

This is the peer reviewed version of the following article: Adamescu GS, Plumptre AJ, Abernethy KA, Polansky L, Bush ER, Chapman CA, Shoo LP, Fayolle A, Janmaat KRL, Robbins MM, Ndangalasi HJ, Cordeiro NJ, Gilby IC, Jeffery K & White L Annual cycles are the most common reproductive strategy in African tropical tree communities, *Biotropica*, 50, pp. 418-430, which has been published in final form at <https://doi.org/10.1111/btp.12561>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

BIOTROPICA

THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Annual cycles are the most common reproductive strategy in African tropical tree communities

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66 Received ____; revision accepted ____.

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68 **ABSTRACT**

69

70 We present the first cross continental comparison of the flowering and fruiting phenology of
71 tropical forests across Africa. Flowering events of 5,446 trees from 196 species across 12 sites,
72 and fruiting events of 4,595 trees from 191 species, across 11 sites were monitored over periods
73 of 6 to 29 years, and analysed to describe phenology at the continental level. To study phenology
74 we used Fourier analysis to identify the dominant cycles of flowering and fruiting for each
75 individual tree and we identified the time of year African trees bloom and bear fruit and their
76 relationship to local seasonality. Reproductive strategies were diverse and no single regular cycle
77 was found in >50% of individuals across all 12 sites. Additionally, we found annual flowering
78 and fruiting cycles to be the most common. Sub-annual cycles were the next most common for
79 flowering whereas supra-annual patterns were the next most common for fruiting. We also
80 identify variation in different subsets of species, with species exhibiting mainly annual cycles
81 most common in West and West-Central African tropical forests, while more species at sites in
82 East-Central and Eastern African forests showed cycles ranging from sub-annual to supra-annual.
83 Despite many trees showing strong seasonality, at most sites some flowering and fruiting
84 occurred all year round. Environmental factors with annual cycles are likely to be important
85 drivers of seasonal periodicity in trees across Africa, but proximate triggers are unlikely to be
86 constant across the continent.

87

88 Key words: Phenology; Annual cycles; Seasonality; Flowers; Fruits; Tropical forest; Africa

89

90 Word count: 5096

91 PLANT PHENOLOGY, THE TIMING OF CYCLICAL BIOLOGICAL EVENTS (PHENOPHASES) SUCH AS
92 LEAFING, flowering and fruiting, is essential for the reproductive success of plants, and equally
93 important for animals that rely on plant resources to survive and reproduce (van Schaik *et al.*
94 1993, Sakai 2001). Phenology is well studied in northern, temperate systems (Visser & Both
95 2005) and changes in phenology associated with climate warming are widespread (Parmesan &
96 Yohe 2003). However, the phenology of tropical plants is poorly understood, due both to the
97 paucity of long-term data sets and the complexity of individual patterns (Gentry 1974, Hudson &
98 Keatley 2009). Ultimately, if we are to understand how phenology is changing in the tropics, it is
99 vitally important to establish how canopy-level patterns emerge from variation at the levels of
100 species and communities.

101
102 Globally, tropical forests are characterised by an exceptionally high diversity of plant species,
103 which can flower or fruit at any time of the year, often with very different patterns to other
104 species within the same forest, including closely related taxa (Bawa *et al.* 2003, Zhou *et al.*
105 2014). Flowering and fruiting events in tropical forests vary from complete intraspecific
106 synchrony to extreme asynchrony, and from constant activity to recurrent short pulses (van
107 Schaik *et al.* 1993). Depending on the environmental conditions, species, individual tree
108 characteristics, location and sometimes year, different phenophases occur at different times of
109 the year, in different seasons, and vary in their frequencies and duration (Sakai *et al.* 1999, Pau *et*
110 *al.* 2013, Bush *et al.* 2017).

111
112 To produce leaves, flowers, or fruits, an adult tree needs to accumulate sufficient nutritional
113 resource before a phenophase onset can be triggered (Opler *et al.* 1976). Consequently, weather

114 conditions that could trigger phenophase onset cannot do so if the tree has not first acquired
115 sufficient resources to enable it to respond (Bullock & Solis-Magallanes 1990). Fruiting events
116 also do not necessarily always follow flowering, as flowers may not be pollinated, may be
117 damaged by weather and herbivores, or trees may abort unripe fruits (Stephenson 1981). These
118 factors make the study of phenological responses in relation to climate extremely challenging.
119 Large and long-term datasets are therefore required to study general phenological patterns, and
120 this is especially needed to offset the high heterogeneity of individual tree responses.

121
122 Regular patterns in phenophase expression can be a first indicator of the factors that drive and
123 mediate plant responses. Analysis of both cycle length and timing of regular patterns in
124 phenology at annual (including supra-annual and sub-annual variants) and seasonal scales is a
125 first step to elucidating potential environmental triggers for various phenophases. In tropical
126 forests, climate is not as seasonally restrictive for plant growth as in temperate areas, with the
127 exceptions of dry forests, which have little or no rainfall for months. Seasonality in the tropics
128 is dominated by the intertropical convergence zone (ITCZ), a band of warm air, which carries
129 precipitation north and south over the equator in annual cycles (National Weather Service 2010),
130 but regular seasonal differences in rainfall and temperature are relatively small for the majority
131 of forests (van Schaik *et al.* 1993).

132
133 Asian and South American studies dominate our current knowledge of tropical phenology (Sakai
134 2001, Chambers *et al.* 2013, Mendoza *et al.* 2017, Morellato *et al.* 2013). In these regions,
135 phenology has been described in terms of timing, duration, synchronicity, and dominant cycles
136 (McEwan & McCarthy 2005). In South-East Asia and South America the highly variable

137 phenology patterns of trees can be triggered by various cues, including sudden drops in solar
138 radiation, plant moisture availability, heavy rain or increased temperatures (Corlett & Lafrankie
139 1998, Sakai *et al.* 1999, Butt *et al.* 2015,). Compared to Asian and Neotropical forests, tropical
140 forests in Africa have been little studied in terms of phenology, and this is mainly because of the
141 relative lack of long-term data sets. As a stark comparison, a recent review of Neotropical
142 phenology studies compiled data from 218 phenology study sites, with 10 sites yielding
143 information from more than a decade (Mendoza *et al.* 2017). In contrast, our efforts to analyse
144 phenological patterns across tropical Africa produced data from just 17 sites, of which only nine
145 have data from more than a decade (Plumptre *et al.* 2012; this study).

146

147 Despite the shortcomings of scant long-term phenological datasets from tropical Africa, what we
148 do know from the few African forests (East and West Africa) that have been previously studied
149 in detail, is that (i) flowering and fruiting frequencies vary from sub-annual to supra-annual
150 (Chapman *et al.* 1999, Polansky & Boesch 2013, Janmaat *et al.* 2016, Bush *et al.* 2017), and (ii)
151 annual flowering cycles were found to be the most common. These important findings from less
152 than a handful of studies representing a narrow range of tropical Africa beckoned for a more in-
153 depth analysis across the continent. In an effort to undertake initial steps towards describing
154 continental patterns in phenological responses and defining likely environmental cues for
155 phenological behaviour in African forests, we here (i) analyze cycles observed in phenophases at
156 different sites, and (ii) examine the site-based relationships between phenophases and seasonal
157 weather cycles that can reliably be extracted from global datasets.

