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

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

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ABSTRACT

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

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

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3 91 PLANT PHENOLOGY, THE TIMING OF CYCLICAL BIOLOGICAL EVENTS (PHENOPHASES) SUCH AS
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5 92  flowering and fruiting, is essential for the reproductive success of plants, and equally
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8 93 important for animals that rely on plant resources to survive and reproduce (van Schaik *et al.*
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10 94 1993, Sakai 2001). Phenology is well studied in northern, temperate systems (Visser & Both
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12 95 2005) and changes in phenology associated with climate warming are widespread (Parmesan &
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14 96 Yohe 2003). However, the phenology of tropical plants is poorly understood, due both to the
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17 97 paucity of long-term data sets and the complexity of individual patterns (Gentry 1974, Hudson &
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19 98 Keatley 2009). Ultimately, if we are to understand how phenology is changing in the tropics, it is
20
21 99 vitally important to establish how canopy-level patterns emerge from variation at the levels of
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24 100 species and communities.

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26 101
27
28 102 Globally, tropical forests are characterised by an exceptionally high diversity of plant species,
29
30 103 which can flower or fruit at any time of the year, often with very different patterns to other
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32 104 species within the same forest, including closely related taxa (Bawa *et al.* 2003, Zhou *et al.*
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34 105 2014). Flowering and fruiting events in tropical forests vary from complete intraspecific
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36 106 synchrony to extreme asynchrony, and from constant activity to recurrent short pulses (van
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38 107 Schaik *et al.* 1993). Depending on the environmental conditions, species, individual tree
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40 108 characteristics, location and sometimes year, different phenophases occur at different times of
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42 109 the year, in different seasons, and vary in their frequencies and duration (Sakai *et al.* 1999, Pau *et*
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44 110 *al.* 2013, Bush *et al.* 2017).

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50 112 To produce leaves, flowers, or fruits, an adult tree needs to accumulate sufficient nutritional
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53 113 resource before a phenophase onset can be triggered (Opler *et al.* 1976). Consequently, weather
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conditions that could trigger phenophase onset cannot do so if the tree has not first acquired sufficient resources to enable it to respond (Bullock & Solis-Magallanes 1990). Fruiting events also do not necessarily always follow flowering, as flowers may not be pollinated, may be damaged by weather and herbivores, or trees may abort unripe fruits (Stephenson 1981). These factors make the study of phenological responses in relation to climate extremely challenging. Large and long-term datasets are therefore required to study general phenological patterns, and this is especially needed to offset the high heterogeneity of individual tree responses.

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

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

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

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

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

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'baiki 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'baiki) 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

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

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

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

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

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

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

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

TESTING FOR DIFFERENCES IN CYCLIC ACTIVITY AMONG SITES — We used the Fourier-derived 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

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

RESULTS

SITE LEVEL FLOWERING AND FRUITING CYCLES - Across 12 sites and 5446 individuals (196 species) for which all data quality control conditions were met, we found 46% of all individual trees showed dominant annual flowering cycles (between 11 and 13 months), 29% of individuals showed sub-annual cycles (typically between 5 and 7 months) and supra-annual cycles (above 13 months) were seen in 25% of trees, with 24-month cycles being the most common. The overall prevalence of annual cycles in individuals was reflected at the site-level in Gombe, Nyungwe, Bwindi, Okapi Lenda, Okapi Edo, Goulougo, Mbeli, Lopé and Taï. Elsewhere annual cycles were not most common, with **M'Baiki** showing mainly supra-annual cycles, Kibale showing a very diverse profile with sub-annual, annual and a variety of mainly supra-annual cycles and Amani showing mainly sub-annual cycles (Fig 2). Remarkably, despite being only 35 km apart and in the same forest type, Okapi Lenda and Edo showed different dominant cycles with far greater diversity in cycle length in Okapi Lenda.

