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1 **Fourier analysis to detect phenological cycles using tropical**

2 **field data and simulations**

3 Fourier analysis for long-term phenology

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16

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.

41 4. There are now a number of large phenology datasets from the tropics, from

42   which insights into current regional and global changes may be gained, if flexible

43   and quantitative analytical approaches are used. However consistent long-term

44   data collection is costly and requires much effort. We provide support for the

45   importance of such research and give suggestions as to how to avoid erroneous

46   interpretation of shorter length datasets and maximize returns from long-term

47   observational studies.

48

49 Key-words:

50 Flowering; Phenophases; Spectral analysis; Tropical forests; Gabon; Time-series data;

51 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 et 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

175 longer gaps we suggest analysing time series in separate parts but more sophisticated

176 forms of interpolation could be used or Lamb normalized periodogram analysis (Press

177 et al. 1992) which allows for unevenly spaced data.

The periodogram

179 The Fourier transform decomposes a time series into a series of **sine and cosine waves**

180 of differing **frequencies**, quantifying the power of each via the **spectral estimate**,

181 visualised in the **periodogram** (Figure 1c). The shortest possible cycle for our data is

182 two months long (twice the observation interval) and the longest is the full length of the

183 data available. Cycles not well supported by the data have low power while cycles well

184 supported by the data have high power.

Smoothing the spectral estimate

186 The **raw** (unsmoothed) **spectral estimate** shows all fine-scale structure and can be

187 overly influenced by certain segments of data. We smooth all spectral estimates using a

188 moving-average smoother - the modified **Daniell kernel** - available within function

189 *spectrum*. The width of the Daniell kernel (known as the **span**) is user-specified and is a

190 compromise between **resolution** and **stability**. The classic text on this method

191 (Bloomfield 2000) recommends a trial and error approach for span-choice relying on

192 visual observation of the periodogram. After much experimentation we found that

193 successively applying the Daniell kernel to achieve a smoothed spectral estimate with a

194 **bandwidth** close to 0.1 gave sufficient resolution to identify **dominant peaks** in the

195 periodogram. For example, applying a Daniell kernel with a span of seven, followed by a

196 kernel with a span of nine to the first *D. macrocarpa* flowering time series of length 353

197 months (figure 1b) resulted in a spectral estimate with bandwidth 0.099. Spans to

198 achieve this resolution vary depending on initial time series length; we provide

199   appropriate spans for data ranging from 24 to 360 months in S6 (line 160). **Smoothed**

200   **spectral estimates** derived from Fourier analysis of flowering data for five example *D.*

201   *macrocarpa* individuals are shown in figure 1c.

202   ### Identifying dominant cycles

203   Interpreting the periodogram begins with observing the general shape of the **spectrum**

204   (e.g. is the data influenced by short or long cycles) and then to identify the peaks with

205   highest power, representing **dominant cycles** within the data. The smoothed spectral

206   estimates derived from flowering data for *D. macrocarpa* show a similar pattern

207   between individuals (figure 1c). The highest peak for each individual is near to 0.056

208   cycles per month (equivalent to a cycle length of 18 months).

209   ### Assigning confidence to dominant cycles

210   Tree phenology studies often rely on monthly canopy observations and are subject to

211   both measurement error (observation uncertainty) and natural variation (process

212   uncertainty). Because of these uncertainties a measure of confidence is needed to

213   differentiate real cycles from the surrounding noise. Bloomfield (2000) suggests that

214   spectral estimates approximate a chi-square distribution, and that 95% confidence

215   intervals can be derived as follows,

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

216   `Eqn. 1`

217   where v is the degrees of freedom (derived from the function output), $\hat{s}(f)$ is the

218   spectral estimate, $s(f)$ is the true spectrum, and $X_v^2(0.975, 0.025)$ are the 2.5% and

219   97.5% quantiles of the chi square distribution with v degrees of freedom.

