY 91 (1st April) and

TABLE 1 Studies evaluating phylogenetic signal on plant phenology, including the metrics calculated and response variable analysed

Reference	Phylogenetic signal metric	Response variable (phenological timing)	Study site vegetation (country)	Number of species	Software/package (function)
Staggemeier, Diniz-Filho & Morellato (2010)	PVR	Linearized phenological variables of flowering and fruiting first and peak dates (scores from PCoA based on circular distance matrix using angular difference), among other variables	Atlantic rainforest (Brazil)	34 Myrtaceae	—
Silva et al. (2011)	Mantel	Matrices with angular differences between pair of species (for flowering and fruiting)	Woodland cerrado (Brazil)	196	—
Chang-Yang et al. (2013)	PVR	Linearized phenological variables of flowering and fruiting (scores from a PCoA considering peak dates and concentration)	Submontane evergreen broadleaf forest (Taiwan)	24–46	R
Davies et al. (2013)	K-statistic	First flower and first leaf dates converted to radians	Northern Hemisphere	~4,000	R/picante (phylosignal)
Seger et al. (2013)	PVR, K-statistic, Mantel	Linearized phenological variables for flowering and fruiting mean dates (scores from PCoA based on distance matrix using sine and cosine values)	Araucaria rainforest (Brazil)	89	R
Lessard-Therrien, Davies & Bolmgren (2014)	K-statistic	Mean flowering date (DOY)	Subarctic vegetation	48	R/picante (phylosignal)
Panchen et al. (2014)	K-statistic, Pagel's Lambda	Adjusted leaf out dates (DOY)	Northern Hemisphere (eighth botanical gardens and arboreta)	1,597	R/phylosig (phytools)
CaraDonna & Inouye (2015)	K-statistic, Pagel's Lambda	First, peak and last flowering date (DOY) and duration	Rocky Mountain perennial herbs (USA)	60	R/picante (phylosignal); geiger
Du et al. (2015)	K-statistic ^a	Mid-point of flowering (transformed onto a circular scale)	Chinese angiosperm flora (China)	19,631	R/picante (phylosignal) ^a
Panchen et al. (2015)	K-statistic, Pagel's Lambda	Leaf senescence dates (days)	Botanical gardens in Asia, Europe and North America	1,360	R/phylosig (phytools)
Staggemeier et al. (2015)	PVR, K-statistic	Linearized phenological variables of flowering and fruiting peak dates (scores from PCoA based on circular distance matrix using angular difference)	Three sites of Atlantic rainforest (Brazil)	24, 26 and 37 species	R/PVR (PVR and PVRdecomp)
Hart, Georgian & Salick (2016)	K-statistic	Mean and first flowering dates (DOY), among others	Himalayan Rhododendron species (China)	9 <i>Rhododendron</i>	R/picante (phylosignal); phytools
Li et al. (2016)	PVR, K-statistic, Pagel's Lambda ^b	First flower budding, first flowering, first fruiting and flowering end (DOY)	Alpine meadows, eastern Tibetan Plateau (China)	40 and 50 species	R/phytools (phylosig)
Razafindratsima & Dunham (2016)	Pagel's Lambda	Scores from 1st axis of PCA based on fruiting mean angle, concentration and duration	Evergreen montane rainforest (Madagascar)	155	R/geiger (fit-Continuous)
Brito et al. (2017)	Mantel	Similarity among species regarding flowering and fruiting phenological curves (% of activity per month)	Atlantic rainforest and campo rupestre (Brazil)	70 Melastomataceae	R/ape (mantel.test); ecodist (mgram)

(Continues)

TABLE 1 (Continued)

Reference	Phylogenetic signal metric	Response variable (phenological timing)	Study site vegetation (country)	Number of species	Software/package (function)
Cortés-Flores, et al. (2017)	PGLS (Pagel's Lambda)	Linearized phenological variables of flowering from a circular distance matrix (scores from ordination)	Seasonal dry tropical forest	154	R/caper (pgls)
Du et al. (2017)	K-statistic	First leaf out and flowering dates (DOY)	Subtropical broad-leaved forest, Heilongjiang Province (China)	47	R/picante (phylosignal)
Heydel & Tackenberg (2017)	K-statistic	Timing of flowering and seed release, among others (growing degree days)	Central Europe	104	R/picante (multiPhylosignal)

^aModified K-statistic significance test to consider the temporal autocorrelation, where the differences for contrasts were based on circular distances rather than absolute distances.