158

159

160 Understanding phenology in African forests has become a fundamental issue in tropical forest
161 ecology and conservation of trees and inter-dependent fauna whose survival is threatened by
162 climate change and other anthropogenic pressures such as logging and hunting (Butt *et al.* 2015).
163 We therefore consider this continental wide analysis as a vital step towards understanding and
164 elucidating phenological patterns of African forest tree species. As such, this study provides a
165 first overview of variability in cycle profiles within and between African sites. It allows initial
166 comparisons between the general characteristics of phenological profiles from African forests
167 with those observed on other continents or outside the tropics. Furthermore, this study lays the
168 foundation for future analyses of the climatic conditions that may be driving phenological
169 responses in flowering and fruiting across different African sites. We use a Fourier analysis of
170 trees from 12 long-term studies in tropical forests to examine the dominant pattern of flowering
171 and fruiting cycles at each site and compare cycle profiles across the African continent. We also
172 explore the seasonal phase of flowering and fruiting events of individual trees at each site.
173
174

175 **METHODS**

176 DATA COLLECTION — We assembled data from 12 long-term research sites across East, Central
177 and West Africa (Fig. 1), including montane, submontane, semi-deciduous, evergreen and
178 swamp forests (Table 1). With the exception of M’baïki, which was in a conservation area within
179 a logging concession, all forest sites were located within protected areas. Site elevation and total
180 protected area around the study trees varied between 80 to 3000 m and from 35 km² to
181 approximately 13,000 km², respectively. Each site experiences two main seasons, dry and wet,
182 each present once or twice a year, depending on the site location. Average minimum and
183 maximum monthly temperatures were between 12 and 30 °C, with maximum rainfall ranging
184 between 200 mm and 700 mm per month (Table 2). Data collection of flowering and fruiting
185 events (data for ripe fruit only are used in these analyses) at each site was done monthly and was
186 accomplished by the investigators and trained field assistants. Each tree was visually monitored
187 for the presence/absence of flowers or ripe fruits. In some sites the phenophase response was
188 quantified, but as different scoring methods were used at different sites, we restricted our
189 analyses to presence/absence. Monitored individuals were originally selected based on different
190 research questions at each site and thus most sites represent a non-random subset of the total
191 forest coverage and species diversity (More information on species diversity in Supplementary
192 material A). One site (M’baïki) selected species important in the timber trade, but with the
193 exception of Amani in Tanzania where phenological transects were randomly located, all other
194 sites preferentially sampled species producing fleshy fruits, as original research questions
195 focussed on resource availability for large mammals, mainly primates or elephants. Although the
196 sample at any site is not limited to fleshy fruit-producing species and includes other traits, such

197 as abiotically-dispersed species, the systematic selection for fleshy fruits means that our total
198 sample is likely to over-represent this trait at a community level.

199

200 DATA PREPARATION — Fourier analysis requires continuous regular data. However, due to the
201 logistical challenges of field data collection, including civil unrest in some regions, there are
202 occasional gaps in the data we have available for individual time series. If gaps were shorter than
203 three months, we interpolated the missing data using a linear estimator. If gaps were longer than
204 3 months we split the data at the gap. Bush *et al.* (2017) show that time series length is a
205 significant predictor of identifying cyclic activity in phenology data. To account for this we only
206 included trees with time series longer than 60 consecutive months after linear interpolation, with
207 a minimum of 10 individuals for each species. We also excluded trees that died or never
208 flowered or fruited.

209

210 FOURIER ANALYSIS OF INDIVIDUAL VARIATION — To assess the major cyclic patterns for
211 flowering and fruiting at the sites, we used Fourier analysis to identify dominant cycles per
212 individual tree. Fourier is a spectral analysis method used to decompose a time series into a sum
213 of sine waves of different frequencies and is a robust analysis for determining plants' dominant
214 cycles (Platt & Denman 1975). Bush *et al.* (2017) showed how it could be used to statistically
215 assess the cycle length and predictability of phenology activity in tropical trees at the individual-
216 level.

217 We calculated the Fourier spectrum for each individual tree using the *R* function spectrum from
218 the *R* base package 'stats' (*R* Core Team 2015). Following the guidelines in Bush *et al.* (2017)
219 we smoothed the raw spectrum using a Daniell kernel (a moving average smoother) with varying

220 spans depending on the time series length to give a bandwidth of 0.1. The 0.1 bandwidth
221 represents one 10th of the length of the available time series of each tree and gives sufficient
222 resolution in the spectral estimate to assess dominant cycles while suppressing irrelevant fine-
223 scale structure (Bush *et al.* 2017).

224 We assessed the smoothed spectral estimate for each individual tree and extracted the cycle
225 frequency with the highest power, representing the strongest cycle in the data. Bush *et al.* (2017)
226 warn that time series with little cyclic activity can sometimes produce Fourier transforms with
227 high power in non-relevant low frequencies (e.g. the full length of the time series). To account
228 for this, we screened out individuals where the dominant cycle identified from the spectrum was
229 greater than half the length of the time series (resulting in exclusion of 9% of trees for flowering
230 and 13% of trees for fruiting). Although 9% of individuals that showed non-cyclical flowering
231 were excluded from our analyses, the bias away from shorter cycles is likely to be minimal, as
232 individuals only flowered once or twice during the whole study period at the site, rather than
233 continuously.

234 These data exclusions following Fourier analysis resulted in final samples of 5,446 individuals
235 (196 species) for the flowering analysis and 4,595 individuals (191 species) for the fruiting
236 analysis. Prior to application of the minimum 60-month threshold, numbers were 11,211
237 individuals (469 unique species) for the flowering analysis and 10,517 individuals (453 unique
238 species) for the fruiting analysis (Table 3). Individual time series ranged from 60 to 339 months
239 long (median= 199.5 months) with site differences in data length.

240

241 TESTING FOR DIFFERENCES IN CYCLIC ACTIVITY AMONG SITES — We used the Fourier-derived
242 estimates for dominant cycle length for each individual tree to determine the differences among

243 sites. To describe the most common flowering and fruiting cycles found at each site and to
244 compare among sites, we plotted the distribution of dominant cycles at each site using violin
245 plots. We treated flowering and fruiting events separately and not as a dependent process. Hence,
246 it is worth noting that not all individuals considered in the flowering analysis were shared in the
247 fruiting analysis. For 851 trees, fruiting was more erratic than flowering and these individuals
248 were excluded from analysis of fruiting, but retained in the flowering analysis. This also led to
249 five species from the flowering analysis to being excluded from the fruiting analysis as less than
250 10 individuals showed regular fruiting.

251
252 COMMUNITY LEVEL SEASONALITY - We assessed the seasonal rainfall pattern at each site by
253 calculating a mean monthly rainfall value (Table 3) over the maximum phenology data collection
254 period (28 years starting in 1986 and finishing in 2014) using rainfall data from the Climate
255 Hazards Group InfraRed Precipitation with Station dataset (CHIRPS) (Funk *et al.* 2015:
256 <http://chg.geog.ucsb.edu/data/chirps/>). This dataset combines ground-based monitoring with
257 satellite derived rainfall data starting in 1986 and finishing in 2014. For the two sites (Lopé and
258 Mbeli) for which rainfall data were available locally the empirically observed monthly time-
259 series data were poorly matched in the CHIRPS dataset. However, seasonal patterns (average
260 monthly rainfall across all years) were strongly correlated ($r > 0.9$ observed at Lopé and Mbeli
261 sites) (data not shown). To standardise across sites, we defined the dry season as any months
262 where rainfall was less than 60 mm (after van Schaik *et al.* 1993). We assessed canopy level
263 flowering and fruiting status for trees at each site, by calculating at each site the proportion of
264 trees in the phenology sample flowering and fruiting within each month and year. To test for
265 seasonality in flowering, fruiting and rainfall data we used Rayleigh tests implemented in the R

266 package circular' (Agostinelly & Lund 2011) with the null hypothesis of uniformity (no
267 seasonality) (Morellato *et al.* 2010). As the Rayleigh test can fail in the presence of strong and
268 symmetric multi-modality, we first visually inspected seasonal patterns to identify potential
269 multi-modality. We then used the function 'Rayleigh.test' from the R package 'circular'
270 (Agostinelly & Lund 2011). At some sites (e.g. Kibale and Amani) rainfall is strongly bimodal,
271 but not symmetrical. Significant seasonality could be identified by the Rayleigh test in such
272 circumstances, although the angle identified is likely to be meaningless (Morellato *et al.* 2010).