220   There are two credible null hypotheses - representing "no cyclicity" - with which to

221   compare the 95% confidence intervals. The first is the ***null continuum*** of the spectrum,

222   which is an extreme smooth of the spectral estimate such that only the underlying

223   shape remains (dotted line, Figure 1d). The second is simply the mean spectrum

224   (otherwise known as the white noise spectrum; Meko 2015). We prefer the null

225   continuum as its use results in fewer false positive results at medium to high noise

226   scenarios (S2).

227   We found we could achieve sufficient smoothness for the null continuum by

228   successively applying the Daniell kernel to give a bandwidth similar to 1 (S1 line 160).

229   Where the lower confidence interval for a specified frequency does not overlap with the

230   null hypothesis, the peak at that frequency can objectively be considered as significantly

231   different from the surrounding noise and representing a real cycle. Bloomfield (2000)

232   cautions against general fishing expeditions for significant peaks because the 95%

233   confidence intervals calculated are not simultaneous. We therefore, only recommend

234   using this method to test the dominant peak, not all local peaks. Occasionally we find

235   that when data are highly irregular, the dominant peak is identified at the longest

236   possible cycle length and is likely to score as "significant" against the null continuum. To

237   avoid these false positive results, we screen Fourier outputs and exclude dominant

238   cycles greater than half the data length.

239   95% confidence intervals for the smoothed spectral estimate derived from one example

240   *D. macrocarpa* time series are shown in figure 1d. We can be confident that the

241   dominant peak at 18 months represents a real flowering cycle because the lower

242   confidence interval doesn't cross the null continuum.

243 **Assessing timing and synchrony**

244 In order to assess timing and synchrony within populations, we developed a method to

245 reference the peak events of tropical phenological cycles in time using a simulated

246 cosine curve within ***co-Fourier analysis***. Co-Fourier allows simultaneous Fourier

247 analysis of any two time series and in addition to normal outputs, gives an estimate for

248 the lag (***phase difference***) between the time series for every possible cycle. Once a

249 dominant cycle has been detected in an empirical time series, we simulate a cosine

250 curve with matching cycle length, by convention for our data peaking on 1st January

251 1986. After co-Fourier analysis of the empirical time series alongside the matching

252 simulated time series, we then extract the phase difference associated with the

253 dominant cycle.

254 In figure 1e we show flowering data for an example *D. macrocarpa* individual alongside

255 a simulated cosine curve with matching cycle length (18 months) and peaking on

256 January 1st 1986. The phase difference between these two time series at the dominant

257 cycle of 18 months is 2.11 ***radians***.

258 Phase difference can be converted to time (an estimate of the first flowering peak, in

259 months since January 1st) by the following,

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

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

260   `Eqn. 2`

261 where Φ is the phase difference and λ is ***wavelength*** in months.

262 It is important to consider that radians are a circular unit and there are 2Π radians in a

263 full cycle no matter how many months are in that cycle. Converting phase to months is

264   very simple when the cycle is annual: one month = $2\Pi/12$ and the first peak month will

265   be the only peak month in a given calendar year. However, for cycle lengths other than

266   12 months, conversion to time will need some careful thought. For a six-month cycle, we

267   would expect two peaks in each calendar year, and for an 18-month cycle we would

268   expect one peak a calendar year but in different months in alternate years.

269   For the *D. macrocarpa* time series used as an example in Figure 1e, the phase difference

270   of 2.11 radians converts to six months since January 1st, placing the first peak at the

271   beginning of July. The next peak in flowering will occur 18 months later, at the

272   beginning of January. We would expect this individual to have flowers in January and

273   July in alternate years.

274   **Calculating mean timing and synchrony for species**

275   Mean phenophase timing can be computed for a sample with the same dominant cycle

276   by taking the ***circular mean*** of the phase difference (in radians) for each individual, as

277   calculated from co-Fourier analysis. Synchrony can be quantified by taking the ***circular***

278   ***standard deviation*** of the mean phase (all circular values calculated using the R

279   package '*circular'* (Agostinelli & Lund 2013)). For the *D. macrocarpa* example, mean

280   phase difference for all individuals with significant dominant cycle at 18 months is

281   0.94± 1.68 SD radians. Converted to time, this references a flowering peak in mid-March

282   and mid-September in alternate years. However synchrony between individuals is so

283   low (SD of peak month is 4.8 months) that "peak flowering" for the population has little

284   biological meaning.

