Fourier analysis to detect phenological cycles using tropical field data and simulations

Fourier analysis for long-term phenology

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Abstract

1. Changes in phenology are an inevitable result of climate change, and will have wide-reaching impacts on species, ecosystems, human society and even feedback onto climate. Accurate understanding of phenology is important to adapt to and mitigate such changes. However, analysis of phenology globally has been constrained by lack of data, dependence on geographically limited, non-circular indicators and lack of power in statistical analyses.
2. To address these challenges, especially for the study of tropical phenology, we developed a flexible and robust analytical approach - using Fourier analysis with confidence intervals - to objectively and quantitatively describe long-term observational phenology data even when data may be noisy. We then tested the power of this approach to detect regular cycles under different scenarios of data noise and length using both simulated and field data.
3. We use Fourier analysis to quantify flowering phenology from newly available data for 856 individual plants of 70 species observed monthly since 1986 at Lopé National Park, Gabon. After applying a confidence test, we find that 59% of the individuals have regular flowering cycles, and 88% species flower annually. We find time series length to be a significant predictor of the likelihood of confidently detecting a regular cycle from the data. Using simulated data we find that cycle regularity has a greater impact on detecting phenology than event detectability. Power analysis of the Lopé field data shows that at least six years of data are needed for confident detection of the least noisy species, but this varies and is often greater than 20 years for the most noisy species.

4. There are now a number of large phenology datasets from the tropics, from which insights into current regional and global changes may be gained, if flexible and quantitative analytical approaches are used. However consistent long-term data collection is costly and requires much effort. We provide support for the importance of such research and give suggestions as to how to avoid erroneous interpretation of shorter length datasets and maximize returns from long-term observational studies.

Key-words:
Flowering; Phenophases; Spectral analysis; Tropical forests; Gabon; Time-series data; Climate change, Circular analysis; Lopé National park

Introduction

Phenology concerns the timing of recurring life-cycle events - such as leaf growth, flowering and fruiting in plants - and has long fascinated ecologists and evolutionary scientists. Questions range from understanding the complex environmental cues and internal mechanisms that initiate phenology events (phenophases) to the adaptive significance of their timing and duration and responses to environmental change. Phenology has wide-reaching influence within ecosystems and determines the nature of many inter-specific interactions (Butt et al. 2015). Changes in global climate will inevitably have long-term impacts on phenology (Parmesan 2006) with knock-on effects for ecosystems and people (Van Vliet 2010). It is also clear that there will be feedbacks between changing phenology and climate, but they are poorly characterised by current climate models (IPCC 2014).

Tropical phenology overlooked in reviews of change

Major reviews of phenological change to date have lent heavily on evidence from temperate, especially Northern hemisphere, regions (Chambers et al. 2013; Cleland et al. 2007; Parmesan 2006). In these regions more phenology data is available and analyses are arguably simpler. The strong seasonality in temperate regions accompanied by a dormant winter season results in broad synchronisation of phenology on the annual cycle. Years can be treated to some extent as independent repeating events and researchers are able to make use of a relatively simple suite of "spring indicators" (e.g. first appearance, first lay-date, bud-burst measured in days since January 1st).

While tropical climates are often seasonal, annual variation is more limited than in temperate regions and vegetative growth and reproduction are possible at any time of

76 the year resulting in more diverse phenology and cycles other than twelve months (van
77 Schaik et al. 1993). Use of simple spring indicators is not appropriate for tropical
78 phenology because of the ***circularity of the data*** (e.g. January 1st is an arbitrarily low
79 value and not meaningfully different from December 31st).
80 Furthermore, phenology is subject to many conflicting demands, for example an
81 organism may receive an environmental signal to reproduce but fail to do so because it
82 lacks critical resources (Obeso 2002). Inconsistencies and gaps in data collection due to
83 observation error are also common in long-term studies, making quantification in many
84 cases harder still. Thus analytical approaches for tropical phenology need to take
85 account of the circularity of the data, be flexible, quantitative and attribute confidence
86 to conclusions.

87 ## Analyses of long-tem tropical plant phenology

88 Published analyses of tropical plant phenology range from simple descriptions and
89 correlations with environmental variables to more recent, quantitative analyses of
90 change (S1). The Newstrom et al. (1994) framework was an important step towards
91 objective inter-site comparisons, however categorisation loses analytical power and
92 visual comparisons lack objective rigour. More computationally intensive methods have
93 included differentiation of species-level reproductive cycles using finite mixture theory
94 and bootstrapping methods (Cannon et al. 2007), modelled autocorrelation functions
95 (Norden et al. 2007), sinusoid-based regression (Anderson et al. 2005), spectral
96 analysis (Chapman et al. 1999), circular statistics (Ting et al. 2008; Zimmerman et al.
97 2007; Wright et al. 1999; Wright & Calderon 1995), generalized linear models (GLMs)
98 (Newbery et al. 2013) and generalized additive mixed models (GAMMs) (Polansky and
99 Robbins 2013). While data has often been collected at the scale of the individual plant

100 (9/18 studies in S1), this is not always reflected in analysis where individuals are
101 clumped into species, guilds, or a percentage score of a whole community, losing power
102 and precluding vital covariate information. The longest tropical phenology dataset
103 analysed to date is 22 years of flowering data (Pau et al. 2013) and 18 years of flowering
104 and fruiting data (Wright & Calderon 2006) from Barro Colorado Island, Panama with
105 many other studies relying on fewer than ten years data (9/18 studies in S1).
106 Addressing the challenges of sample size, data quality, circularity and pseudo-
107 replication is of paramount importance to quantify tropical phenology and compare
108 between sites and over time. Consensus as to the most suitable way to analyse these
109 data, what length of data is necessary to identify cycles and how to attribute confidence
110 to results has been missing, although progress is being made (Hudson & Keatley 2010).
111 In this article, we apply statistical theory to both field and simulated data, to
112 develop and demonstrate objective methods – based on ***Fourier analysis*** - to detect and
113 quantify confidence in regular phenological cycles. We also test the likelihood of
114 detecting cycles under different data noise and length scenarios and discuss
115 opportunities for incorporating the resulting insights into research and policy.
116 Explanations of technical terms related to Fourier analysis used in this paper are given
117 in the glossary in Table 1 and their first use in the text is indicated in ***bold italics***.
118

119 ## Introduction to Fourier analysis for phenology

120 The Fourier transform is a mathematical method used to identify regular ***cycles*** in ***time***
121 ***series*** data by comparing fluctuations in the data with ***sinusoids*** (Bloomfield 2000) and
122 has been used extensively in disciplines such as engineering and mathematics. The
123 Fourier transform calculates the tendency (hereafter known as ***power***) of all possible