273

274 **RESULTS**

275

276 SITE LEVEL FLOWERING AND FRUITING CYCLES - Across 12 sites and 5446 individuals (196
277 species) for which all data quality control conditions were met, we found 46% of all individual
278 trees showed dominant annual flowering cycles (between 11 and 13 months), 29% of individuals
279 showed sub-annual cycles (typically between 5 and 7 months) and supra-annual cycles (above 13
280 months) were seen in 25% of trees, with 24-month cycles being the most common.

281 The overall prevalence of annual cycles in individuals was reflected at the site-level in Gombe,
282 Nyungwe, Bwindi, Okapi Lenda, Okapi Edo, Goualougo, Mbeli, Lopé and Taï. Elsewhere
283 annual cycles were not most common, with M'Baiki showing mainly supra-annual cycles, Kibale
284 showing a very diverse profile with sub-annual, annual and a variety of mainly supra-annual
285 cycles and Amani showing mainly sub-annual cycles (Fig 2). Remarkably, despite being only 35
286 km apart and in the same forest type, Okapi Lenda and Edo showed different dominant cycles
287 with far greater diversity in cycle length in Okapi Lenda.

288

289 Across the 11 sites and 191 species (4,595 individuals), 42% of individuals showed annual
290 fruiting cycles. In contrast to the flowering analysis, supra-annual fruiting cycles were nearly as
291 common as annual cycles (35% of individual trees), with the most frequent dominant fruiting
292 cycle being 24 months. Sub-annual cycles were encountered only in 23% of individuals with the
293 most common cycle being 6 months. At most sites we found species with differing cycle lengths
294 (Fig. 4). In sites in West and West Central Africa we found that most trees recorded an annual
295 fruiting cycle.

296

297 FLOWERING AND FRUITING SEASONALITY - Due to considerable variation between individuals
298 and both within and between species, flowering patterns at the community level at most sites
299 showed weak seasonality (some trees flower during both the wet and dry season) despite
300 considerable seasonal differences in rainfall between sites (Fig 3, 5 and Table 5). Seasonality in
301 flowering (flowering triggered by a certain environmental cue, such as heat or rainfall) was not
302 observed in Amani, Kibale, Nyungwe, Bwindi, and Tai, while we detected significant flowering
303 seasonality at the canopy level in the rest of sites (Fig 3 and Table 5). Among the remaining
304 seven sites, the strongest seasonal flowering patterns were encountered at Gombe, M'Baiki,
305 Lope, Goualougo, Okapi Lenda and Okapi Egoro sites (Fig 5). All sites showed significant
306 seasonality in rainfall (Table 4).

307

308 With regard to fruiting, we found constant fruit patterns a feature of several sites. Amani, Kibale,
309 Nyungwe and Bwindi were sites that exhibited no significant seasonality in flowering, and also
310 showed no statistically significant seasonality in fruiting patterns ($p > 0.01$, Table 5). However,
311 although Lope showed strong significant seasonality in flowering, it did not show seasonality in

312 fruiting (although the p value = 0.01). In contrast, Tai, which showed no seasonality in
313 flowering, showed strong seasonality in fruiting. Most inter-month variation (highest seasonality)
314 in fruiting was found in Tai, Okapi Lenda, M’Baïki, and Gombe. For Amani, Nyungwe,
315 M’Baïki, Mbeli and Tai, peak fruiting occurred during the dry season. At Kibale, peak fruiting
316 was at the transition from wet to dry seasons, and for the rest of the sites, peak fruiting occurred
317 during the wet season (Fig 5).

318

319

320 **DISCUSSION**

321

322 Using Fourier based analysis we effectively estimated flowering patterns for 5446 individual
323 trees of 196 species, and fruiting patterns for 4595 trees of 191 species, across 12 and 11 sites,
324 respectively. This was performed both at the site level and among tropical forests spanning from
325 western to eastern Africa. We found that across all sites, more trees flowered and fruited
326 annually than supra or sub-annually; however, sub-annual flowering cycles and supra-annual
327 fruiting patterns were present at all sites and common in many. Although some sites had few
328 individual trees reproducing annually, all sites had some annually reproductive trees, as expected
329 from previous analyses of dominant reproductive cycles in Lopé (Bush *et al.* 2017) and Kibale
330 (Chapman *et al.* 1999).

331

332 Overall, 46% of trees showed annual flowering frequencies across all 12 sites. Our results
333 contrast with those previously reported from tropical forests of Central and South America, as
334 well as Southeast Asia, where, depending on the region, sub-annual and supra-annual

335 frequencies have previously been reported as the most frequent strategies (Newstrom *et al.* 1994,
336 Sakai 2001, McEwan & McCarthy 2005, Wright *et al.* 2005). However, more recent work in
337 South America has now shown some sites where annual cycles in fruiting are dominant (Norden
338 *et al.* 2007, Mendoza *et al.* 2018). Evolutionary histories and pressures driving flowering and
339 fruiting are likely to be different in forests on different continents and, equally, even at a
340 continental scale, may contrast greatly between western and eastern Africa (Slik *et al.* 2018).
341 There is certainly room for further work on the evolution of cyclicity and current drivers of
342 cyclicity on all continents before robust inter-continental comparisons can be made.
343 Fruiting showed similar patterns to flowering, with 42% of trees at 11 sites showing annual
344 cycles, also as previously reported for Africa (Chapman *et al.* 1999, Takenoshita *et al.* 2008,
345 Bush *et al.* 2017). This result was not as strong as the annual flowering pattern, presumably
346 because many flowering cycles do not result in production of mature fruit. Our dataset shows
347 that fruiting cycles are slightly more likely to be supra-annual than flowering cycles, which may
348 be the result of resource deficiencies, stochastic weather events, flower or fruit predation, or
349 disease all playing a role in modifying annual cycles by preventing fruiting after a flowering
350 event.

351

352 SITE LEVEL FLOWERING AND FRUITING PATTERNS — We assume that the prevalence of annual
353 cycles suggests that a regular, external annual cycle, sometimes moderated by the resource base
354 available to each individual, and additional extra-annual environmental variation, perhaps, such
355 as the El Niño phenomenon (Chapman *et al.* 2018, Dunham *et al.* 2018) drives the observed
356 phenological pattern in many trees. Annual phenological cycles have previously been reported to
357 be initiated by annual cycles in environmental conditions such as day length, seasonal rainfall

358 and temperature (Borchert 1983, Pau *et al.* 2013). It is difficult to disentangle exactly which cues
359 were responsible for triggering phenological events at our sites due to the lack of data on
360 environmental conditions. Factors mediating the trees' ability to respond to an environmental
361 cue, such as carbohydrate storage (Borchert 1983), or phosphorus accumulation (Corlett 2016),
362 have not been measured at any of our sites. The lack of data on local weather at a sufficient level
363 of precision (Maidment *et al.* 2015, Abernethy *et al.* 2016) is also problematic for robust
364 definition of environmental cues in African sites. However, despite these limitations, we did find
365 annual cycles in rainfall in most sites and consider it likely that annually cycling local
366 environmental cues are important in driving African tree phenology across the continent. It is
367 important to remember that although annual cycles were the most common patterns at most sites,
368 annual cycles were not shown by a majority of trees: there were individuals at every site showing
369 either sub- or super-annual cycles, and across the whole dataset more trees showed non-annual
370 than annual cycles. African forests show a high level of diversity in phenological behaviours
371 both within and between species. Although there was no clear effect of forest type, longitude,
372 latitude or altitude on the phenological profile at a site, the more westerly sites showed stronger
373 dominance of annual cycles than those in the west and south, and sites closest to the current edge
374 of the rainforest extent showed the highest diversity in cyclic behaviour.