285

286   In S4 we include a detailed description of Fourier analysis for the flowering cycles of

287   two additional species (*Antidesma vogelianum Muell. Arg.* flowering on a six-month

288   cycle, and *Pentadesma butyracea Sabine* flowering on an annual cycle) and a comparison

289   of Fourier alongside four other commonly used methods for seasonal phenology

290   analysis – graphical representations, circular statistics, autocorrelation analysis and

291   GAMs.

Scaling up – quantifying flowering phenology among many individuals and species

294   ### Methods

295   We used the methods developed above to quantitatively describe flowering data for all

296   species monitored as part of the Lopé study. We preselected 856 individuals (70 species

297   of 26 families) with the following criteria; greater than five years continuous data, at

298   least one flowering event and no persistent records of disease (species list given in S3).

299   Where we found isolated gaps longer than three months, we excluded data before or

300   after (whichever was shorter) from further analysis. Linear interpolation for gaps

301   shorter than three months was necessary for 95% of the individuals in the sample. Time

302   series' length ranged from 60 to 353 months (mean = 249 months).

303   To quantitatively describe regular cycles, we ran Fourier analysis and a confidence test

304   of the dominant flowering cycle for each tree. To allow comparison between individuals

305   for the power of the dominant cycle, we normalised the spectrum so that the mean

306   power across frequencies was equal to one (Polansky et al. 2010).

307   To summarise at the species-level we calculated the modal cycle length for species with

308   more than five individuals with significant dominant cycles. To estimate the level of

309   synchrony at the species-level, we ran co-Fourier analysis for each individual with a

310   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),

16

334 with others flowering on a 6-month (4 species, e.g. *A. vogelianum,* S4) and an 18-month

335 basis (1 species, *D. macrocarpa,* S4) (Figure 2c, Figure 3 and S3: Table 2).

336 To assess modal level of synchrony between species we used a subsample of 39 species

337 (402 individuals). The majority of species had flowering cycles well synchronised

338 between individuals, (38 species with standard deviation of mean peak less than one

339 month) (Figure 2d, S3: Table 2).

340 Species showed considerable inter- and intra-specific variation in flowering phenology

341 (Figure 3). Some species were split between different cycle length strategies; e.g. for a

342 sample of 19 *Uapaca guieensis Muell. Arg.* trees, the dominant flowering cycle was

343 annual for 13 trees and six months for six trees. Species also varied in the power of their

344 dominant flowering cycles. Despite all individuals shown in Figure 3 having significant

345 flowering cycles, some species such as *Maranthes glabra (Oliv.) Prance* (mean power =

346 9.3 ± 1.6 S.D.) and *Xylopia aethiopica (Dunal) A. Richard* (mean power = 8.1 ± 2.6 S.D.)

347 tended to have much stronger, less noisy cycles than others such as *Klainedoxa*

348 *gabonensis Baill.* (mean power = 2.1 ± 0.4 S.D.) and *Pseudospondias microcarpa (A Rich.)*

349 *Engl.* (mean power = 2.4 ± 0.7 S.D.) (S3: Table 2).

350

Testing Fourier under different scenarios using both simulated and field data

Methods

354 To test the impact of noise and sample length on cycle detectability, we undertook a

355 power analysis of simulated phenology data. We simulated 10,000 individual time

356 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

383   The power analysis of simulated phenology data (Figure 4) showed that as time series'

384   length increased, from 5 to 15 years, so did likelihood of confidently detecting the

385   annual cycle. For example, for a mid-level noise scenario (cycle regularity 2SD; zero

386   replacement 20%) the proportion of the sample with a significant annual cycle was zero

387   after 5 years, 57% after 10 years and 81% after 15 years. However, at relatively low-

388   noise scenarios, (highly regular cycles <1SD; low zero replacement < 20%), the effect of

389   time series length saturated quickly, with 100% likelihood of detecting a significant

390   annual cycle after just five years. In contrast at high-noise scenarios (highly irregular

391   cycles >4SD; zero replacement > 60%), likelihood of detecting a significant annual cycle

392   never rose above 20% even after 15 years. For highly regular cycles (SD<2), even poor

393   event detectability (zero replacement 40 – 60%) had little impact on likelihood of

394   detecting the cycle.