124 cycles to appear in the data and can therefore be used to quantify seasonal phenology
125 data without the need for prior knowledge or hypotheses of ***cycle length***. However it
126 has been rarely used in the context of phenology analysis and never for long-term
127 observational phenology data. Chapman et al. (1999) used Fourier to identify dominant
128 reproductive cycles from six years of data for a tropical tree community, but did not use
129 a confidence test. More recently Zalamea et al. (2011) used Fourier to identify flowering
130 cycles from reconstructed 12-month series of herbarium data for a genus of neotropical
131 tree, attributing confidence to cycles using a bootstrapping method.
132 Compared to other data for which Fourier has been used, phenology data are often
133 comparatively short and collected at low resolution due to the costs and effort incurred.
134 However, in the field of movement ecology, Wittemyer et al. (2008) and Polansky et al.
135 (2010) successfully used Fourier to confidently identify regular cycles in animal
136 movements by comparing outputs with a null hypothesis of random movement and
137 95% confidence intervals.
138 In this paper we build on Wittemyer et al.'s (2008) analytical framework to extend the
139 existing uses of Fourier for the field of long-term phenology research. First we
140 demonstrate appropriate application of Fourier to phenology data by quantifying
141 flowering cycle confidence, length, power, timing and ***synchrony*** for individuals of a
142 single species from the Lopé long-term observational study of tropical forest plants
143 (1986 – 2016). Second, we up-scale this Fourier-based approach to analyse flowering
144 phenology using newly available data for all species from the Lopé study (856
145 individuals, 70 species). Third, we recognize that while the Lopé study is one of the
146 longest and most consistent of its kind in the tropics, data is still often noisy or short for
147 certain individuals and/or species. In order to apply this framework elsewhere, and to
148 inform best practice for data collection, we test the ability of the Fourier method to

149 detect regular phenology under different scenarios using both simulated data and field
150 data with realistic noise.

How to detect and describe flowering cycles using Fourier analysis

The Lopé long-term observational phenology study.

Since 1986, researchers from the Station d'Études des Gorilles and Chimpanzées (SEGC), Lopé National Park, Gabon, have observed individual plants of 88 different species each month and noted the proportion of each canopy covered by new, mature and senescing leaves, flowers, unripe and ripe fruits. Canopy coverage for a particular phenophase is assessed from the ground using binoculars and recorded as a score from 0 to 4. The study area experiences an equatorial climate, where seasonality is determined by movements of the inter-tropical convergence zone to form two dry and two wet seasons annually. See Tutin and White (1998) for detailed site description including local climate and vegetation.

In this first section we demonstrate Fourier analysis using flowering data for tree species *Duboscia macrocarpa* Bocq. (Malvaceae, n=11). Initial observation of species-level data shows no apparent seasonality in flowering (figure 1a-b). However this is because the true flowering cycle for this species is 18 months long and is not synchronised between individuals. This unusual reproductive phenology is useful to demonstrate the explicitly circular basis of Fourier analysis, and how analysis at the individual-level allows for quantification of complex tropical phenology. R scripts are provided in supporting information (S6) and follow this description.

Data input requirements

For all Fourier analyses we used the function *spectrum* from the R base package '*stats*' (R Core Team 2015). The method requires regular time intervals between observations, so we interpolated data for gaps up to three data points long using a simple linear estimator, *interpNA* from R package '*timeSeries*' (Rmetrics Core Team et al. 2015). For

longer gaps we suggest analysing time series in separate parts but more sophisticated forms of interpolation could be used or Lamb normalized periodogram analysis (Press et al. 1992) which allows for unevenly spaced data.

The periodogram

The Fourier transform decomposes a time series into a series of ***sine and cosine waves*** of differing ***frequencies***, quantifying the power of each via the ***spectral estimate***, visualised in the ***periodogram*** (Figure 1c). The shortest possible cycle for our data is two months long (twice the observation interval) and the longest is the full length of the data available. Cycles not well supported by the data have low power while cycles well supported by the data have high power.

Smoothing the spectral estimate

The ***raw*** (unsmoothed) ***spectral estimate*** shows all fine-scale structure and can be overly influenced by certain segments of data. We smooth all spectral estimates using a moving-average smoother - the modified ***Daniell kernel*** - available within function *spectrum*. The width of the Daniell kernel (known as the ***span***) is user-specified and is a compromise between ***resolution*** and ***stability***. The classic text on this method (Bloomfield 2000) recommends a trial and error approach for span-choice relying on visual observation of the periodogram. After much experimentation we found that successively applying the Daniell kernel to achieve a smoothed spectral estimate with a ***bandwidth*** close to 0.1 gave sufficient resolution to identify ***dominant peaks*** in the periodogram. For example, applying a Daniell kernel with a span of seven, followed by a kernel with a span of nine to the first *D. macrocarpa* flowering time series of length 353 months (figure 1b) resulted in a spectral estimate with bandwidth 0.099. Spans to achieve this resolution vary depending on initial time series length; we provide

appropriate spans for data ranging from 24 to 360 months in S6 (line 160). ***Smoothed spectral estimates*** derived from Fourier analysis of flowering data for five example *D. macrocarpa* individuals are shown in figure 1c.

Identifying dominant cycles

Interpreting the periodogram begins with observing the general shape of the ***spectrum*** (e.g. is the data influenced by short or long cycles) and then to identify the peaks with highest power, representing ***dominant cycles*** within the data. The smoothed spectral estimates derived from flowering data for *D. macrocarpa* show a similar pattern between individuals (figure 1c). The highest peak for each individual is near to 0.056 cycles per month (equivalent to a cycle length of 18 months).

Assigning confidence to dominant cycles

Tree phenology studies often rely on monthly canopy observations and are subject to both measurement error (observation uncertainty) and natural variation (process uncertainty). Because of these uncertainties a measure of confidence is needed to differentiate real cycles from the surrounding noise. Bloomfield (2000) suggests that spectral estimates approximate a chi-square distribution, and that 95% confidence intervals can be derived as follows,

$$\frac{v\hat{s}(f)}{\mathrm{X}^2_v(0.975)} \leq s(f) \leq \frac{v\hat{s}(f)}{\mathrm{X}^2_v(0.025)}$$

Eqn. 1

where v is the degrees of freedom (derived from the function output), $\hat{s}(f)$ is the spectral estimate, $s(f)$ is the true spectrum, and $\mathrm{X}^2_v(0.975,0.025)$ are the 2.5% and 97.5% quantiles of the chi square distribution with v degrees of freedom.

There are two credible null hypotheses - representing ”no cyclicity” - with which to compare the 95% confidence intervals. The first is the ***null continuum*** of the spectrum, which is an extreme smooth of the spectral estimate such that only the underlying shape remains (dotted line, Figure 1d). The second is simply the mean spectrum (otherwise known as the white noise spectrum; Meko 2015). We prefer the null continuum as its use results in fewer false positive results at medium to high noise scenarios (S2).