^bK-statistic and Pagel's Lambda were used to estimate phylogenetic signal. PVR was applied to separate the variation explained by ecology and phylogeny.

DOY 273 (30th September), respectively, with highest synchrony in the middle of temperate spring. The non-resting systems' FFDs were spread throughout the year, with a mean date around the tropical spring (Sep–Nov). Based on the simulated FFDs, we calculated the FFD peak for each simulated community (average of the 100 FFDs) using DOY and angles under linear and circular statistics respectively. To estimate the circular mean angle for each community, each DOY was first converted to an angle ($\text{angle} = \text{DOY} \times 360 \text{ degrees} / 365 \text{ days}$). Each angle is converted in cartesian coordinates (x, y) where x is the cosine of the angle, and y is the sine (Fisher, 1995; Jammalamadaka & SenGupta, 2001). The mean angle for each community is the arctangent from the average of all sines divided by the average of all cosines (see details in Supporting Information). We also calculated rho values, or the length of the r vector, which is the degree of data concentration around the mean angle or mean date and can be interpreted as the degree of seasonality of each

community (Morellato et al., 2010; Morellato et al., 2000). The rho varies from 0 to 1—a value of 0 means data are spread over the year or circle, with no concentration around the mean date or angle, and is interpreted as 'no seasonality'; a value of 1 represents the highest concentration around the mean date and is interpreted as 'strong seasonality'.

Mean dates or angles were compared between two phenological scenarios: resting (temperate) versus non-resting (tropical) systems. We used Wilcoxon paired test (Zar, 2010) to verify whether FFD peaks estimated by linear and circular statistics differed.

The phenological seasonality of resting systems was high as expected, with $\rho = 0.79 \pm 0.04$ (min: 0.62; max: 0.90), FFD peak on DOY 178 ($N = 1,000$; Figure 4a) and mean angle of 175.3° (Figure 4c), equivalent to DOY 178. Hence, the FFD peaks estimated by circular and linear statistics for each resting community were congruent, with 99% of communities showing a difference of 3 days or less