375

376 Our results underscore the complexity and inter-individual variation in flowering and fruiting at
377 the community level, previously reported at different sites in Africa (Tutin & Fernandez 1993,
378 Plumptre 1995). In this analysis a different set of species was monitored at each site. Since
379 species are not distributed at random among sites and tree selection criteria varied at different
380 sites (see Methods), it is plausible that differences among sites are more reflective of differences

381 in species selection than fundamental differences in geography. Unfortunately, we cannot
382 estimate the degree of bias this generates post hoc, but further research into functional or
383 taxonomic group responses to environmental triggers may elucidate the potential effects of each.
384 We saw variability in flowering and fruiting patterns among species within the same forest site,
385 presumably associated with selection for responses to differing environmental drivers. This may
386 be expected when different functional traits mediate the response to environmental drivers of
387 phenological patterns: e.g. different animal-plant relationships (Takenoshita *et al.* 2008);
388 different modes of seed dispersal (e.g. wind dispersed seeds tend to ripen during drier periods,
389 fleshy fruits in wetter ones: Chapman *et al.* 2001) or differences in endogenous factors mediating
390 the response (which may reflect genetic differences: Staggemeier *et al.* 2015). Although our
391 study is the first to present and compare the range of phenological profiles at tropical forest sites
392 across Africa, the question of *why* predominant cycle length varies across the continent remains
393 unanswered. Further analyses including factors such as climate change, rare weather events, soil
394 types, interspecific interactions, genetic variation, forest history and geographical position should
395 be considered by researchers wishing to advance this discipline.

396

397 FLOWERING AND FRUITING SEASONALITY — As reported elsewhere in Africa (Chapman *et al.*
398 1999), we found that timing of flowering and fruiting between species was highly variable at
399 most sites, such that at the canopy level some individuals may always be found in flower or in
400 fruit. Visually, Bwindi and Kibale showed the least seasonal flowering patterns (Fig 3), but even
401 here there may be some slightly bimodal seasonal patterns that are cannot be detected by the
402 Rayleigh test. We confirmed that for the majority of sites, flowering activity peaked at the
403 beginning or during the middle of one of the two wet seasons (Anderson *et al.* 2005, Polansky &

404 Boesch 2013). In five of our sites, peak fruiting occurred during the wet season (c.f. Sun *et al.*
405 1996), a pattern also common in South and Central America (Smythe 1970) and Asia (Medway
406 1972). However, in another five sites, peak fruiting occurred in the dry season, and for one site,
407 fruiting peaked in the transition from wet to dry. There was no discernible pattern in the
408 geographic distribution, seasonality, or rainfall characteristics of wet vs. dry season fruiting sites.
409
410 Phenological complementarity between plants and animals is crucial for ecosystem organisation,
411 process and function (Cleland *et al.* 2007), and the importance of phenological events in
412 understanding the ecology and evolution of species within their communities has been previously
413 demonstrated (Chapman *et al.* 2005, Visser & Both 2005). Changes in plant phenology can lead
414 to cascading effects across the entire ecosystem by causing phenological mismatches between
415 the cycles followed by plants and the animals that rely on them (Newstrom *et al.* 1994, Sakai
416 2001, Morellato *et al.* 2016). Mismatches have already been observed in temperate regions
417 where phenology has changed differently for animals and plant communities, due to recent rapid
418 changes in climate (Brown *et al.* 2016). Morellato *et al.* (2016) and Mendoza *et al.* (2017) review
419 the evidence and likelihood of such mismatches arising in neotropical forests. Chapman *et al.*
420 (2005), Polansky & Boesch (2013), Dunham *et al.* (this issue) and Chapman *et al.* (this issue)
421 consider the consequences of mismatches in African forests. All conclude that primate foragers
422 have developed behavioural patterns in response to the predictability of fruit resources, and are
423 likely to suffer population declines if fruit phenology cycles become less regular.

424

425 CONCLUDING REMARKS - Our study shows that annual cycling, as opposed to supra- or sub-
426 annual cycling, is the most common flowering and fruiting strategy in African tree reproduction

427 across the continent. However, both supra- and sub-annual strategies exist in every site alongside
428 annually cycling trees, and non-annual patterns (of supra and sub-annual combined) are common
429 overall and at many individual sites. Seasonality at most sites covers two wet and two dry
430 seasons, providing potential for environmental cues at a sub-annual cycle length, but we found
431 relatively low frequencies of sub-annual cycling. Our results provide an important baseline from
432 which future changes in seasonality, community phenological profiles and individual or species
433 average cycle length can be assessed. We show for the first time that there is considerable
434 variation in the frequency of phenological cycle types at different tropical African sites and that
435 there is some geographic patterning in the distribution of site-specific phenological cycle
436 profiles, although trends are not strong.

437
438 With this study, we bring African data to bear in global comparisons of tropical forest behaviour.
439 We show similarities and differences in flower and fruit cycles between African, Asian and
440 Neotropical forests. We also show the complexity of observed phenology cycles within and
441 among sites in Africa and the lack of explanatory power found in the currently available
442 environmental data. In order for the environmental drivers of phenology patterns in Afrotropical
443 forests to be more clearly understood we make the following research recommendations: 1)
444 encourage the collection of more detailed and precise environmental data (weather, soils, nutrient
445 flux etc.) at phenology data collection sites; 2) assess and improve the potential of African
446 climate models to provide interpolated climate-data for specific sites; 3) resolve differences in
447 observational methodologies such that inter-site comparisons become more robust; 4) expand
448 data collection to include a more representative selection of tree species and 5) increase the
449 collection of functional trait data for the species targeted for phenology data collection.

450 Furthermore, we encourage future work that addresses questions of variability within tree
451 species. Finally, we note that although more work has been undertaken in Asian and Neotropical
452 forests than in Africa to date, it seems likely that application of new analytical methods such as
453 those used here may identify previously overlooked patterns in these better known forests too.

454

455 **ACKNOWLEDGEMENTS**

456 We thank ESA CCI Land Cover project for permission to use the land cover data to create our
457 map. Thanks are due to the following organisations and individuals for assistance with funding,
458 permits, permissions and fieldwork at each of the sites:

459

460 AMANI - Permits and permissions from COSTECH and Amani Nature Reserve; fieldwork from
461 University of Dar es Salaam, Roosevelt University and the Field Museum, Thomas Challenge,
462 Bakari Mtui, and Mwanaidi Kijazi.

463

464 GOMBE - We thank the Tanzania Wildlife Research Institute (TAWIRI) and Commission on
465 Science and Technology (COSTECH) for permission to conduct this research, and Gen
466 Yamakoshi, who initiated collection of phenology data at Gombe. We thank the Jane Goodall
467 Institute, NSF grants IOS-1052693 and BCS-0648481, the University of Minnesota, Harris Steel,
468 and Duke University for supporting fieldwork and data entry.

469

470 KIBALE - Funding from Canada Research Chairs Program, Wildlife Conservation Society,
471 Natural Science and Engineering Research Council of Canada, National Geographic, National

472 Science Foundation, and Fonds Québécois de la Recherche sur la Nature et les Technologies.

473 Fieldwork: Richard Wrangham.

474 LOPÉ - Funding from the International Centre for Medical Research in Franceville (CIRMF)
475 (1986-2010), the University of Stirling (1986-present) and Gabon's National Parks Agency
476 (ANPN) (2011-present). Permission and permits from the CIRMF Scientific Council and the
477 Ministry of Water and Forests (1986 – 2010), and by ANPN and the National Centre for
478 Research in Science and Technology (CENAREST) (2011 – present). We also thank Richard
479 Parnell, Liz Williamson, Rebecca Ham and Patricia Peignot for significant periods of data
480 collection.