We found we could achieve sufficient smoothness for the null continuum by successively applying the Daniell kernel to give a bandwidth similar to 1 (S1 line 160). Where the lower confidence interval for a specified frequency does not overlap with the null hypothesis, the peak at that frequency can objectively be considered as significantly different from the surrounding noise and representing a real cycle. Bloomfield (2000) cautions against general fishing expeditions for significant peaks because the 95% confidence intervals calculated are not simultaneous. We therefore, only recommend using this method to test the dominant peak, not all local peaks. Occasionally we find that when data are highly irregular, the dominant peak is identified at the longest possible cycle length and is likely to score as “significant” against the null continuum. To avoid these false positive results, we screen Fourier outputs and exclude dominant cycles greater than half the data length.

95% confidence intervals for the smoothed spectral estimate derived from one example *D. macrocarpa* time series are shown in figure 1d. We can be confident that the dominant peak at 18 months represents a real flowering cycle because the lower confidence interval doesn’t cross the null continuum.

Assessing timing and synchrony

In order to assess timing and synchrony within populations, we developed a method to reference the peak events of tropical phenological cycles in time using a simulated cosine curve within ***co-Fourier analysis***. Co-Fourier allows simultaneous Fourier analysis of any two time series and in addition to normal outputs, gives an estimate for the lag (***phase difference***) between the time series for every possible cycle. Once a dominant cycle has been detected in an empirical time series, we simulate a cosine curve with matching cycle length, by convention for our data peaking on 1st January 1986. After co-Fourier analysis of the empirical time series alongside the matching simulated time series, we then extract the phase difference associated with the dominant cycle.

In figure 1e we show flowering data for an example *D. macrocarpa* individual alongside a simulated cosine curve with matching cycle length (18 months) and peaking on January 1st 1986. The phase difference between these two time series at the dominant cycle of 18 months is 2.11 ***radians***.

Phase difference can be converted to time (an estimate of the first flowering peak, in months since January 1st) by the following,

$$if\ \Phi_{radians} > 0, \qquad \Phi_{months} = \frac{\Phi_{radians}}{(2\Pi/\lambda)}$$

$$if\ \Phi_{radians} < 0, \qquad \Phi_{months} = \frac{\Phi_{radians} + 2\Pi}{(2\Pi/\lambda)}$$

Eqn. 2

where Φ is the phase difference and $\boldsymbol{\lambda}$ is ***wavelength*** in months.

It is important to consider that radians are a circular unit and there are 2Π radians in a full cycle no matter how many months are in that cycle. Converting phase to months is

very simple when the cycle is annual: one month = $2\Pi/12$ and the first peak month will be the only peak month in a given calendar year. However, for cycle lengths other than 12 months, conversion to time will need some careful thought. For a six-month cycle, we would expect two peaks in each calendar year, and for an 18-month cycle we would expect one peak a calendar year but in different months in alternate years.

For the *D. macrocarpa* time series used as an example in Figure 1e, the phase difference of 2.11 radians converts to six months since January 1st, placing the first peak at the beginning of July. The next peak in flowering will occur 18 months later, at the beginning of January. We would expect this individual to have flowers in January and July in alternate years.

Calculating mean timing and synchrony for species

Mean phenophase timing can be computed for a sample with the same dominant cycle by taking the ***circular mean*** of the phase difference (in radians) for each individual, as calculated from co-Fourier analysis. Synchrony can be quantified by taking the ***circular standard deviation*** of the mean phase (all circular values calculated using the R package '*circular*' (Agostinelli & Lund 2013)). For the *D. macrocarpa* example, mean phase difference for all individuals with significant dominant cycle at 18 months is 0.94$\pm$ 1.68 SD radians. Converted to time, this references a flowering peak in mid-March and mid-September in alternate years. However synchrony between individuals is so low (SD of peak month is 4.8 months) that "peak flowering" for the population has little biological meaning.

In S4 we include a detailed description of Fourier analysis for the flowering cycles of two additional species (*Antidesma vogelianum Muell. Arg.* flowering on a six-month

cycle, and *Pentadesma butyracea Sabine* flowering on an annual cycle) and a comparison of Fourier alongside four other commonly used methods for seasonal phenology analysis – graphical representations, circular statistics, autocorrelation analysis and GAMs.

Scaling up – quantifying flowering phenology among many individuals and species

Methods

We used the methods developed above to quantitatively describe flowering data for all species monitored as part of the Lopé study. We preselected 856 individuals (70 species of 26 families) with the following criteria; greater than five years continuous data, at least one flowering event and no persistent records of disease (species list given in S3). Where we found isolated gaps longer than three months, we excluded data before or after (whichever was shorter) from further analysis. Linear interpolation for gaps shorter than three months was necessary for 95% of the individuals in the sample. Time series' length ranged from 60 to 353 months (mean = 249 months).

To quantitatively describe regular cycles, we ran Fourier analysis and a confidence test of the dominant flowering cycle for each tree. To allow comparison between individuals for the power of the dominant cycle, we normalised the spectrum so that the mean power across frequencies was equal to one (Polansky et al. 2010).

To summarise at the species-level we calculated the modal cycle length for species with more than five individuals with significant dominant cycles. To estimate the level of synchrony at the species-level, we ran co-Fourier analysis for each individual with a significant dominant cycle equal to the modal cycle length for that species (only

311 including species with more than five such individuals). From the co-Fourier outputs we
312 calculated the standard deviation of mean phase difference in radians and converted to
313 months using Eqn. 2 for each species.
314 We present whole sample summaries for time series length and sample size per species
315 and compare these between all individuals and those for which we could detect
316 significant cycles. We then present the most common flowering cycles and level of
317 synchrony (standard deviation of mean phase difference) per species. We also tested
318 the impact of time series length as a predictor of detecting significant regular phenology
319 using a binomial Generalized Linear Mixed Model (GLMM) with species as a random
320 effect.

321 ## Results

322 We detected significant regular flowering cycles for 509 out of 856 individuals in our
323 sample, 79% of which were annual. Of those for which we could not confidently detect
324 regular cycles, 22 came from five species for which no significant cycles were detected
325 (e.g. *Baillonella toxisperma Pierre* and *Dacryodes normandii nornandii Aubr. & Pell.,* S3:
326 Table 2).
327 When only trees with significant cycles were included, the sample distribution shifted
328 toward longer time series (Figure 2a), and mean sample size per species for all trees (12
329 individuals $\pm$ 8.1 SD) was reduced (seven individuals $\pm$ 5.8 SD) (Figure 2b). We found
330 time series' length to be a significant positive predictor (z value = 6.42, $p<0.001$) of the
331 likelihood of detecting a significant regular cycle from the data (GLM outputs in S5).
332 To assess modal cycle length we used a subsample of 42 species (458 individuals). The
333 modal flowering cycle for most species was annual (37 species, e.g. *P. butyracea,* S4),

with others flowering on a 6-month (4 species, e.g. *A. vogelianum,* S4) and an 18-month basis (1 species, *D. macrocarpa,* S4) (Figure 2c, Figure 3 and S3: Table 2).

To assess modal level of synchrony between species we used a subsample of 39 species (402 individuals). The majority of species had flowering cycles well synchronised between individuals, (38 species with standard deviation of mean peak less than one month) (Figure 2d, S3: Table 2).