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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Boesch 2013). In five of our sites, peak fruiting occurred during the wet season (c.f. Sun *et al.* 1996), a pattern also common in South and Central America (Smythe 1970) and Asia (Medway 1972). However, in another five sites, peak fruiting occurred in the dry season, and for one site, fruiting peaked in the transition from wet to dry. There was no discernible pattern in the geographic distribution, seasonality, or rainfall characteristics of wet vs. dry season fruiting sites.

Phenological complementarity between plants and animals is crucial for ecosystem organisation, process and function (Cleland *et al.* 2007), and the importance of phenological events in understanding the ecology and evolution of species within their communities has been previously demonstrated (Chapman *et al.* 2005, Visser & Both 2005). Changes in plant phenology can lead to cascading effects across the entire ecosystem by causing phenological mismatches between the cycles followed by plants and the animals that rely on them (Newstrom *et al.* 1994, Sakai 2001, Morellato *et al.* 2016). Mismatches have already been observed in temperate regions where phenology has changed differently for animals and plant communities, due to recent rapid changes in climate (Brown *et al.* 2016). Morellato *et al.* (2016) and Mendoza *et al.* (2017) review the evidence and likelihood of such mismatches arising in neotropical forests. Chapman *et al.* (2005), Polansky & Boesch (2013), Dunham *et al.* (this issue) and Chapman *et al.* (this issue) consider the consequences of mismatches in African forests. All conclude that primate foragers have developed behavioural patterns in response to the predictability of fruit resources, and are likely to suffer population declines if fruit phenology cycles become less regular.

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

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

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

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

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500

501 **DATA AVAILABILITY STATEMENT**

502 The summary data from this study will be available via the WCS data portal website (doi: xxx

503  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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TABLES

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

	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

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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)

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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
										653

654

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
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659 Bujo, Corneille Ewango and Terese Hart; Lopé **Reserve**, Gabon – Kate Abernethy, Emma Bush, Edmond Dimoto, Jean-
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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
Taï	10	380	19	34

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 ones presented in the text because in this summary we considered all species, including the ones present at multiple sites (therefore species may appear more than once)

Site (South East to North West)	Original sample		Detected cycle sample		Characteristics of detected cycles					
					Sub annual		Annual		Supra annual	
	N Species	N trees	N Species	N trees	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
Taï	108	1000	44	2049	43	663	43	973	39	413
Total	669	7693	258	5446	208	1620	231	2479	216	1311

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

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

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
Taï	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