395

396   Similar to the simulated data, we found that as time series' length increased, so did

397   likelihood of detecting regular cyclic behaviour for our field data (Figure 5). We found

398   that for the species in our sample with the most positive slope estimates for time series

399   length (*M. glabra and Pycnanthus angolensis Welw.) Warb.,* S5), just six and seven years

400   of data respectively were required before the annual flowering cycle could be detected

401   with greater than 95% likelihood. However species ranged widely, with 19 species not

402   reaching this 95% threshold until after 20 years. The species with the least positive

403   slope estimates were *Detarium macrocarpum Harms* and *Greenwaydodendron*

404   *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.

Data Accessibility:

504   R scripts: uploaded as online supporting information

505   Individual- and species-level flowering data: University of Stirling's DataSTORRE

506   (https://datastorre.stir.ac.uk) doi: XXXX

Author contributions:

508   EB, NB, KA and AJ conceived the ideas for this manuscript; CT, LW and KA designed the

509   field methodology; ED, JTD, CT, KA, LW and KJ collected the data; EB, NB and KA

510   analysed the data; EB, NB, KA and AJ led the writing of the manuscript. All

511   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.
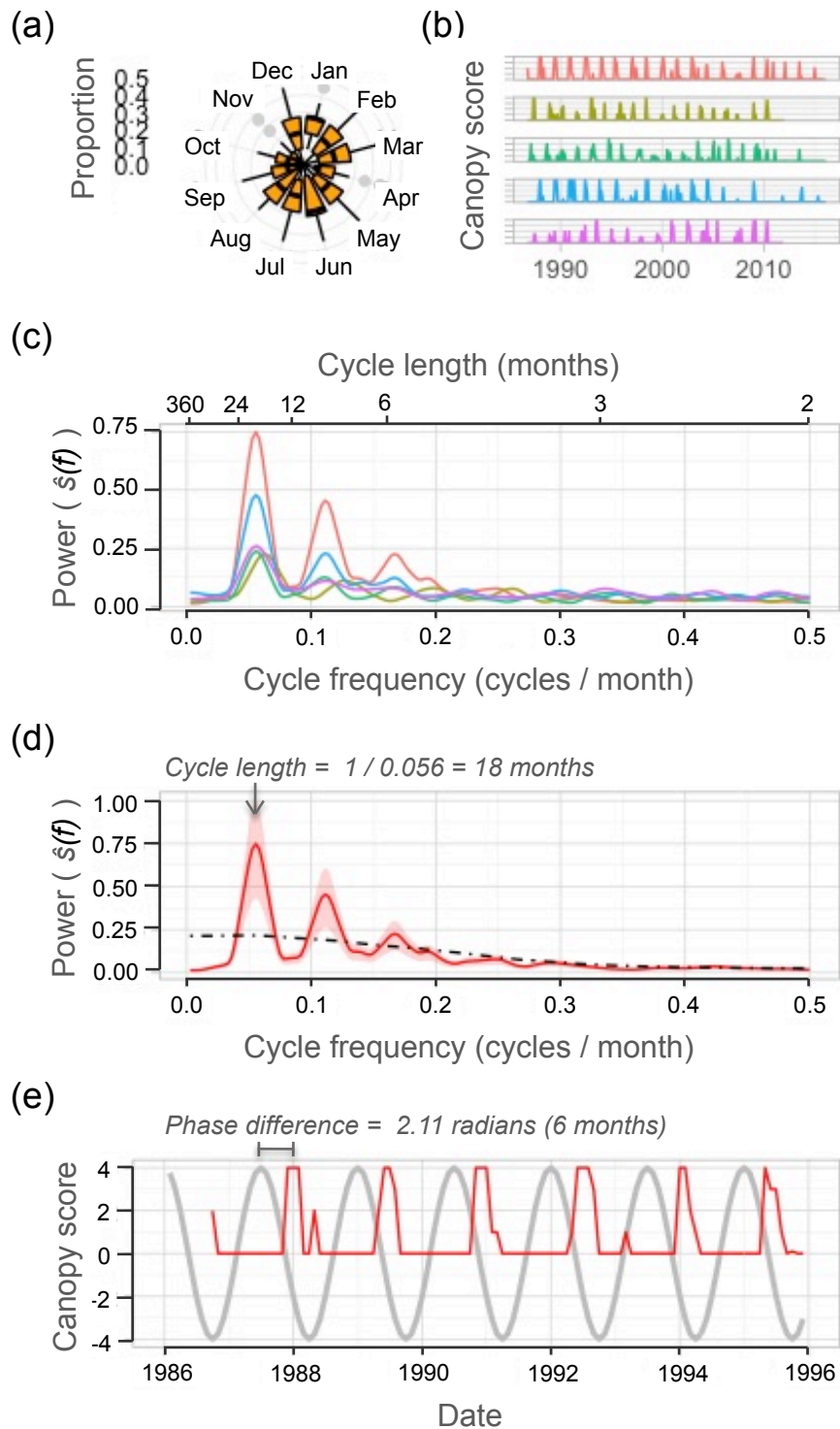
S5: GLM outputs