Species showed considerable inter- and intra-specific variation in flowering phenology (Figure 3). Some species were split between different cycle length strategies; e.g. for a sample of 19 *Uapaca guieensis Muell. Arg.* trees, the dominant flowering cycle was annual for 13 trees and six months for six trees. Species also varied in the power of their dominant flowering cycles. Despite all individuals shown in Figure 3 having significant flowering cycles, some species such as *Maranthes glabra (Oliv.) Prance* (mean power = 9.3±1.6 S.D.) and *Xylopia aethiopica (Dunal) A. Richard* (mean power = 8.1±2.6 S.D.) tended to have much stronger, less noisy cycles than others such as *Klainedoxa gabonensis Baill.* (mean power = 2.1±0.4 S.D.) and *Pseudospondias microcarpa (A Rich.) Engl.* (mean power = 2.4 ±0.7 S.D.) (S3: Table 2).

Testing Fourier under different scenarios using both simulated and field data

Methods

To test the impact of noise and sample length on cycle detectability, we undertook a power analysis of simulated phenology data. We simulated 10,000 individual time series representing an annually repeating flowering cycle peaking in June, with three

357 key parameters allowed to vary between “individuals”; 1) the regularity of the peak
358 month (representing process uncertainty), 2) the detectability of flowering events
359 (representing observation uncertainty) and 3) the length of data recorded. For each
360 year of data, we generated monthly flowering scores of zero and a peak of three-months
361 duration with positive scores randomly chosen from a distribution similar to that found
362 in our field data. We varied levels of regularity by randomly choosing the peak
363 flowering month each year from a truncated normal distribution (ranging from two to
364 11, with mean six and standard deviation randomly selected from 0.1 to six). The
365 standard deviation of the distribution was consistent between years but allowed to vary
366 between individuals. We then varied levels of detectability by replacing a certain
367 percentage of randomly chosen positive flowering scores with zeros (from zero to
368 60%). Finally, a window of data (five, ten or 15 years) was randomly cut from each full-
369 length time series prior to Fourier analysis (example simulated data are plotted in S2).
370 We assessed the dominant cycle using a 95% confidence test and whether it fell within
371 the expected interval for an annual cycle (11-13 months).
372 To demonstrate the impact of data length with realistic noise we also conducted a
373 power analysis using all individual time series from the Lopé study longer than 20
374 years, from which we had previously detected significant annual flowering cycles and
375 for species with more than five such individuals (233 individuals of 30 different
376 species). We randomly chose individual time series from this sub-sample and cut
377 shorter windows of data (window length randomly selected from the range 2:20 years
378 with randomly selected start date), repeating 10,000 times. We analysed the windowed
379 time series with Fourier as described above and recorded if the dominant cycle was
380 significant and fell within the expected interval for an annual cycle (11-13 months). We
381 fitted binomial GLMs to compare the effect of time series’ length between species.

Results

The power analysis of simulated phenology data (Figure 4) showed that as time series' length increased, from 5 to 15 years, so did likelihood of confidently detecting the annual cycle. For example, for a mid-level noise scenario (cycle regularity 2SD; zero replacement 20%) the proportion of the sample with a significant annual cycle was zero after 5 years, 57% after 10 years and 81% after 15 years. However, at relatively low-noise scenarios, (highly regular cycles <1SD; low zero replacement < 20%), the effect of time series length saturated quickly, with 100% likelihood of detecting a significant annual cycle after just five years. In contrast at high-noise scenarios (highly irregular cycles >4SD; zero replacement > 60%), likelihood of detecting a significant annual cycle never rose above 20% even after 15 years. For highly regular cycles (SD<2), even poor event detectability (zero replacement 40 – 60%) had little impact on likelihood of detecting the cycle.

Similar to the simulated data, we found that as time series' length increased, so did likelihood of detecting regular cyclic behaviour for our field data (Figure 5). We found that for the species in our sample with the most positive slope estimates for time series length (*M. glabra and Pycnanthus angolensis Welw.) Warb.,* S5), just six and seven years of data respectively were required before the annual flowering cycle could be detected with greater than 95% likelihood. However species ranged widely, with 19 species not reaching this 95% threshold until after 20 years. The species with the least positive slope estimates were *Detarium macrocarpum Harms* and *Greenwaydodendron suaveolens Engl. & Diels.* (S5).

Discussion

Detectability and power

The flowering phenology of trees observed at Lopé National Park, Gabon, is dominated by annual cycles (88% species), in contrast with forests from the neotropics that appear to be dominated by sub-annual reproductive cycles and the Dipterocarp forests of South-East Asia that are dominated by supra-annual reproductive cycles (Sakai 2001). We could not confidently describe regular cycles for many individuals in our sample (41%), where either flowering is regular but the data were too noisy or too short for detection or glowering is irregular. Observation length was shown to be a significant positive predictor of detecting regular cycles in both field data and simulations. Even when cycles were confidently described, we found that the power attributed to cycles ranged widely, meaning that the flowering phenology of some species is much noisier than others. However the source of this noise is difficult to differentiate for field data. To explore this further we simulated two forms of noise associated with both process and observation uncertainty and found that cycle regularity has a greater effect on ability to detect a significant cycle than event detectability: Fourier analysis can be used to detect the cycle even if the observer misidentifies 60% of flowering months. There are likely to be additional sources of noise in the field, such as false recording of non-existent phenophases, however we consider these to occur less often.

We attributed cycle characteristics to the species-level when we had five or more individuals with significant cycles, under the biological assumption that phenology is an evolutionarily adaptive trait and likely to be constraining con-specifics in a similar way. However, true levels of intraspecific variation are unknown. We find considerable intraspecific variation for some species (i.e. *Uapaca guineensis*) and further research

429 may reveal that phenology is not necessarily a stable trait within a species or an
430 individual's lifetime.

431 Our results can be used to inform effective collection, processing and analysis of
432 phenological data. We have shown that where suitable data is available, objective
433 analyses can be used to confidently detect regular phenology and that frequency-based
434 outputs – cycle length, power, timing and level of synchrony – give a suite of indicators
435 that could be used to quantitatively describe and compare phenology globally.

436 ## Development for causation and change research

437 The indicators derived from Fourier analysis can be used to address research questions
438 such as the proximate and ultimate causes of adaptive phenology and detection of
439 change. Where data is available, analysis at the individual-level allows for inclusion of
440 covariates (e.g. location, age, size of individuals etc.) in subsequent statistical models,
441 either in combination with random effects and best linear unbiased predictors (BLUPs)
442 to account for variation (for example between different sites, genera or functional
443 groups) or as fixed effects to test hypotheses of the causes of variation between
444 individuals' phenology. Co-Fourier analysis would allow testing of other cyclic factors
445 (such as climate data) alongside phenology to measure synchrony. The advantage of
446 these spectral approaches is that they explicitly model the circular nature of phenology
447 and weather data without losing power by clumping data points into arbitrary time
448 periods or pseudo-replication.