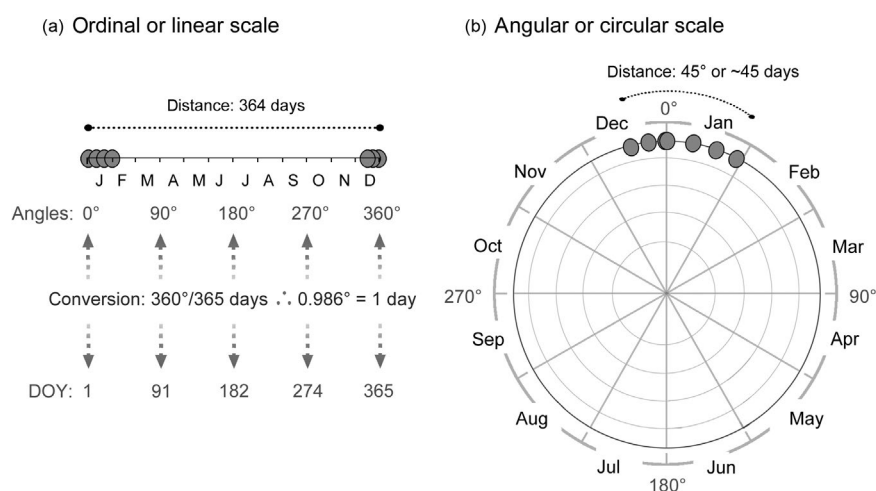
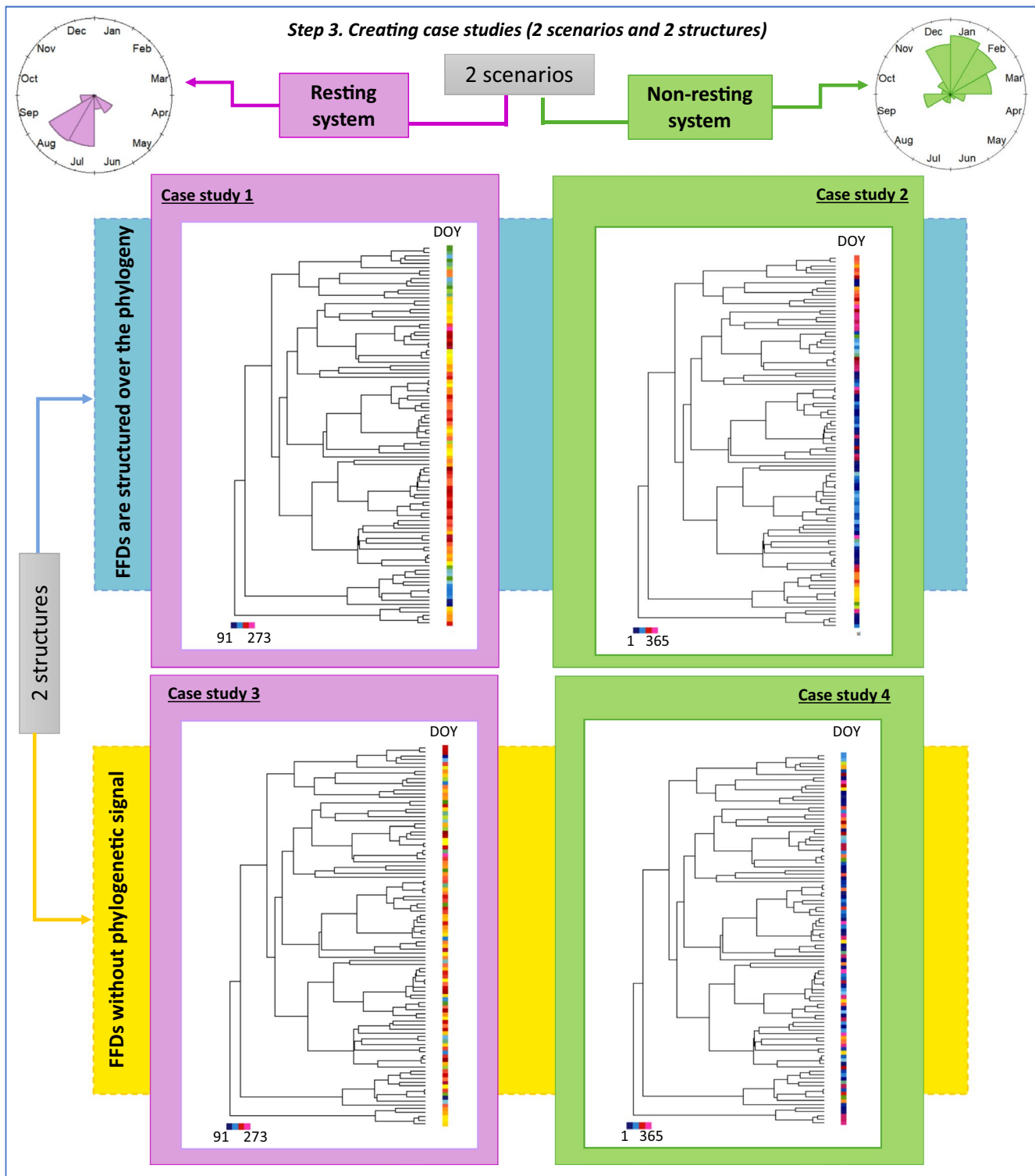


FIGURE 2 Two representations, linear and circular, of the 365 days of the year (DOY), demonstrating how the temporal distance between events must be interpreted in phenological studies. (a) Ordinal or linear scale: the largest possible interval is the distance between phenological events (grey dots) on days of the year between January and December; and (b) angular or circular scale: dates were converted into angles (see text for details), resulting in tightly clustered phenological events, showing that December and January are actually close on the circular temporal scale, representing the shortest possible interval between events in the same dataset

Step 1. Simulating 1 000 trees with 100 species each

Step 2. Simulating 100 dates in accordance with the expectancies from Brownian model for each phylogeny

Step 3. Creating case studies (2 scenarios and 2 structures)



Step 4. Comparisons using linear raw date (DOY) versus circular transformed date (scores) for each case study with 4 metrics