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 estimate* 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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FIGURE 1: Using Fourier analysis to detect flowering phenology for a single species *Duboscia macrocarpa*.

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

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

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638   b) ***Time series*** plots showing flowering canopy scores every month since 1986 to 2016

639   (five individuals shown as an example). There appears to be some regular flowering

640   cycles for individuals.

641   c) ***Periodogram*** displaying the ***smoothed spectral estimates*** (***bandwidth***=0.1) derived

642   from ***Fourier analysis*** for each individual flowering time series in (b). The x-axis of the

643   shows all possible cycle ***frequencies*** (from one cycle every two months to the full length

644   of the series). The y-axis shows the ***power*** of each cycle. The highest peak in each

645   ***spectrum*** occurs at a frequency of 0.056 cycles per month (indicating a flowering cycle

646   length of 18 months).

647   d) Periodogram displaying smoothed spectral estimate derived from Fourier analysis

648   for the first flowering time series shown in (b) (red line). The 95% confidence intervals

649   for the spectral estimate (red shades) show that the ***dominant peak*** (grey arrow) at

650   0.056 cycles per month is different from the null hypothesis of no cyclicity (the null

651   continuum: black dashed line). We can be confident that the 18-month cycle is different

652   from surrounding noise and represents a real flowering cycle.

653   e) Demonstration of ***co-Fourier*** analysis to derive the relative phase of the flowering

654   cycle identified in (d). The flowering time series (red line) is decomposed alongside a

655   regular ***cosine curve***, simulated to have the same ***cycle length*** as the flowering data (18

656   months) and by convention for our data peaking on the 1st January 1986 (grey line). The

657   ***phase difference*** (2.11 ***radians***) between the two time series can be converted to time

658   (6 months).

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(a)

(b)

(c)