481

482 M'BAÏKI - Fieldwork by ARF Project (Appui la Recherche Forestière) funded by six partners:
483 AFD (Agence Française de Développement), CIRAD (Centre de Coopération Internationale en
484 Recherche Agronomique pour le Développement), ICRA (Institut Centrafricain de Recherche
485 Agronomique), MEFCP (Ministère centrafricain des Eaux, Forêts, Chasse et Pêche),
486 SCAC/MAE (Service de Coopération et d'Actions Culturelles, Ministère des Affaires
487 Etrangères), and SCAD (Société Centrafricaine de Déroulage).

488

489 MBELI BAI - Funding from The Columbus Zoo and Aquarium, Cincinnati Zoo and Botanical
490 Garden, Cologne Zoo, Disney Worldwide Conservation Fund, Dublin Zoo, Sea World and Busch
491 Gardens Conservation Fund, Toronto Zoo, Wildlife Conservation Society and Woodland Park
492 Zoo. Permits from Ministry of Sustainable Development, Forest Economy and Environment and
493 the Ministry of Scientific Research of the Republic of Congo.

494

495 Tai - Funding from Max Planck Institute for Evolutionary Anthropology. Permits from the
496 Ministère de la Recherches Scientifiques, the Ministère de l'Environnement et des Eaux et
497 Forêts, the Office Ivoirien des Parcs et Réserves. Support in the field from the staff of the Tai
498 Chimpanzee Project, Centre Suisse de Recherche Scientifique, C. Boesch, D. P. Anderson, and
499 Z.B. Goné Bi.

500

501 **DATA AVAILABILITY STATEMENT**

502 The summary data from this study will be available via the WCS data portal website (doi: xxx
503 xxxxx). Data for the Lopé site is stored at (DataSTORRE; <http://hdl.handle.net/11667/103>),
504 under a 10 year open-access embargo. Access to embargoed data may be requested by contacting
505 the relevant authors (see affiliations).

506

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636 **TABLES**

637

638 TABLE 1. Characteristics of the 12 African study sites, including country, geographical coordinates and monitoring period for
 639 flowering and fruiting phenology of tropical trees. Sites are organised from East to West. Latitude and longitude are expressed in
 640 decimal degrees. FL = flowering; RF= fruiting; SD= Standard deviation.

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	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean Altitude	Mean time series length for flower	Mean time series length for fruit
1	Amani Nature Reserve	Tanzania	-5.13	38.62	7 (2006 – 2012)	Moist submontane forest	950 m	78 (SD=0)	78 (SD=0)
2	Kibale Forest National Park	Uganda	0.56	30.36	11 (2005 – 2015)	Moist submontane forest	1500 m	148 (SD=23.7)	142 (SD=27.9)
3	Okapi Wildlife Reserve Lenda site	Democratic Republic of the Congo	1.26	28.64	20 (1993 – 2012)	Humid mixed evergreen forest	750 m	OL: 200 (SD= 53.3)	OL: 200.9 (SD=53.1)
4	Okapi Wildlife Reserve Edoro sites	Democratic Republic of the Congo	1.26	28.64	20 (1993 – 2012)	Humid mixed evergreen forest	750 m	152 (SD=57.9)	No data

5	Bwindi Impenetrable National Park	Uganda	-1.05	29.77	6 (2008 – 2014)	Montane forests	2240 m	93 (SD=5.9)	93 (SD=7.4)
6	Nyungwe Forest National Park	Rwanda	-2.43	29.26	13 (1996 – 2008)	Montane forest	2260 m	150 (SD=15.3)	184 (SD=21.6)
7	Gombe National Park	Tanzania	-4.61	29.64	13 (1997 – 2009)	Evergreen riverine forest, deciduous woodland, and grassland	1000 m	98 (SD=5.4)	97 (SD=5.5)
8	M’Baïki forest	Central African Republic	3.90	17.90	21 (1991 – 1995, 1998 – 2003, 2005 – 2011)	Semi- deciduous - tropical forest	560 m	82 (SD=0.9)	81 (SD=0.4)
9	Goualougo Triangle Nouabalé- Ndoki National Park	Republic of Congo	2.21	16.52	11 (2002 – 2012)	Semi- deciduous rain forest	300 m	69 (SD=2.7)	70 (SD=2.1)

10	Mbeli Bai Nouabalé- Ndoki National Park	Republic of Congo	2.26	16.41	12 (2004 – 2015)	Semi- deciduous rain forest	300 m	134 (SD=22.8)	140 (SD=13.6)	644
										645
										646
11	Lopé National Park	Gabon	-1.09	11.16	29 (1986 – 2014)	Semi- evergreen, tropical lowland rainforest	300 m	237 (SD=91.1)	236 (SD=90.5)	647
										648
										649
										650
12	Taï National Park	Côte d'Ivoire	5.84	-7.31	15 (1997 – 2011)	Diverse moist evergreen and semi- evergreen forest	80 m	68 (SD=4.1)	68 (4.1)	651
										652
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655 Sources: **Amani Nature Reserve**, Tanzania – Henry Ndangalasi and Norbert Cordeiro; **Gombe Stream National Park** ,
656 Tanzania – Ian Gilby, Anne Pusey, Michael Wilson and Baraka Gilagiza; **Nyungwe National Park**, Rwanda – Felix
657 Mulindahabi; **Bwindi Impenetrable National Park**, Uganda – Badru Mugerwa, Frederick Ssali, Douglas Sheil and Martha
658 Robbins; **Kibale National Park**, Uganda – Colin Chapman, **Okapi Wildlife Reserve**; Democratic Republic of Congo – Flory
659 Bujo, Corneille Ewango and Terese Hart; Lopé **Reserve**, Gabon – Kate Abernethy, Emma Bush, Edmond Dimoto, Jean-
660 Thoussaint Dikangadissi, Kath Jeffery, Caroline Tutin and Lee White; **Mbeli Bai**; Nouabalé-Ndoki National Park, Republic of
661 Congo– Mireille Breuer-Ndoundou Hockemba and Thomas Breuer; **M’Baïki**, Central African Republic – Adeline Fayolle, **Taï**
662 **National Park**; Ivory Coast – Christophe Boesch, Leo Polansky; **Goualougo**, Republic, Republic of Congo– Sydney Ndolo,
663 Dave Morgan, and Crickette Sanz.

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668 TABLE 2. Monthly minimum and maximum temperature and precipitation values at each of the 12 African sites taken from CHIRPS.
 669

	Minimum precipitation (mm)	Maximum precipitation (mm)	Minimum temperature (°C)	Maximum temperature (°C)
Amani	49	341	18	33
Kibale	45	209	15	30
Okapi	57	221	17	31
Bwindi	21	161	9	23
Nyungwe	13	203	11	24
Gombe	1	212	15	30
M'Baiki	29	232	17	34
Goualougo	47	224	18	32
Mbeli	46	226	18	31
Lope	0	349	18	30
Tai	10	380	19	34

670 TABLE 3. Number of individual trees and species at each African site in the original and Fourier datasets. Total number of species do not match the
 671 ones presented in the text because in this summary we considered all species, including the ones present at multiple sites (therefore species may
 672 appear more than once)

Site (South East to North West)	Original sample		Detected cycle sample		Characteristics of detected cycles					
	N Species	N trees	N Species	N trees	Sub annual		Annual		Supra annual	
					N Species	N trees	N Species	N trees	N Species	N trees
Amani	70	935	14	410	14	252	7	23	14	135
Gombe	13	277	11	192	7	13	10	146	7	33
Nyungwe	74	1000	45	794	35	187	43	326	42	245
Bwindi	33	319	8	80	6	40	6	18	8	22
Kibale	75	311	10	85	8	29	7	13	10	43
Okapi Lenda	49	570	27	354	17	60	27	251	19	43
Okapi Egoro	61	850	30	439	27	111	24	140	29	188
M'Baiki	30	769	6	155	6	55	5	36	6	64
Goualougo	28	284	3	43	2	19	3	20	1	4
Mbeli	44	438	12	112	10	24	11	55	11	33
Lope	84	940	48	733	33	167	45	478	30	88
Tai	108	1000	44	2049	43	663	43	973	39	413
Total	669	7693	258	5446	208	1620	231	2479	216	1311

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TABLE 4. Rayleigh test of uniformity (Z), and p value for non-uniformity of monthly precipitation at 12 sites in tropical Africa. All sites show significant seasonality.