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

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FIGURE LEGENDS

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

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

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

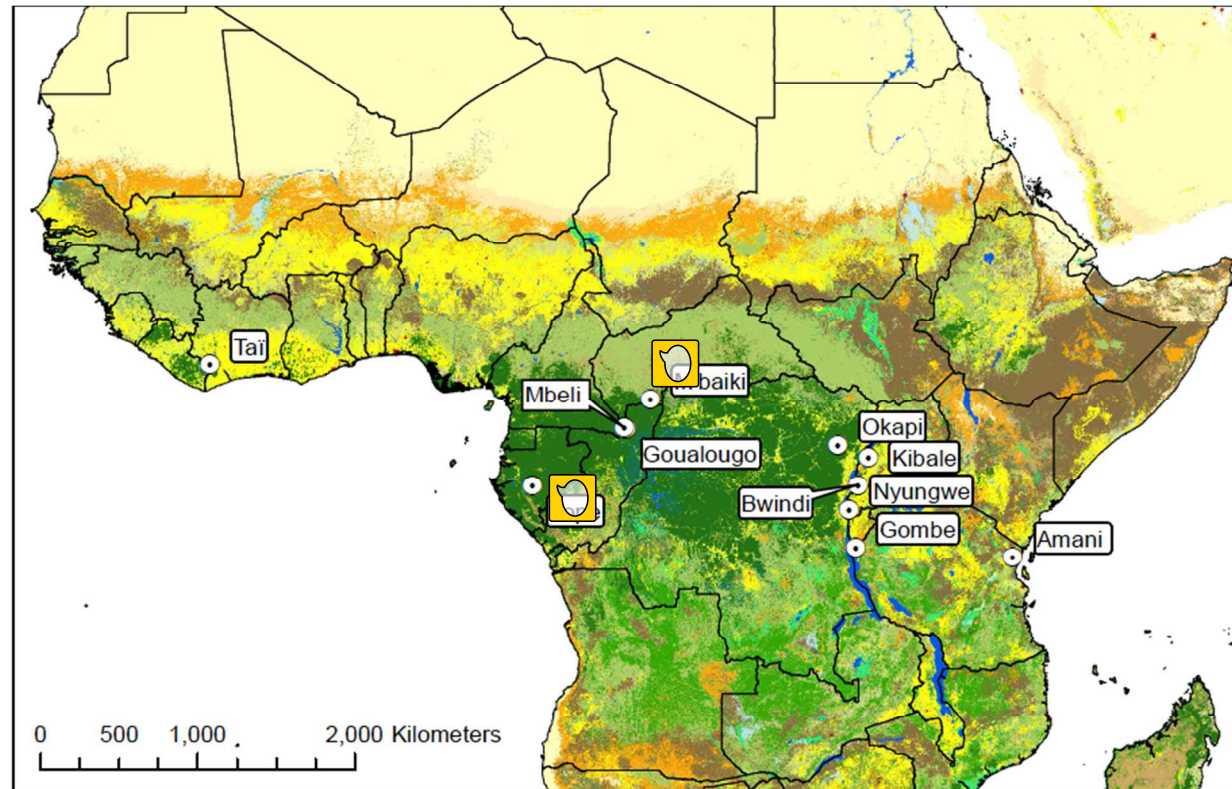
FIGURE 4. Violin plot showing the density of fruiting frequency of all individual trees present at each African site. (Species present after Fourier analysis was applied for each site: Amani = 11, Gombe = 10, Nyungwe = 49, Bwindi = 7, Kibale = 7), Okapi Lenda = 20, M'baiki = 6,

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

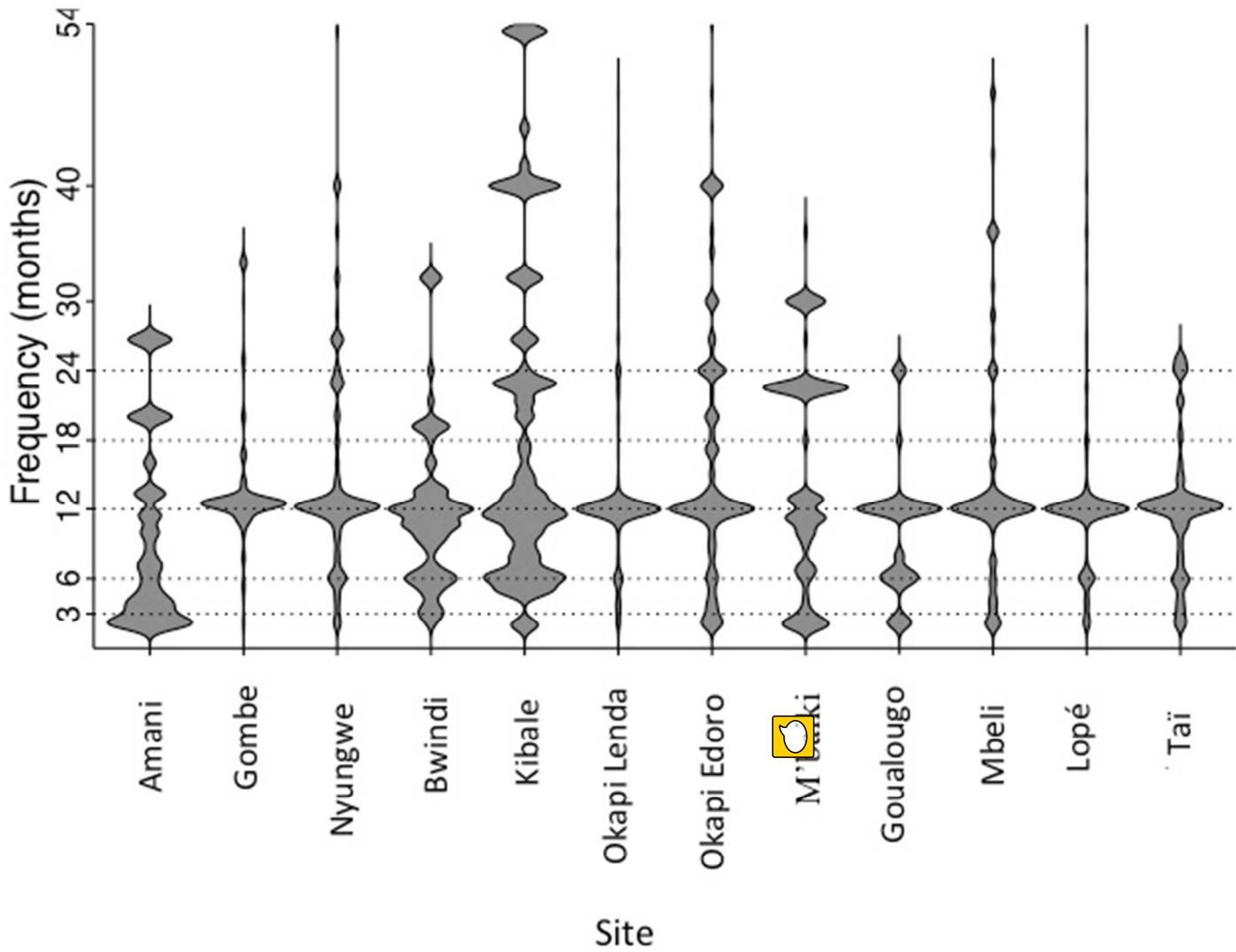
734 FIGURE 5. Fruiting seasonality at 11 sites in Africa. Black graph represents the rainfall for
735 each month normalised to the rainfall of the wettest month. Circular plots show the proportion
736 of individual trees flowering in each month for 11 sites. Sites are labelled above each circular
737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