(d)
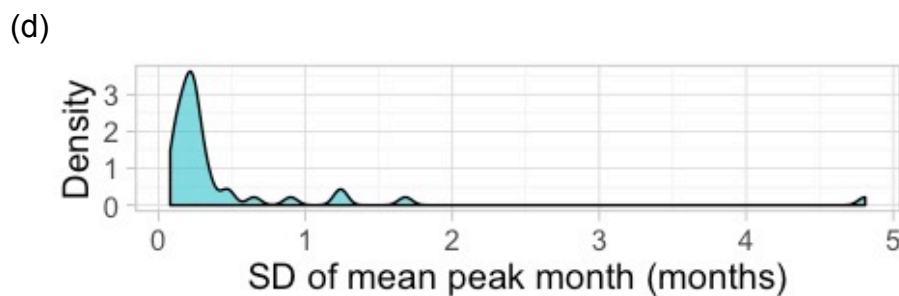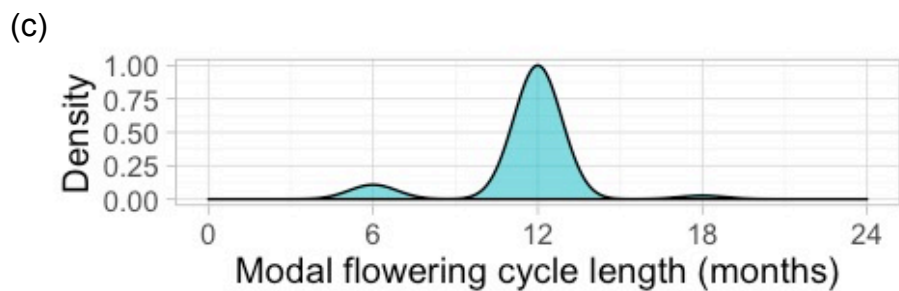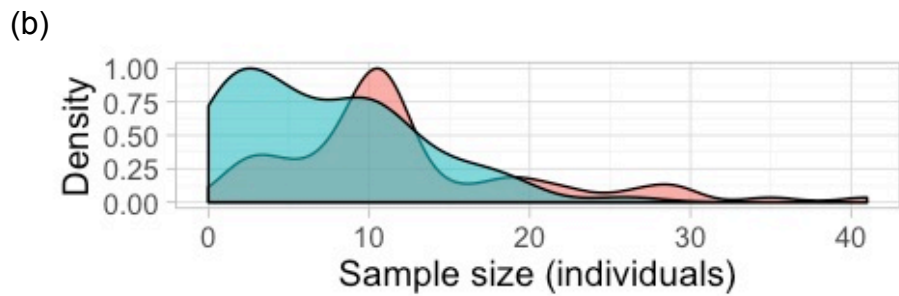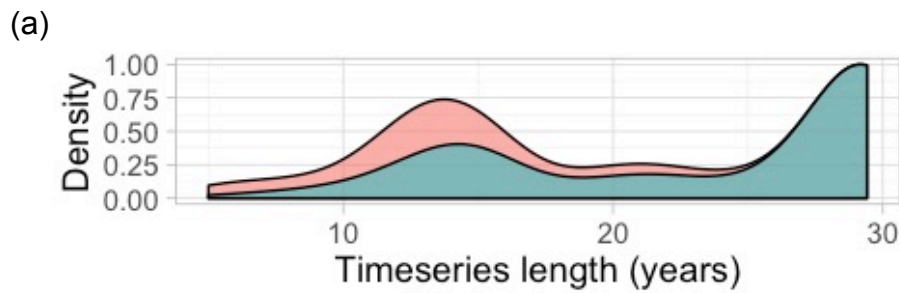
All individuals
Individuals with significant flowering cycle

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**FIGURE 2: Summary of flowering phenology for all tree species monitored at Lopé NP, Gabon.**

    a) Density plot of time series' length for all individuals analysed (red, 856 individuals) compared to individuals with significant flowering cycles (blue, 509 individuals).

667 b) Density plot of number of individuals per species for all individuals (red, 856

668   individuals, 70 species) compared to individuals with significant flowering cycles

669   (blue, 509 individuals, 65 species).

670 c) Density plot of most common flowering *cycle length* (mode) per species, for a

671   subsample of 42 species, each more than five individuals with significant

672   flowering cycles (458 individuals).

673 d) Density plot of *synchrony* (standard deviation of mean peak month) per species,

674   for a subsample of 39 species, each with more than five individuals with

675   significant dominant cycle equal to the species modal cycle length (402

676   individuals).