Site	Z	P value
Amani	0.206	0
Kibale	0.113	0
Okapi	0.120	0
Bwindi	0.092	0
Nyungwe	0.243	0
Gombe	0.458	0
M'Baiki	0.312	0
Goualago	0.190	0
Mbeli Bai	0.206	0
Lopé	0.078	0
Taï	0.288	0

701 TABLE 5. Rayleigh test of uniformity (Z), and p value of significance of deviation from uniformity. P values of less than 0.01 are
 702 considered significant.
 703

Site	Z	P value
Flowering		
Amani	0.248	0.039
Kibale	0.034	0.80
Okapi Egoro	0.238	0.001
Okapi Lenda	0.551	0.001
Bwindi	0.039	0.308
Nyungwe	0.117	0.02
Gombe	0.193	0.001
M'Baiki	0.448	0.001
Goualougo	0.294	0.001
Mbeli Bai	0.316	0.003
Lopé	0.275	0.001
Tai	0.057	0.389
Fruiting		
Amani	0.246	0.03
Kibale	0.105	0.210
Okapi Lenda	0.256	0.001
Bwindi	0.160	0.05
Nyungwe	0.181	0.012
Gombe	0.238	0.001
M'Baiki	0.182	0.009

Goualougo	0.201	0.001
Mbeli Bai	0.168	0.002
Lopé	0.104	0.010
Taï	0.304	0.001

705 **FIGURE LEGENDS**

706

707 FIGURE 1. Geographical position of the 12 long-term, cross-continental phenology studies in
708 Africa. Okapi Wildlife Reserve is represented by two sites: Okapi Lenda and Egoro. Due to the
709 scale of the map, dots for Goualogo and Mbeli overlap, as do the dots for Bwindi and Nyungwe.
710 Colors indicate spatial variation in land cover on a spectrum of high (green) to low (orange)
711 cover (data downloaded from ESA at 5° x 5° resolution (Arino *et al.* 2009).

712

713 FIGURE 2. Violin plot showing the density of flowering frequency of all individual trees present
714 at 12 African sites ordered from East to West. (Species present after Fourier analysis was applied
715 for each site: Amani = 14, Gombe = 11, Nyungwe = 45, Bwindi = 8, Kibale = 10, Okapi Lenda =
716 27, Okapi Egoro = 30, M'baiki = 6, Goualougo = 3, Mbeli = 12, Lopé 48, Tai = 44; Number of
717 trees present at each site: Amani = 410, Gombe = 192, Nyungwe = 792, Bwindi = 80, Kibale =
718 85, Okapi Lenda = 354, Okapi Egoro = 439, M'Baiki = 155, Goualougo = 43, Mbeli = 112, Lopé
719 = 733, Tai = 2049)

720

721 FIGURE 3. Flowering seasonality at 12 different sites in Africa. Black graph represents the
722 rainfall for each month normalised to the rainfall of the wettest month. Circular plots indicate the
723 proportion of individual trees flowering in each month in each month for 12 sites. Sites are
724 labelled above each circular plot.

725

726 FIGURE 4. Violin plot showing the density of fruiting frequency of all individual trees present at
727 each African site. (Species present after Fourier analysis was applied for each site: Amani = 11,
728 Gombe = 10, Nyungwe = 49, Bwindi = 7, Kibale = 7), Okapi Lenda = 20, M'baiki = 6,

729 Goualougo = 6, Mbeli = 9, Lopé = 48, Tai = 49; Amani = 321, Gombe = 165, Nyungwe = 842,
730 Bwindi = 60, Kibale = 57, Okapi Lenda = 265, M'baiki = 132, Goualougo = 64, Mbeli = 66,
731 Lopé = 709, Tai = 1914). Okapi Egoro was not included in the fruiting analysis because it did
732 not pass the condition of the 60-month threshold.

733

734 FIGURE 5. Fruiting seasonality at 11 sites in Africa. Black graph represents the rainfall for
735 each month normalised to the rainfall of the wettest month. Circular plots show the proportion
736 of individual trees flowering in each month for 11 sites. Sites are labelled above each circular
737 plot. Okapi Egoro was not included in the fruiting analysis because it did not pass the
738 condition of the 60-month threshold.