FIGURES

FIGURE 1.



751 **FIGURE 2.**



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753 **FIGURE 3.**

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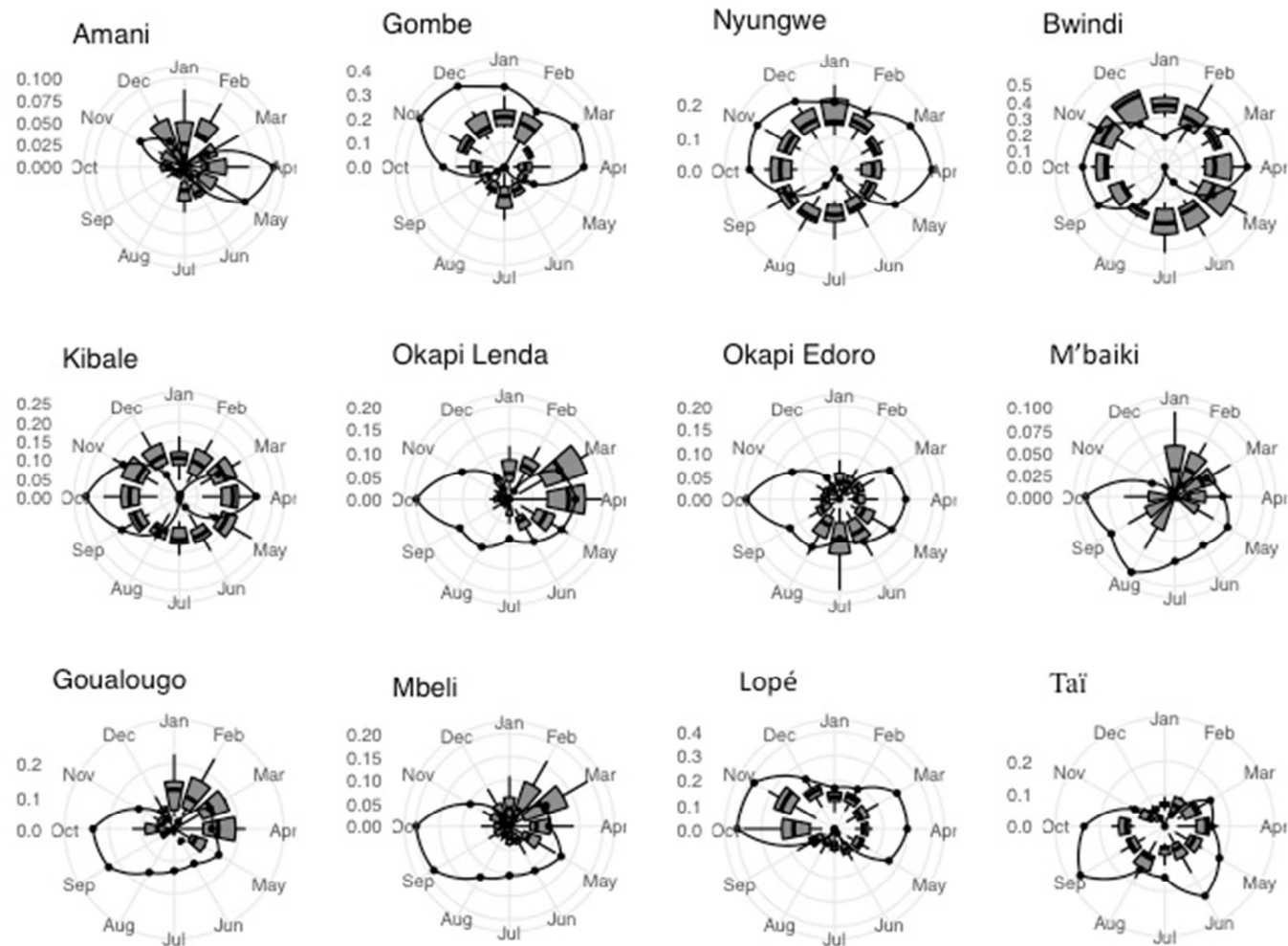
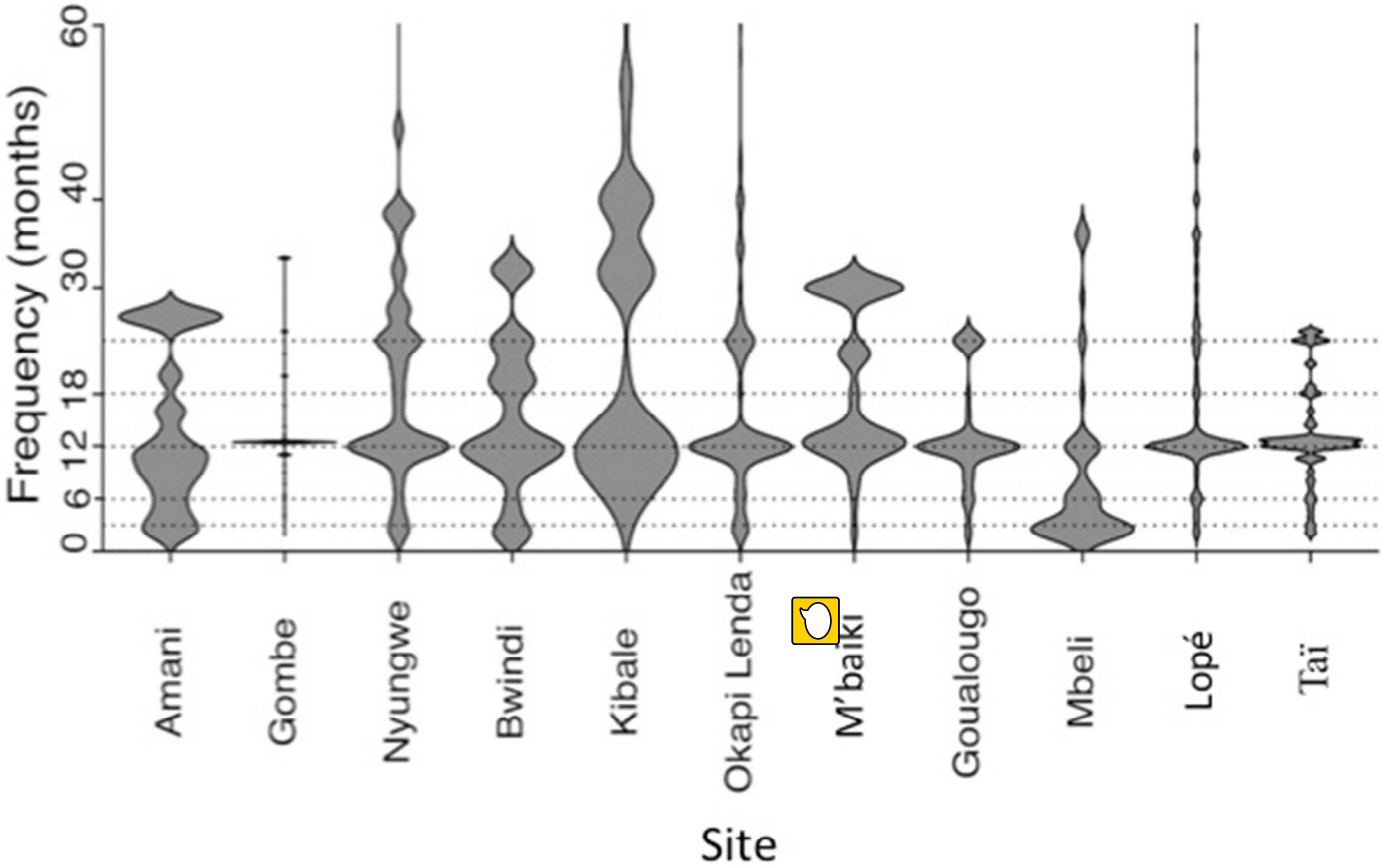