Blomberg's K statistic, Pagel's lambda, PVR, Mantel correlation

FIGURE 3 Framework applied to simulate communities with known phenological and phylogenetic information. *Step 1:* 1,000 phylogenies with 100 species were simulated under birth-death process. *Step 2:* 100 FFDs (first flowering dates) were simulated based on each phylogeny under Brownian model (BM) expectancies; that is, the differences in the day of the year (DOY) for two species is proportional to the divergence time between them. *Step 3:* FFD vector for each community was rescaled to represent resting systems where the FFD occurs between DOY 91 and 273 (case studies 1 and 3), and non-resting systems where the flowering dates occurs throughout the year (case studies 2 and 4). For case studies 1 and 2, the FFDs are phylogenetically structured (i.e. follow the BM expectancy); for case studies 3 and 4, the FFDs were randomized over the tips of the phylogeny to represent communities with phenological patterns not phylogenetically structured. *Step 4:* comparisons inside each community were conducted for four metrics of phylogenetic signal, contrasting analyses based on linear raw date (DOY) versus circular transformed date (angles were converted into linear scores by PCoA on the angular distance matrix to consider the circular temporal distribution of the phenological information). Methodological details for the simulations are described in the Supporting Information

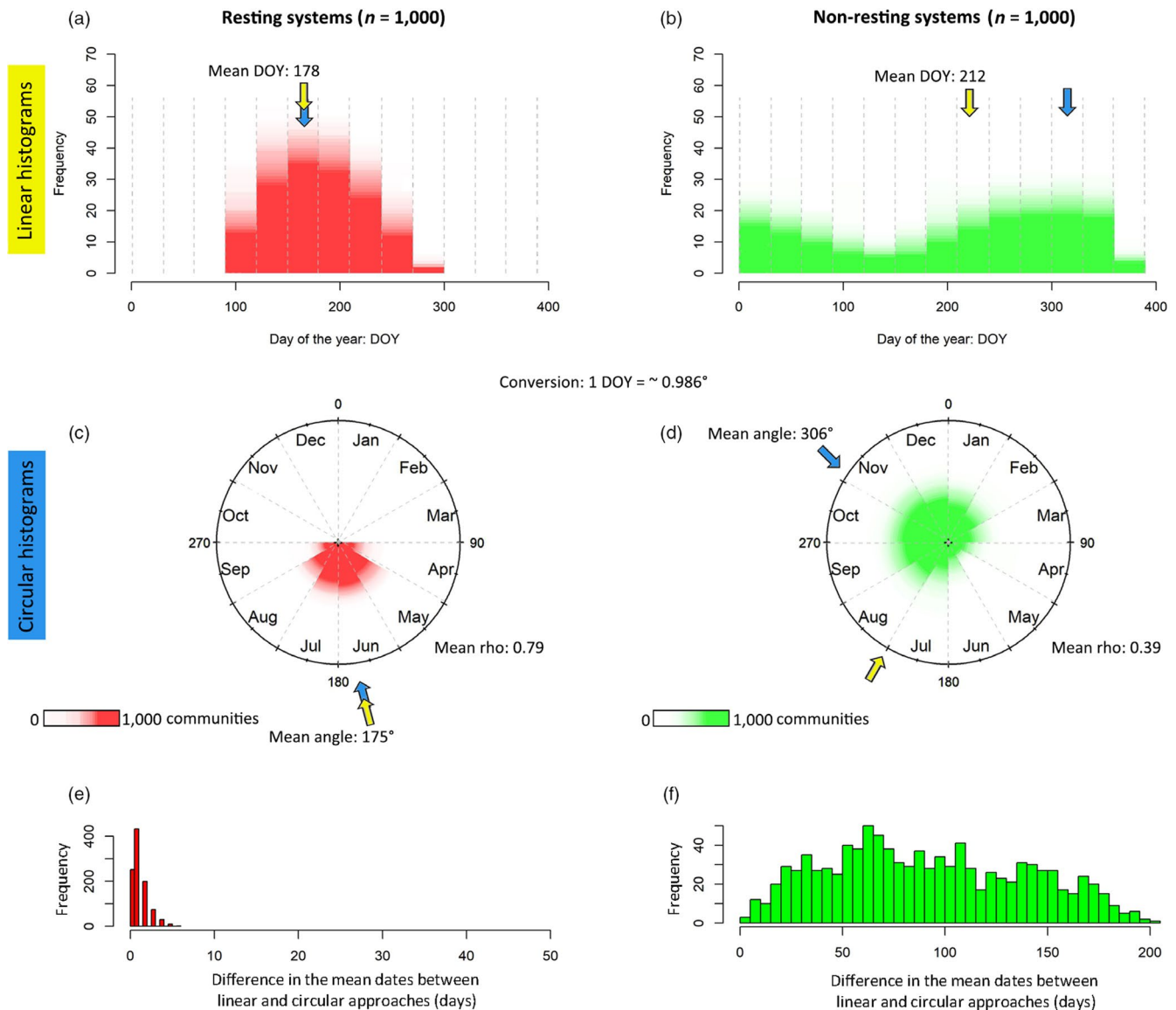


FIGURE 4 Linear (a, b) and circular (c, d) histograms representing the distribution of simulated FFD (first flowering date) for 1,000 temperate communities affected by a resting season, during which species cannot reproduce (a, c), and for 1,000 non-resting tropical communities, where species can reproduce throughout the year (b, d). Absolute differences in the mean dates of FFD per community, estimated by linear (yellow arrows) and circular (blue arrows) statistics, were negligible for resting communities (e). On the other hand, absolute differences were larger for non-resting communities (f), demonstrating the error of using a linear scale for circular measures of recurrent events. The linear FFD mean date of non-resting systems differed from the circular mean date and fell outside the phenological activity peak (Sep–Dec)