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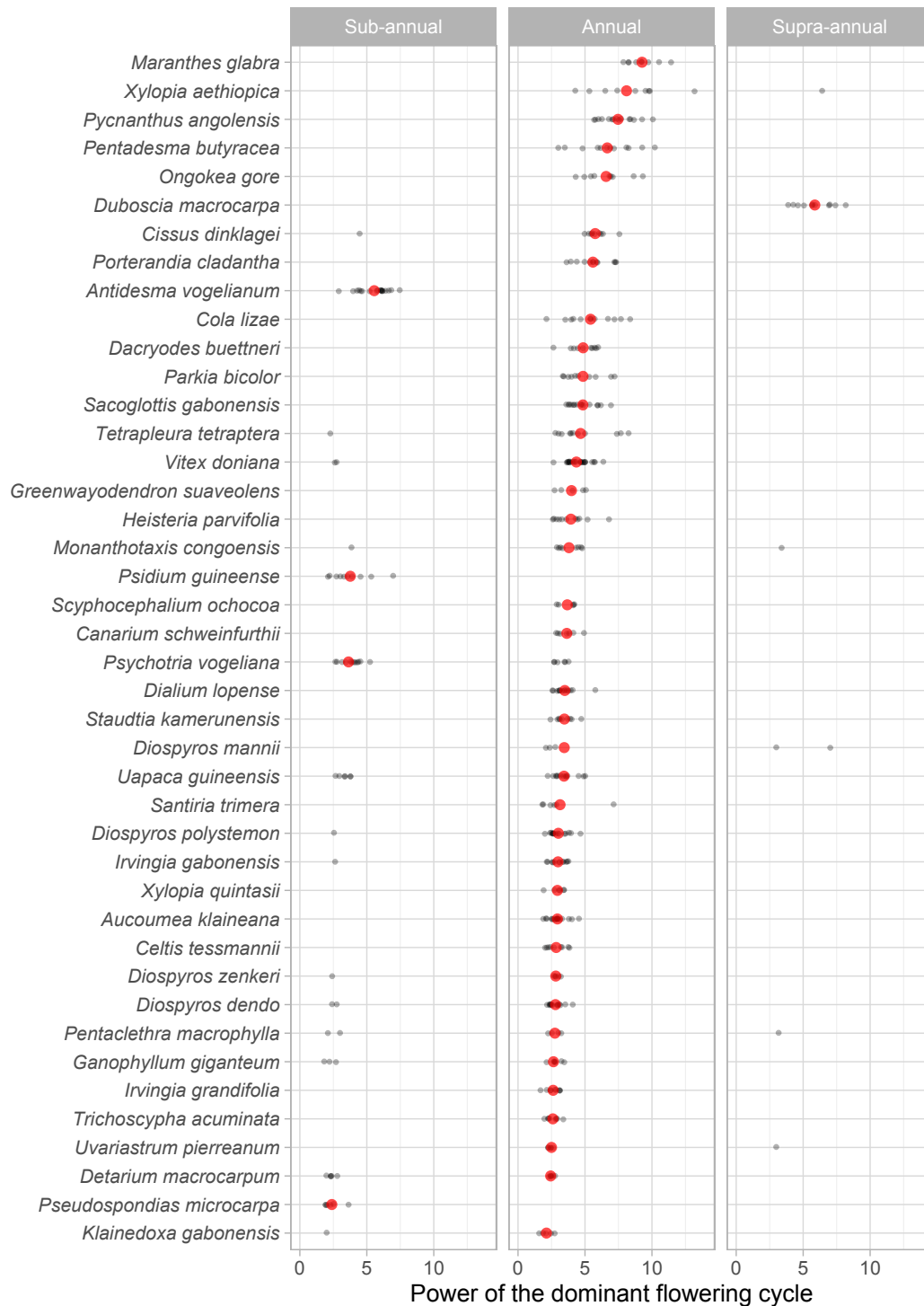
FIGURE 3: Inter- and intra-specific variation in flowering phenology for tree

species monitored at Lopé NP, Gabon.