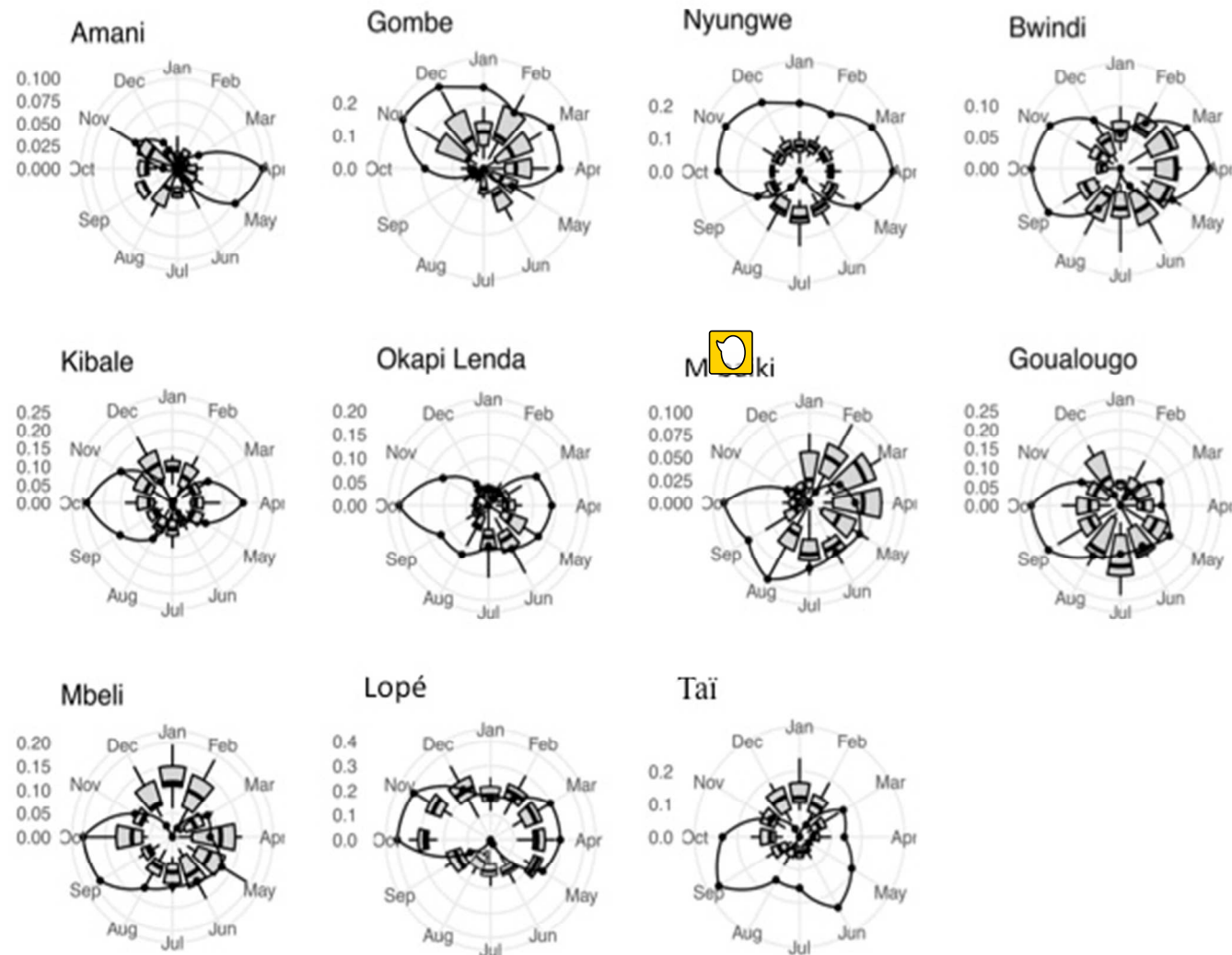
FIGURE 4.