between circular and linear estimates (min: 0, mean: 1.2 day; max: 6 days; Figure 4e). Conversely, non-resting systems showed weak seasonality on average, with $\rho = 0.39 \pm 0.12$ (min: 0.03; max: 0.71). The linear and circular estimates of FFD peaks differed, with 80% of non-resting communities showing more than 1 month of difference (min: 3 days; mean: 92 days; max: 201 days; Figure 4f). The average FFD peaks for non-resting communities on the linear scale was DOY 213 (Figure 4b); on circular scale, the angle was 306.8° , equivalent to DOY 312 is about 100 days apart (Figure 4d).

We conclude that linear statistics calculates a mean date outside the community peak for non-resting communities (Figure 4). Linear statistics does not accurately represent the phenology of non-resting environments, while circular statistics is a good descriptor for any community with or without a resting season. We stress, however, that circular and linear estimates are congruent for very seasonal systems in which the peaks are concentrated in the middle of the year. For temperate seasonal communities in the Southern Hemisphere (examples in Aizen & Vazquez, 2006), where activity peaks between November and February, we emphasize the application of circular statistics (see S2 in Supporting Information).

3 | METRICS OF PHYLOGENETIC SIGNAL IN PLANT PHENOLOGY: A REVIEW AND EVALUATION

We conducted a non-exhaustive review of papers estimating phylogenetic signal in phenological timing (18 articles, Table 1). Our survey shows no consensus on the best way to conduct this analysis. The most frequent metrics were the *K*-statistic (Blomberg, Garland, & Ives, 2003) and Pagel's λ (Pagel, 1999), followed by phylogenetic eigenvector regression (PVR: Phylogenetic EigenVector Regression; Diniz-Filho, Sant'Ana, & Bini, 1998; Diniz-Filho et al., 2012) and Mantel correlation (Harmon & Glor, 2010). All four metrics were designed for linearly scaled data.

Some phenological studies have emphasized the importance of considering the year as a continuum, working with angles and applying a linearization of angular variables before conducting linear statistical analyses (Table 1). Staggemeier, Diniz-Filho, and Morellato (2010) first proposed an ordination metric to linearize angles, and further studies applied this approach with minor modifications (Chang-Yang, Lu, Sun, & Hsieh, 2013; Seger, Duarte, Debastiani, Kindel, & Jarenkow, 2013; Silva, Silva, Carvalho, & Batalha, 2011; Staggemeier et al., 2015).