449 Detecting long-term changes in phenology is challenging and field observations
450 (Plumptre 2011) are vital to stimulate hypotheses and further analysis. However it will
451 be increasingly important to measure the statistical confidence of detected changes. To
452 date, studies of change in tropical phenology are few (S1), due to the paucity of long-

453 term data. Wavelet analysis is the natural extension of Fourier into the time-frequency
454 domain (Hudson et al. 2010; Polansky et al. 2010; Wittemyer et al. 2008), overcoming
455 assumptions of stationarity, to estimate the spectrum as a function of time (Cazelles et
456 al. 2008). For phenology research, this could enable analysis of whether individuals or
457 species reproduce more or less frequently (e.g. change in dominant cycle length),
458 reproduce at the same frequency but with more or less certainty (e.g. change in the
459 power of the dominant cycle) or shift phase and become more or less synchronised over
460 time. The power of a cycle may be a more subtle and effective indicator for change than
461 frequency to track increasing uncertainty over time, especially in the shorter term.
462 In a formal comparison of this Fourier-based method with other commonly used
463 methods for quantifying phenology (S4), we found Fourier is flexible to diverse
464 phenology and provides a suite of quantitative information to describe seasonal activity
465 with attribution of variance and confidence.

466 ## Steps forward

467 We have shown that at least six years of data are necessary to confidently detect
468 reproductive cycles amongst our species sample. For data-collection scenarios resulting
469 in noisier data – those with high likelihood of measurement error (e.g. inconspicuous
470 flowers), systematic error (e.g. high inter-observer uncertainty) or natural variation
471 that cannot be controlled for (e.g. diverse array of phenological responses within a
472 population) – it will be necessary to invest in large samples of individuals over a longer
473 time period to detect cycles confidently. To effectively monitor the response of tropical
474 forests to global change, it will be necessary to focus efforts on suitable indicator
475 species – those with good signal to noise ratios - to maximise analytical power over
476 relatively short time periods.

For many phenology research questions, collecting sufficient data will be a challenge and require significant research effort. Ways to achieve this include: formation of research networks and greater coordination of methods and objectives between sites, internet-based citizen-science data collection networks and technical solutions to data collection, such as automated canopy photography and GIS.

Conclusions

Phenology is a key adaptive trait shown to determine species distributions (Chuine 2010) and as such will shape how ecosystems respond to rapidly increasing regional and global changes including human pressure. With the emergence of long-term tropical phenology data, the need also emerges for appropriate analytical methods to improve our understanding of the functioning of ecosystems. We present a Fourier-based method that can be further developed and tested, to give simple, flexible and quantifiable indicators for phenology activity, and demonstrate the importance of consistent long-term investment in phenological research.

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Data Accessibility:

R scripts: uploaded as online supporting information

Individual- and species-level flowering data: University of Stirling's DataSTORRE (https://datastorre.stir.ac.uk) doi: XXXX

Author contributions:

EB, NB, KA and AJ conceived the ideas for this manuscript; CT, LW and KA designed the field methodology; ED, JTD, CT, KA, LW and KJ collected the data; EB, NB and KA analysed the data; EB, NB, KA and AJ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

S1: Review of methods from the literature

Review of key literature analysing long-term tropical plant phenology data, detailing the phenophase of interest, site, data length, analytical methods used and the scale of data collection and analysis.

S2: Null hypothesis choice and example simulated data

Power analysis of simulated data to show the impact of null hypothesis choice (null continuum vs. white noise spectrum) for detecting periodicity.

S3: Species list from Lopé long-term phenology study

List of families (n=26), species (n=70) and individuals (n=856) observed as part of the Lopé long-term phenology study included in Fourier analysis and summarised Fourier outputs at the species level.

S4: Demonstration of Fourier analysis and comparison with other methods

Demonstration of Fourier analysis for three case study species - *Antidesma vogelianum, Pentadesma butyracea, Duboscia macrocarpa* - and comparison with other common methods for quantifying flowering phenology.

S5: GLM outputs

GLM outputs for effect of time series length on likelihood of detecting significant cycle from all available field data and from power analysis of annually cycling species.

S6: R code for Fourier analysis of phenology

631 **Table 1: Glossary to technical terms**

Term	Definition
Bandwidth	The distance at which two peaks in the ***periodogram*** can be distinguished from each other, a quantitative measure of ***resolution***. For example a bandwidth of 0.1 means that cycles can be distinguished from each other when the difference between their frequencies is at least 0.1.
Circular mean	A mean value calculated for ***circular data*** where the arithmetic mean would be inappropriate. For example, the circular mean of 5° and 355° is 0°, in comparison to the arithmetic mean which is 180°.
Circular standard deviation	A measure of dispersion calculated for ***circular data*** where the arithmetic standard deviation would be inappropriate.
Circular data	Data from circular distributions (e.g. months, hours, directions etc.) where there is no true zero and "high" and "low" values are arbitrary (e.g. Figure 1a).
Co-Fourier analysis	Simultaneous ***Fourier analysis*** of two ***time series***. Additional outputs include relative ***phase difference*** between the time series at every possible ***cycle*** (Figure 1e).
Cycle	A pattern of repeating events in a regular order
Cycle length / ***Wavelength***	The time taken for a whole ***cycle*** to repeat itself (e.g. number of months between repeating flowering events)
Daniell kernel	A moving-average smoother used to eliminate fine detail from the ***raw spectral estimate*** to make the output more ***stable*** and easier to interpret (e.g. ***smoothed spectral estimate*** in Figure 1c)
Dominant cycle	The ***cycle length*** associated with the ***dominant peak***.
Dominant peak	The point in the ***spectral estimate*** with highest ***power***
Fourier analysis	Decomposition of a ***time series*** into a series of ***sinusoidal*** functions. The ***power*** of each ***cycle*** in the series can be used to identify ***dominant cycles*** (Figure 1c).
Frequency	The rate at which something occurs (e.g. number of flowering cycles per month or per year)
Null continuum	A ***spectral estimate***, derived from the data series, that has been smoothed extensively so that only the underlying shape remains, and no fine detail can be identified (Figure 1d).