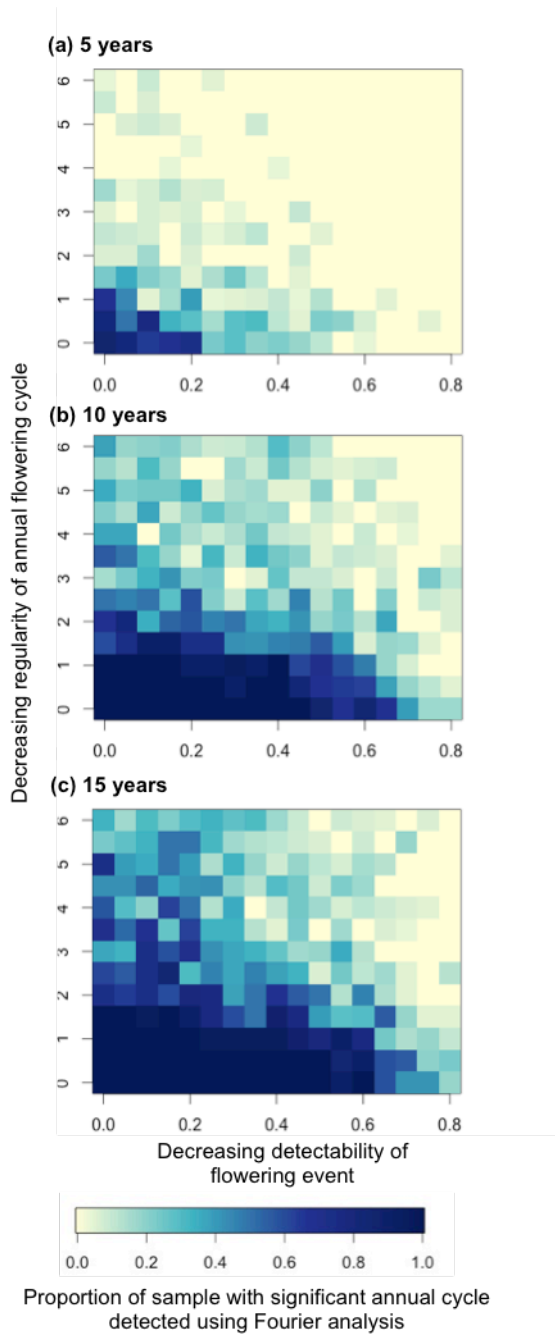*Cycle length* (sub-annual, annual and supra-annual) and ***power*** for each individual

(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).

686

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).

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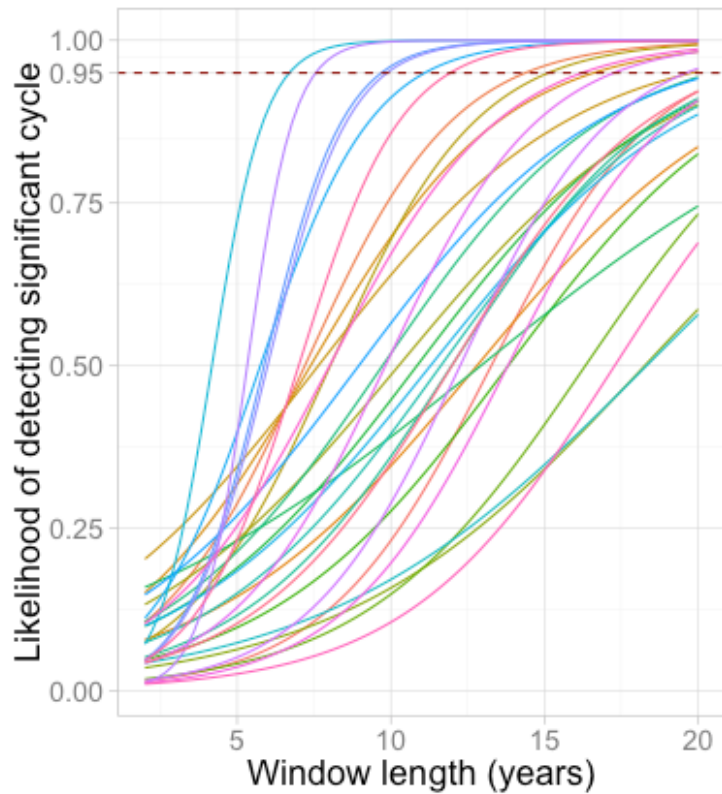
FIGURE 5: Power analysis of annually flowering phenology data from Lopé NP to show the impact of time series length (2-20 years window length) on cycle detection using Fourier analysis (10,000 random samples from 233 individuals of 30 species). Generalised linear model (GLM) predictions (family=binomial,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

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