In order to linearize the circular data, the phenological angles are represented by scores extracted from orthogonal vectors based on the Principal Coordinate Analysis (PCoA) of the matrix of angular distance between species, as described in Staggemeier et al. (2010) and graphically illustrated in Staggemeier et al. (2015). These scores represent the angular position of the species on a linear scale. When the first PCoA vector explains more than 70% of phenological variation, it is assumed that the first vector is sufficient to represent the position of the species in the phenological space, otherwise the two

first vectors must be interpreted. Species variation can be plotted in a graph, where x-axis represents the phylogenetic position according to the significant phylogenetic vector (defined by PVR analysis) and y-axis represents the scores of flowering dates. If the community is phylogenetically structured, this graph will show phenological clusters of related species, in other words, smallest phenological distances among species correspond to closest phylogenetic distances. Other studies discussed alternative approaches, for example, Davies et al. (2013) suggest that conversion to angles or radians is important, although they did not mention how they dealt with radians in the phylogenetic contrast when estimating the *K*-statistic. Du et al. (2015) suggest a modification of the significance test for *K*-statistic that takes into account the temporal circularity by using the angular distance to estimate the phylogenetic contrasts. However, this modification only slightly changes the p-value. In addition, *K*-statistic was not modified to consider circularity, and the resultant *K*-values are not comparable across studies.

To evaluate the impact of neglecting the circular nature of phenological data in comparative phylogenetic analyses, we calculated the most common metrics of phylogenetic signal for 1,000 communities of 100 species under four situations, hereinafter termed 'case studies' (Figure 3): resting and non-resting systems with FFD phylogenetically structured (case studies 1 and 2 respectively) and FFD not phylogenetically structured (case studies 3 and 4). The phylogenetic information came from 1,000 phylogenetic trees simulated under birth-death process with 100 species per community, every simulation resulting in one community (step 1, Figure 3). The phenological information was simulated to recreate FFDs following the expectancies of Brownian evolutionary model (BM; step 2 in Figure 3). Under BM, the differences in FFDs between species are expected to be proportional to the divergence time between species.

We found that the FFDs of communities simulated to evolve by Brownian evolutionary model showed phylogenetic signal as expected, while the communities' FFDs randomized among the tips showed no phylogenetic signal (Figure 5). The phylogenetic signal for resting communities was similar for analyses conducted on linear raw date (DOY) and circular transformed date (scores from PCoA; Figure 5). However, we found differences between raw and transformed data analyses for non-resting communities (Figure 5). The phylogenetic signal calculated based on linear raw data was underestimated in 94% of the non-resting communities by the *K*-statistic, in 62% by the λ statistic, in 92% by the PVR and in 88% by Mantel correlation (Figure 6).

We conclude that the phylogenetic signal is estimated accurately only when the circular nature of the temporal data is considered, that is, when using the circular transformed data.

As guideline for future studies, we suggest graphically exploring the phenological patterns in datasets and calculating basic descriptive statistics (including descriptors at species level, because species with continuous reproduction or non-seasonal patterns cannot be represented by the mean date, the most common response variable used in studies evaluating PS in plant phenology). Despite the criticism of Mantel test as a measure of phylogenetic