739

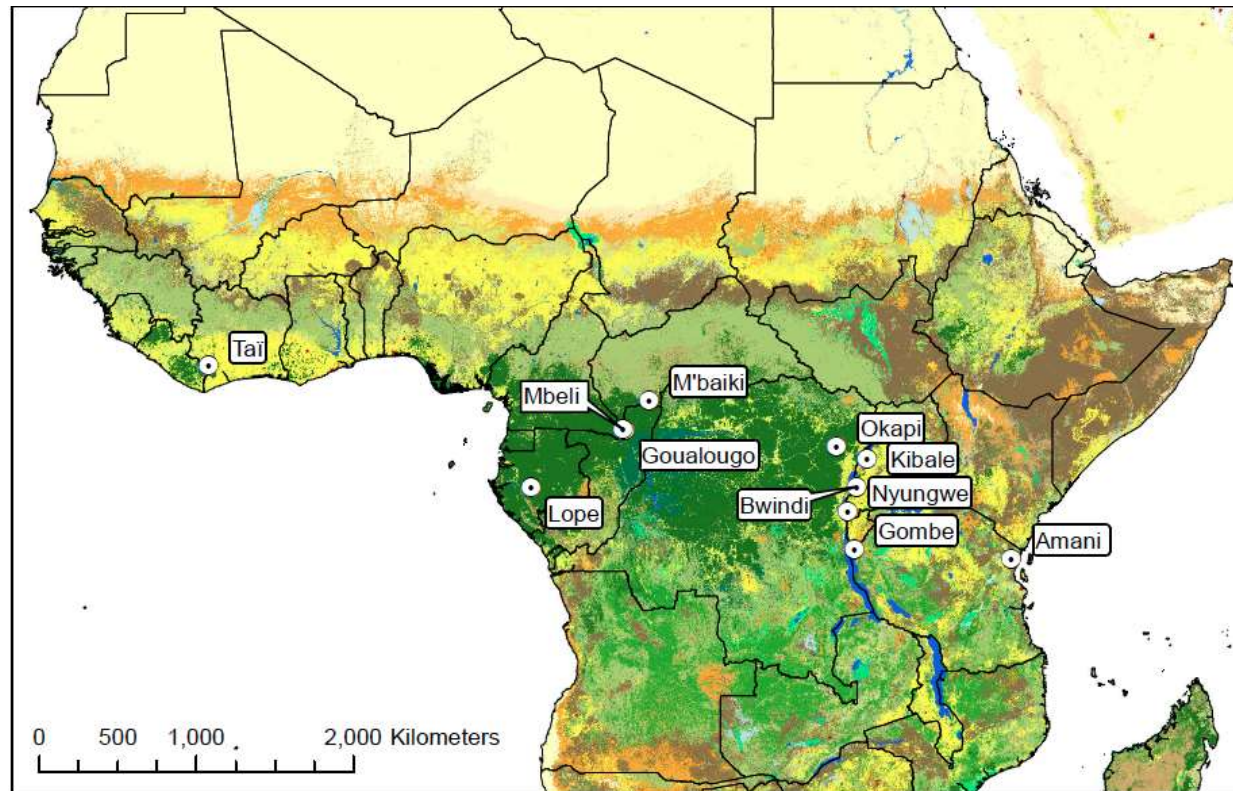
740

741 **FIGURES**

742

743 **FIGURE 1.**

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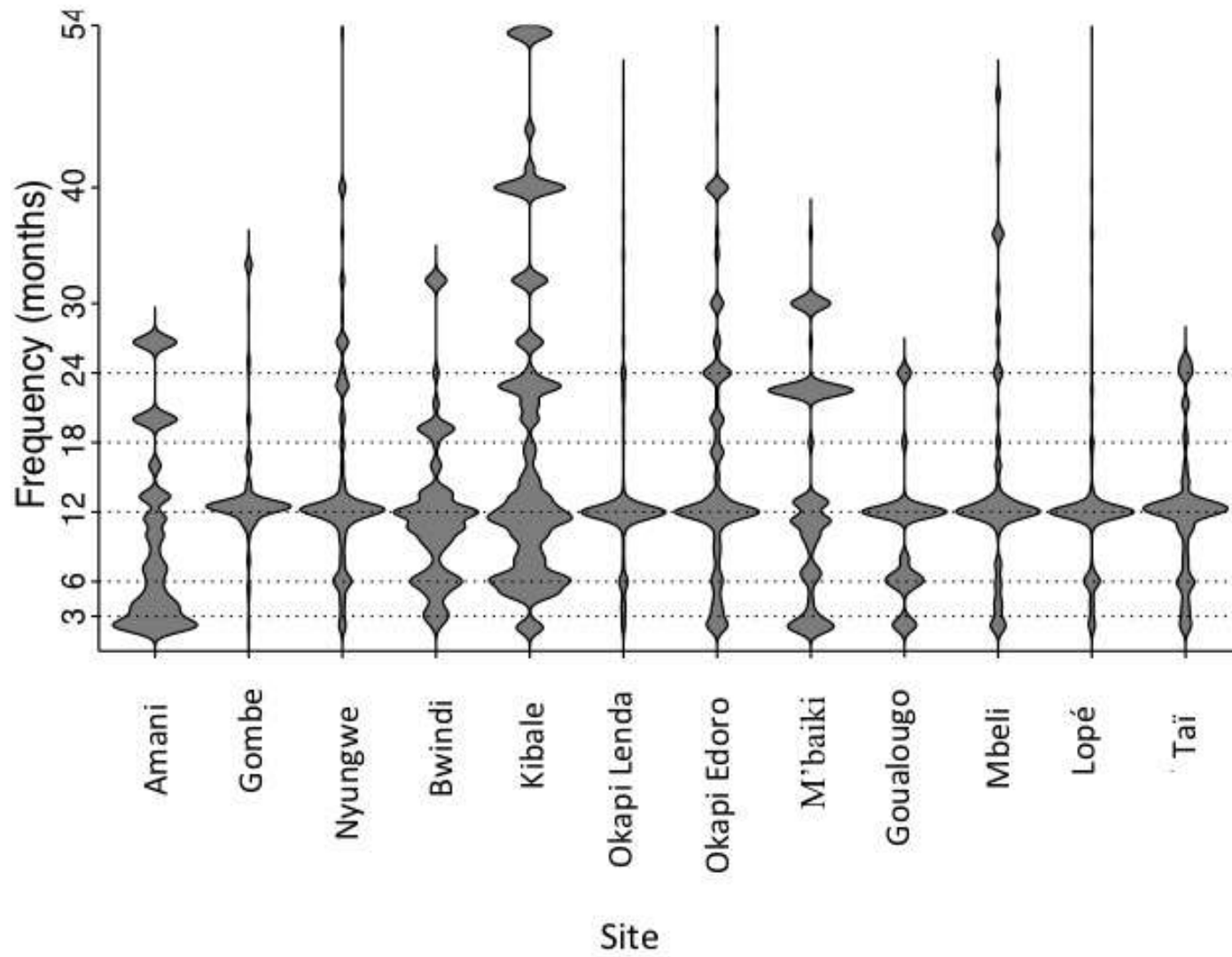
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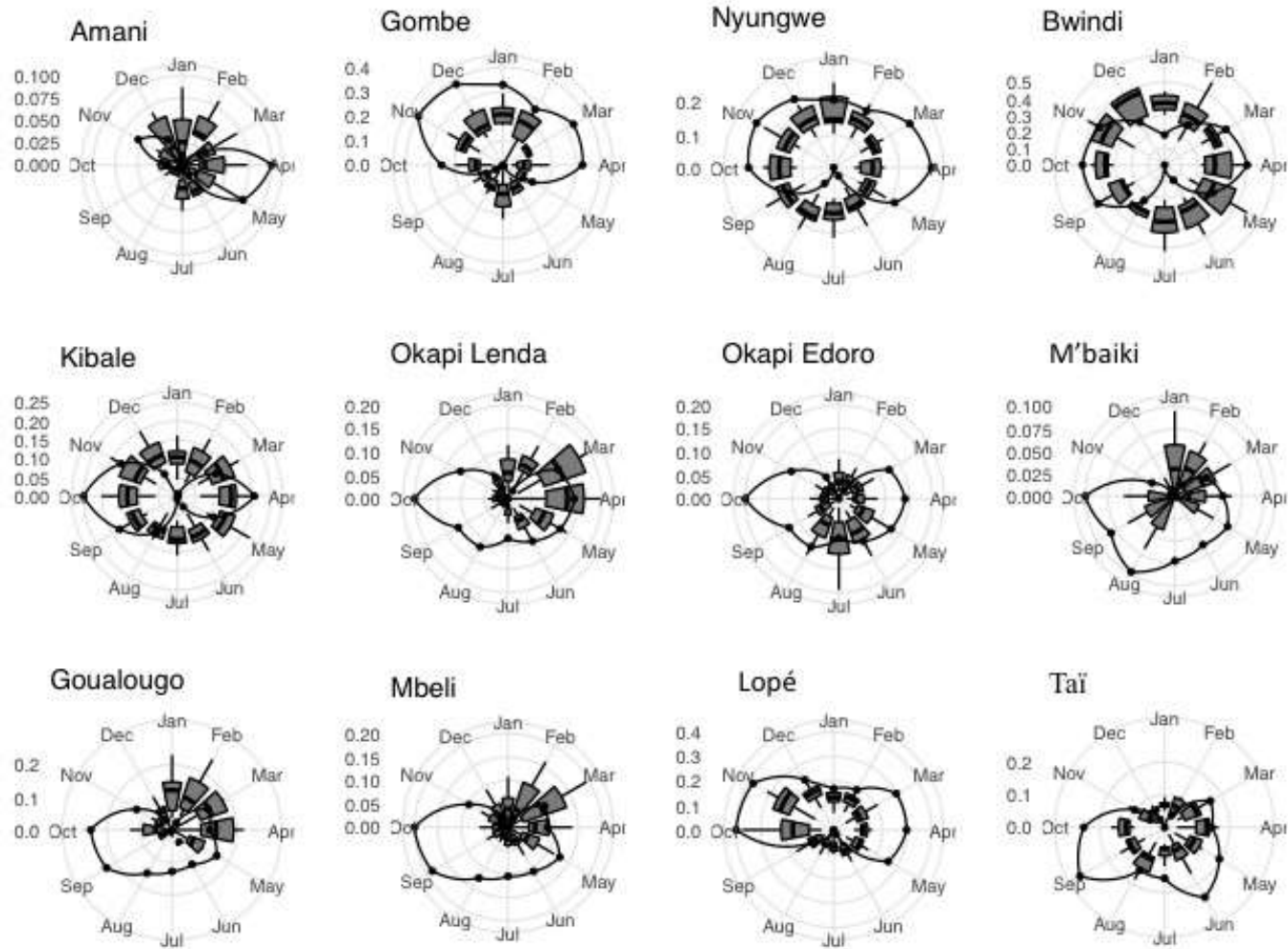
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751 **FIGURE 2.**