Periodogram	The visual output of the ***spectral estimate*** derived from ***Fourier analysis*** (Figure 1c-d)
Phase difference	The distance between the peaks in two ***cycles*** of matching ***frequency*** and referenced in time (Figure 1e).
Power	The relative tendency of all possible ***cycles*** to appear in the data. Estimated in the ***spectral estimate*** and plotted in the y-axis of a ***periodogram*** (Figure 1c). Cycles not well supported by the data have low power, while cycles well supported by the data have high power
Radians	The standard unit of angular measures; 2π radians = 360°.
Raw spectral estimate	The default output of ***Fourier analysis*** where all fine-scale structure is included, and can be overly influenced by certain segments of the data.
Resolution	The ability to represent fine structure and distinguish between close peaks in the ***spectral estimate*** derived from ***Fourier***, quantified as the ***bandwidth*** (Bloomfield 2000). Spectral estimates with high resolution will show all peaks including minor ones, where as spectral estimates with very low resolution may show no peaks at all, but rather the general shape of the data (e.g. the ***null continuum*** in Figure 1d). Increased resolution reduces stability and visa versa.
Sinusoid / Sine wave / Cosine wave	A smooth repeating pattern occurring every 2π radians (or 360°) (e.g. the simulated curve in Figure 1e).
Smoothed spectral estimate	The output of ***Fourier analysis*** after a moving-average smoother is applied to the ***raw spectral estimate*** (Figure 1c-d).
Spans	The user-specified widths of the ***Daniell kernel*** smoother, specifically how many data points are used to smooth the ***spectral estimate*** in each local window.
Spectral estimate / Spectrum	The output of ***Fourier analysis*** showing the tendency of all possible ***cycles*** to appear in the data, from twice the observation interval to the full length of the series (Figure 1c-d).
Stability	Extent to which small fluctuations in certain segments of the data influence the ***spectral estima***te derived from ***Fourier***. Greater stability reduces ***resolution*** and visa versa. (Bloomfield 2000).
Synchrony	The simultaneous occurrence of two or more events.
Time series	A sequence of data points arranged in time order

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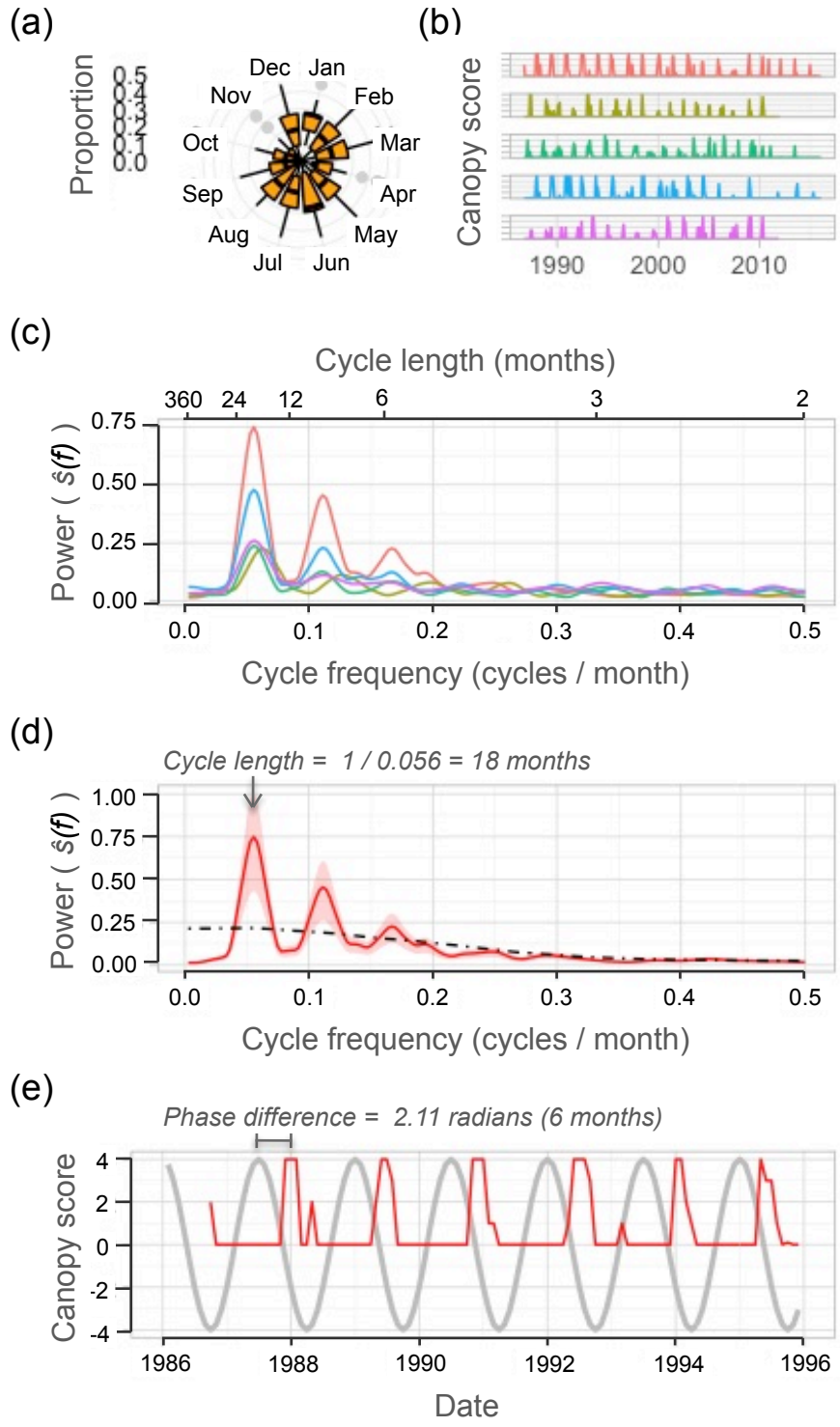


633

634 **FIGURE 1: Using Fourier analysis to detect flowering phenology for a single**

635 **species *Duboscia macrocarpa*.**

636 a) Boxplots showing the proportion of individuals (n=11) in flower each month from