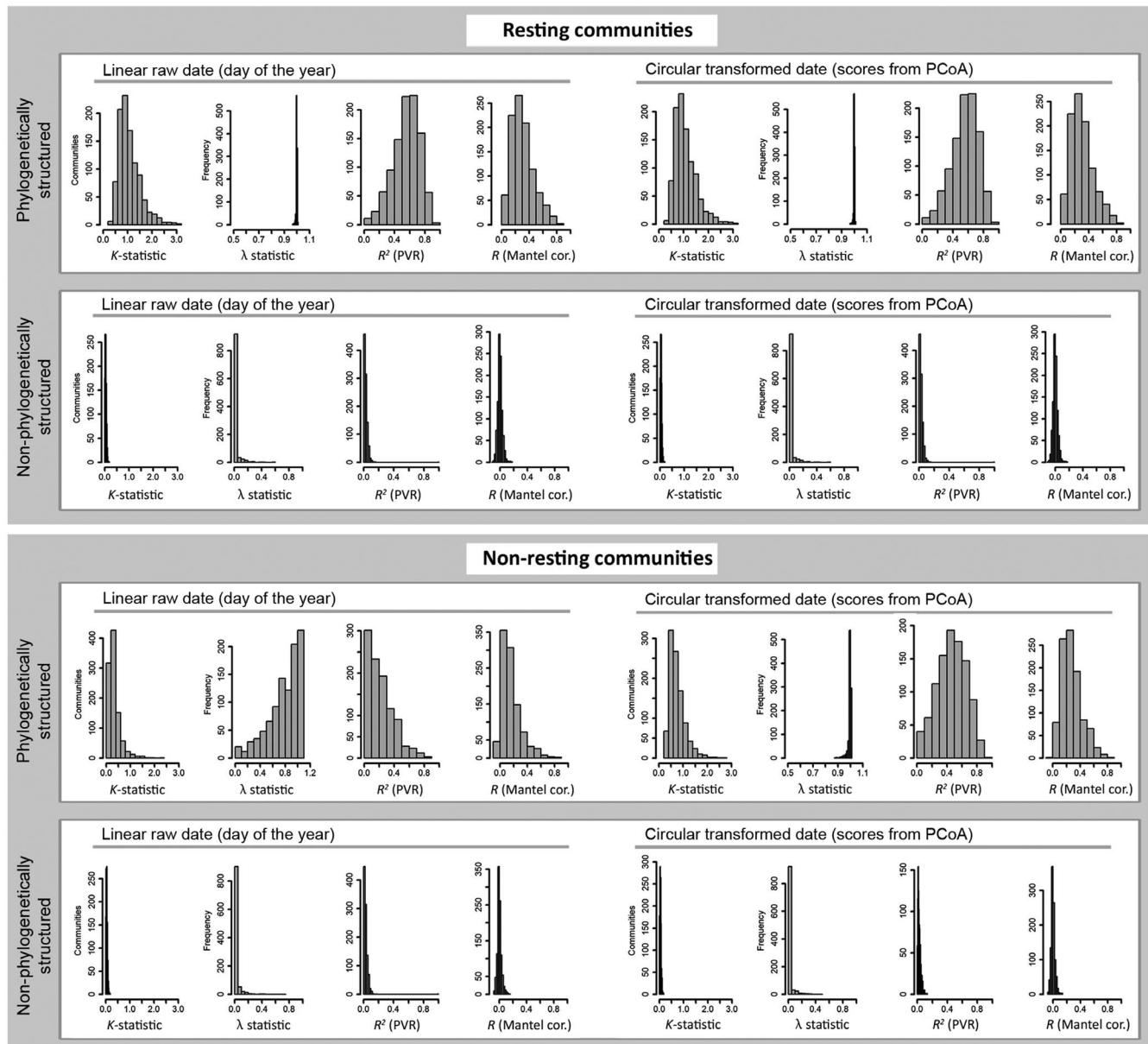


FIGURE 5 Phylogenetic signal estimated for 1,000 simulated resting and non-resting communities, with contrasting analyses conducted using linear raw date (day of the year) and circular transformed date (scores from Principal Coordinates Analysis based on the angular distances, see details in Supporting Information)

signal in comparative analyses (see Harmon & Glor, 2010), this method is still useful for analysing communities containing species that exhibit sub-annual or continuous phenology, as demonstrated in Brito et al. (2017). We also recommend reporting results based on more than one phylogenetic signal metric, because they are based on distinct assumptions (Münkemüller et al., 2012; Seger et al., 2013). Finally, for global analyses comparing the phenological pattern (e.g. onset date, peak date and mean date) between hemispheres, it is necessary to standardize the zero point of the dataset, prior to analysis, to account for differences between austral and boreal seasons (see Keogan et al., 2018). For example, when studying species occurring in mid-North and mid-South latitudes, the zero point of the circular analyses should be standardized to

the date (or angle) of minimum daylight hours (winter solstice). In Dryad, we provide the R script to calculate basic statistics at community level, graphically explore datasets and estimate phylogenetic signal with the four metrics compared in the present study.

Finally, we are aware that transforming angles into a linear scale and applying multivariate analyses is not the only solution to the problem of circular nature of the recurrent phenological events, since the transformed data may not represent all variation in the original dataset. However, this is the best analytical approach available. We highlight the urgent necessity for developing comparative phylogenetic methods—for example, including a wrapped normal distribution (Pewsey, Neuhauser, & Ruxton, 2013) in the MCMCglmm framework (Hadfield, 2010)—to properly deal with the circular nature of phenological data.