752

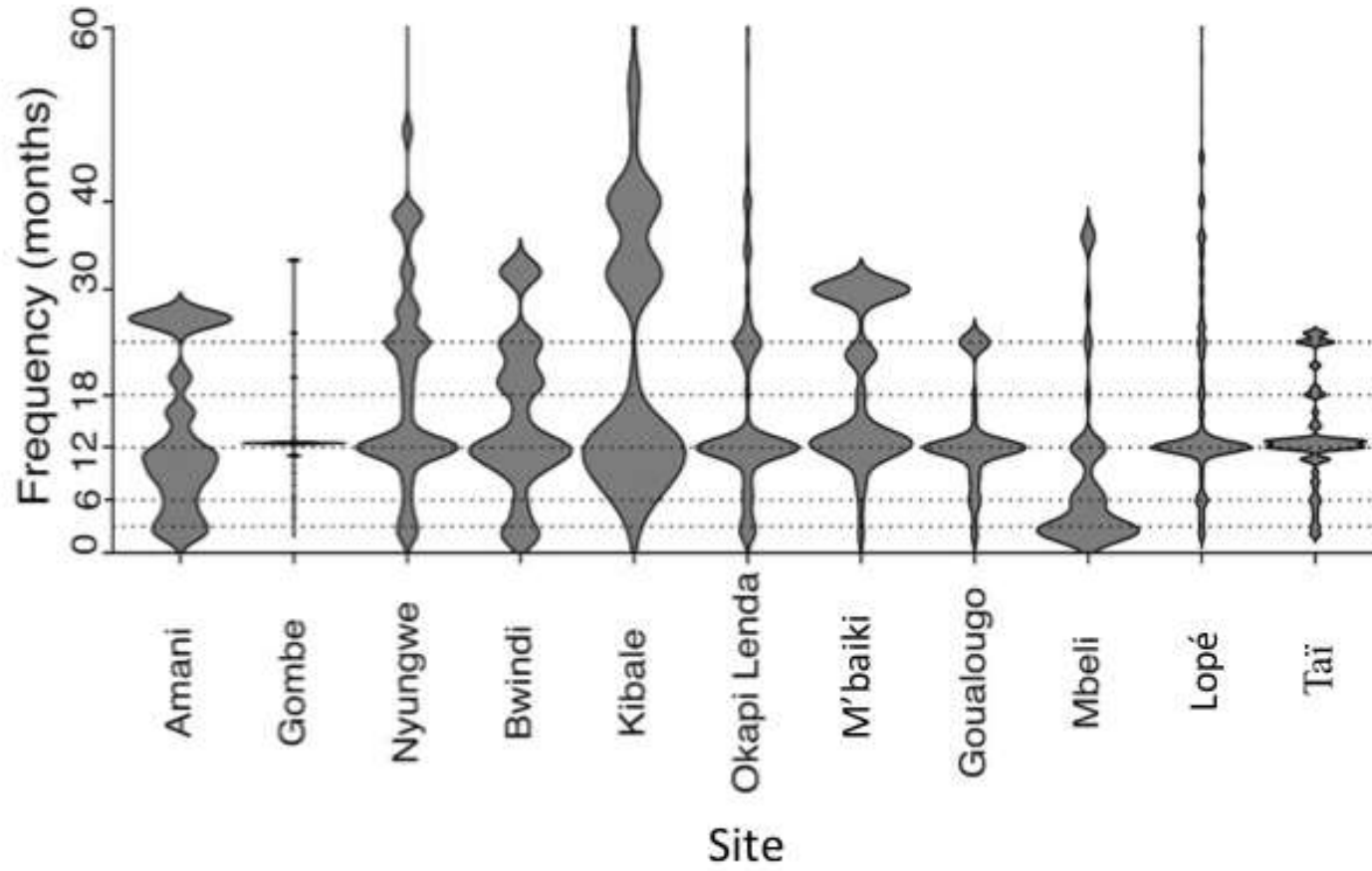
753 **FIGURE 3.**
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755

756

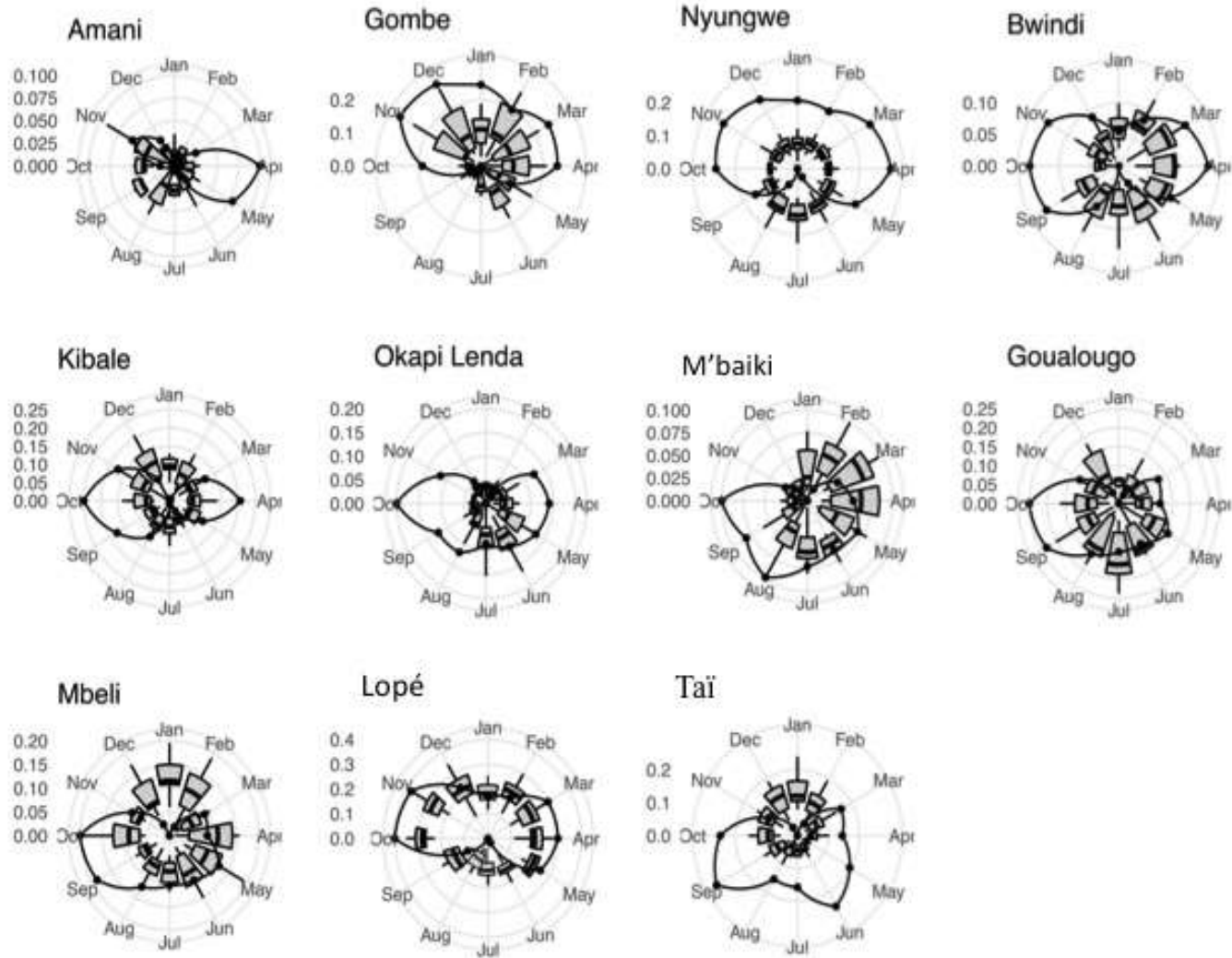
FIGURE 4.



757

758

FIGURE 5.



759