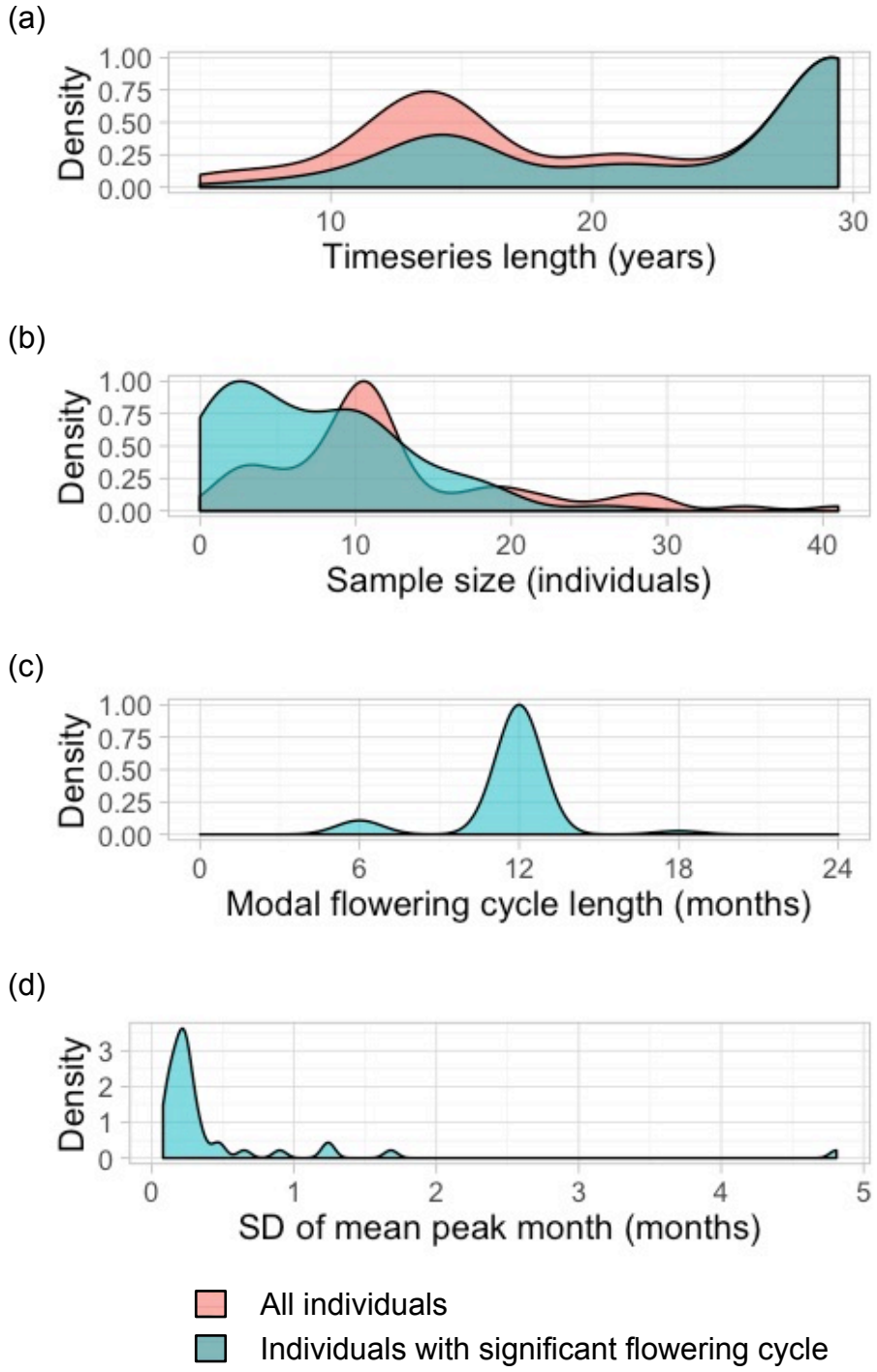
637 1986 to 2016. There is no obvious seasonal flowering pattern for this species.

b) ***Time series*** plots showing flowering canopy scores every month since 1986 to 2016 (five individuals shown as an example). There appears to be some regular flowering cycles for individuals.

c) ***Periodogram*** displaying the ***smoothed spectral estimates*** (***bandwidth***=0.1) derived from ***Fourier analysis*** for each individual flowering time series in (b). The x-axis of the shows all possible cycle ***frequencies*** (from one cycle every two months to the full length of the series). The y-axis shows the ***power*** of each cycle. The highest peak in each ***spectrum*** occurs at a frequency of 0.056 cycles per month (indicating a flowering cycle length of 18 months).

d) Periodogram displaying smoothed spectral estimate derived from Fourier analysis for the first flowering time series shown in (b) (red line). The 95% confidence intervals for the spectral estimate (red shades) show that the ***dominant peak*** (grey arrow) at 0.056 cycles per month is different from the null hypothesis of no cyclicity (the null continuum: black dashed line). We can be confident that the 18-month cycle is different from surrounding noise and represents a real flowering cycle.

e) Demonstration of ***co-Fourier*** analysis to derive the relative phase of the flowering cycle identified in (d). The flowering time series (red line) is decomposed alongside a regular ***cosine curve***, simulated to have the same ***cycle length*** as the flowering data (18 months) and by convention for our data peaking on the 1st January 1986 (grey line). The ***phase difference*** (2.11 ***radians***) between the two time series can be converted to time (6 months).



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662 **FIGURE 2: Summary of flowering phenology for all tree species monitored at Lopé**

663 **NP, Gabon.**

664 a) Density plot of time series' length for all individuals analysed (red, 856

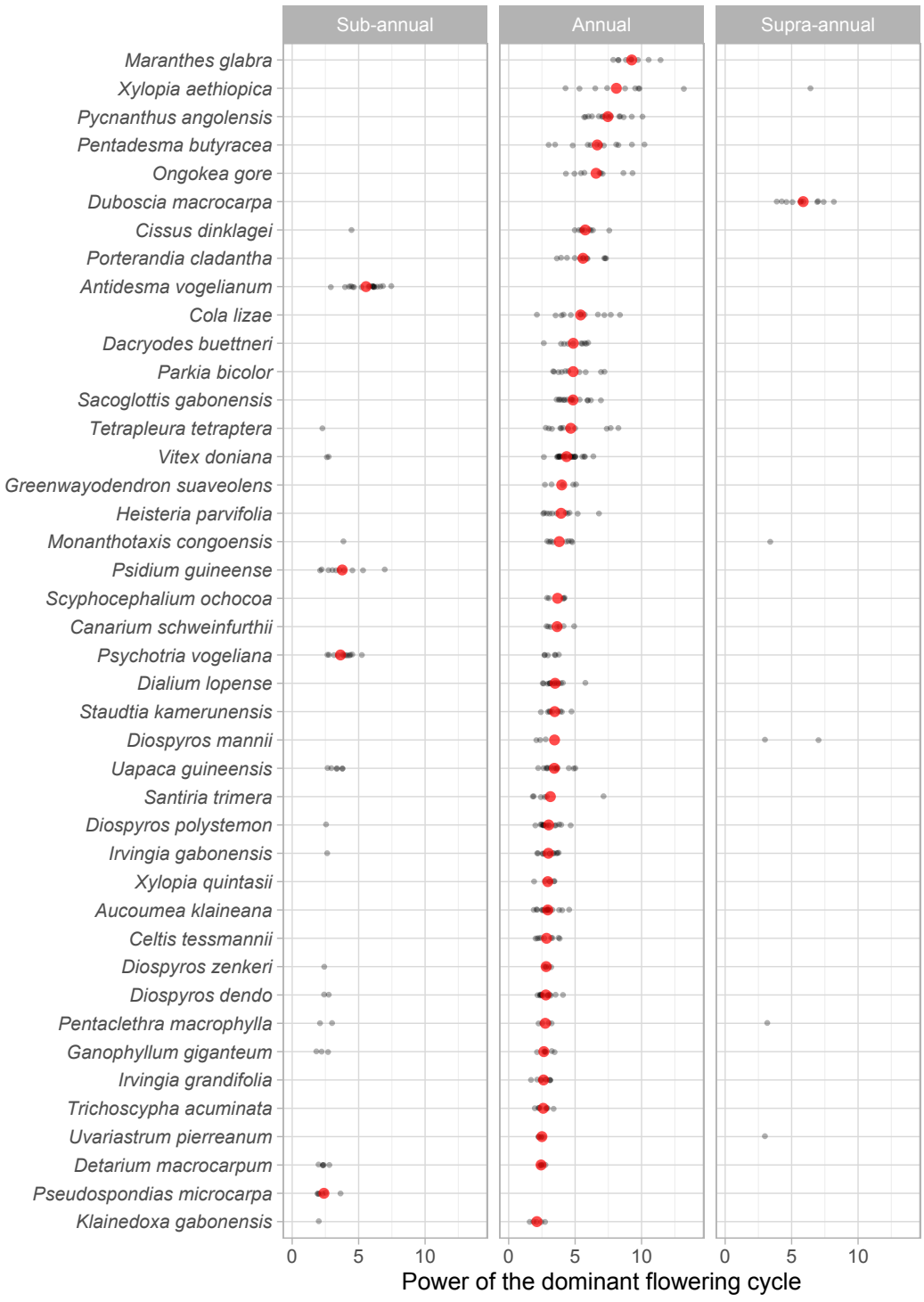
665 individuals) compared to individuals with significant flowering cycles (blue, 509