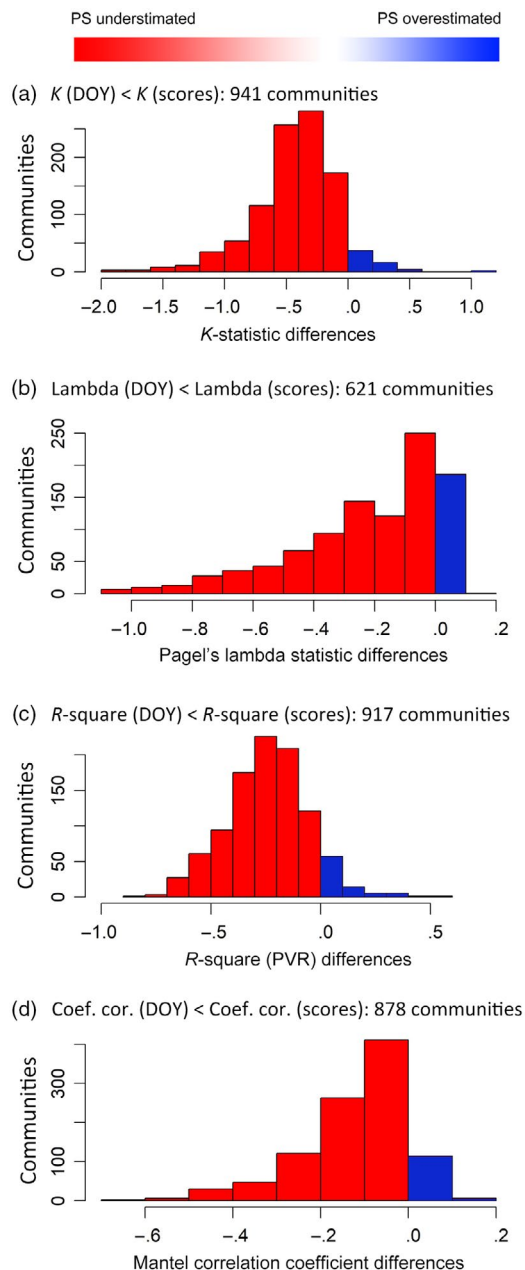


FIGURE 6 Differences in the phylogenetic signal (PS) estimated by four metrics (a–d) for non-resting communities with first flowering dates structured over the phylogeny contrasting circular and linear approaches (linear minus circular) that estimate PS based on circular transformed date (scores) and linear raw date (DOY), respectively

4 | CONCLUDING REMARKS

The high species diversity of the tropics has yielded a complexity of phenological patterns and a great variety of reproductive strategies (Morellato et al., 2013). We demonstrated the importance of applying statistical metrics that deal with the low climate seasonality, and the absence of a resting season, to describe and analyse phenology and detect triggers through global analyses involving communities with a wide variety of phenological patterns. We show that

circular statistics precisely estimates the FFD peak for temperate and tropical vegetation, and that considering the recurrence of plant phenology leads to accurate comparisons across communities with or without a resting season. An increasing number of phenological datasets and phylogenetic data are becoming available, enabling comparisons of phenological trends and phylogenetic signal across communities and continents (Abernethy et al., 2018); an important potential application of the analytical approach we proposed.

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AUTHORS' CONTRIBUTIONS

V.G.S., M.G.G.C., J.A.F.D.-F. and L.P.C.M. conceived the themes for this manuscript; V.G.S., M.G.G.C. and L.P.C.M. led the writing with J.A.F.D.-F., R.F. and L.J. contributing equally to the text for each section. V.G.S. and L.J. conducted all analytical section with contribution of R.F. All authors provided critical reviews of each draft before giving approval for submission of the final version.


DATA AVAILABILITY STATEMENT

This paper does not use real data. The R-script, including data exemplifying the four study cases and the function to estimate phylogenetic signal on phenological data, is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.64r8fc0> (Staggemeier et al., 2019) enabling people to run all the analyses developed here.


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