666 individuals).

b) Density plot of number of individuals per species for all individuals (red, 856 individuals, 70 species) compared to individuals with significant flowering cycles (blue, 509 individuals, 65 species).

c) Density plot of most common flowering ***cycle length*** (mode) per species, for a subsample of 42 species, each more than five individuals with significant flowering cycles (458 individuals).

d) Density plot of ***synchrony*** (standard deviation of mean peak month) per species, for a subsample of 39 species, each with more than five individuals with significant dominant cycle equal to the species modal cycle length (402 individuals).



679

680 **FIGURE 3: Inter- and intra-specific variation in flowering phenology for tree**

681 **species monitored at Lopé NP, Gabon.**

682 ***Cycle length*** (sub-annual, annual and supra-annual) and ***power*** for each individual

683 (grey dots) and modal cycle length and mean power per species (red dots) from a sub-

684 sample of 42 species with more than five individuals with significant flowering cycles

685 (458 individuals).

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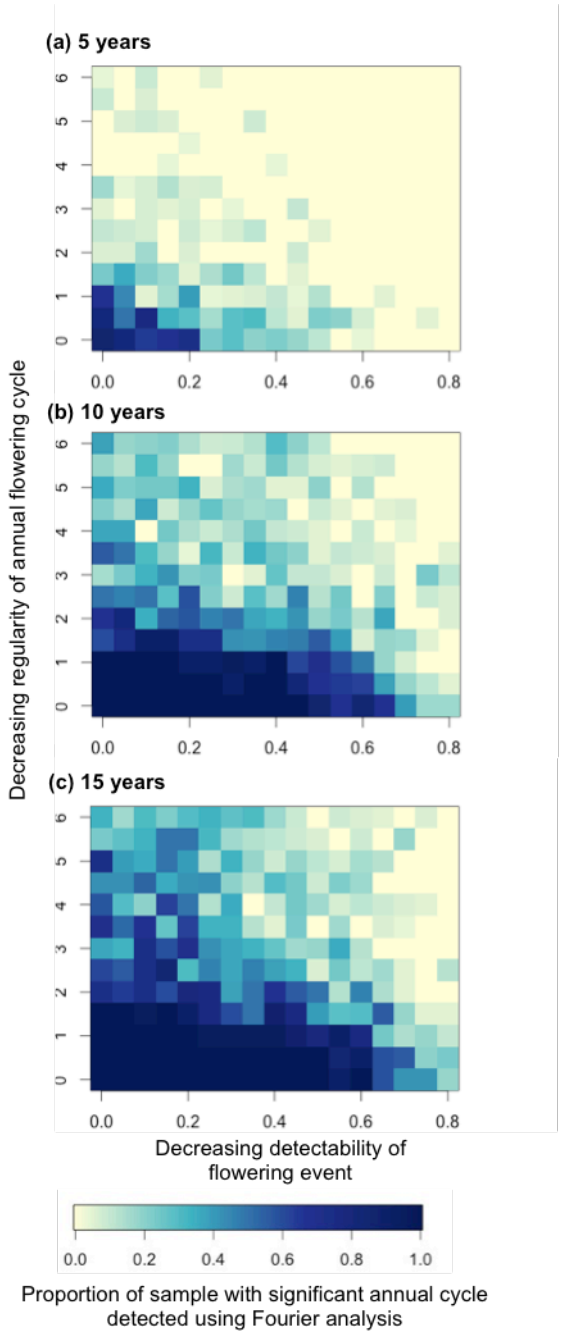

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689 **FIGURE 4: Power analysis of simulated phenology data (n=10,000) to show the**

690 **impact of data noise and length (5, 10 and 15 years; (a)-(c)) on likelihood of**

691 **detecting cycles using Fourier analysis**.

692 Noise simulated as cycle regularity (y-axis: standard deviation - 0.1: 6 - of mean month

693 of annual flowering event) and event detectability (x-axis: proportion – 0: 60% - of

694 positive flowering events replaced by zeros).

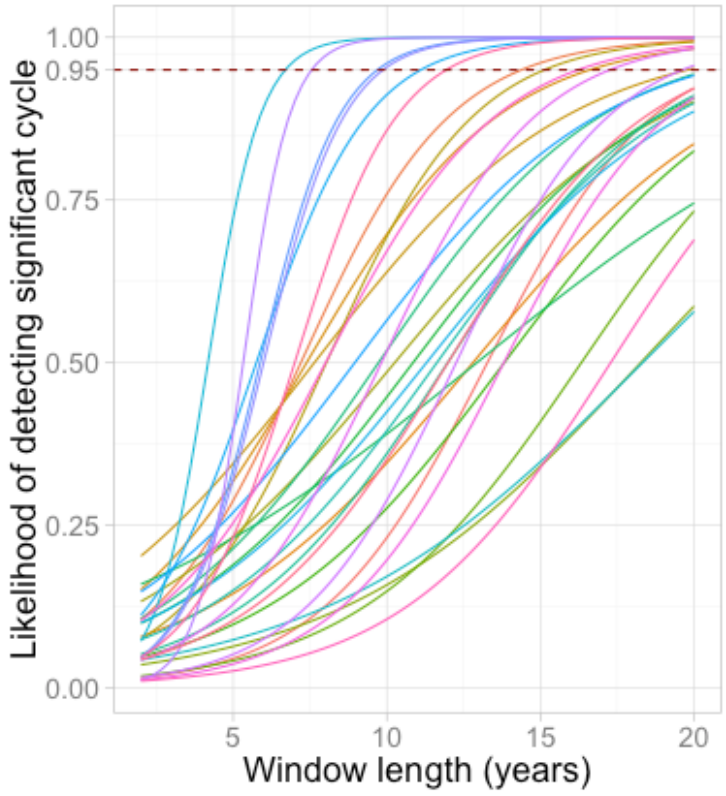

FIGURE 5: Power analysis of annually flowering phenology data from Lopé NP to show the impact of time series length (2-20 years window length) on cycle detection using Fourier analysis (10,000 random samples from 233 individuals of 30 species). Generalised linear model (GLM) predictions (family=binomial, link=logit) for each species (see S5, for species key and GLM outputs).

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