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FIGURE 5.



Supplementary Material A

Table 1. Species characteristics

Species	Site	Family	Genus	Dioecious	Liana	Dispersal	Pod / Capsule	Fleshy Fruit	Nut	Winged Seed
Afzelia bella	Tai	Fabaceae	Afzelia	0	0	auto	1	NA	NA	NA
Agelaea paradoxa	Tai	Connaraceae	Agelaea	0	0	zoo	1	1	NA	NA
Alangium chinense	Nyungwe	Alangiaceae	Alangium	0	0	zoo	NA	1	NA	NA
Albizia gummifera	Okapi Lenda	Fabaceae	Albizia	0	0	wind	1	NA	NA	NA
Albizzia grandibracteata	Kibale	Fabaceae	Albizia	0	0	wind	1	NA	NA	NA
Allanblackia stuhlmannii	Amani	Clusiaceae	Allanblackia	1	0	zoo	NA	NA	1	NA
Alsodeiopsis schumannii	Amani	Icacinaceae	Alsodeiopsis	0	0	zoo	NA	1	NA	NA
Alstonia boonei	Okapi Lenda	Apocynaceae	Alstonia	0	0	wind	1	NA	NA	NA
Alstonia boonei	Okapi Lenda	Apocynaceae	Alstonia	0	0	wind	1	NA	NA	NA
Anisophyllea obtusifolia	Amani	Anisophyllaceae	Anisophyllea	1	0	zoo	NA	1	NA	NA
Anonidium mannii	Mbeli	Annonaceae	Anonidium	0	0	zoo	NA	1	NA	NA
Anthonotha macrophylla	Okapi Edozo	Fabaceae	Anthonotha	0	0	auto	1	NA	NA	NA
Antidesma vogelianum	Lope	Euphorbiaceae	Antidesma	1	0	zoo	NA	1	NA	NA
Apodytes dimidiata	Okapi Edozo	Icacinaceae	Apodytes	0	0	zoo	NA	1	NA	NA
Apodytes dimidiata	Okapi Edozo	Icacinaceae	Apodytes	0	0	zoo	NA	1	NA	NA
Aucoumea klaineana	Lope	Burseraceae	Aucoumea	1	0	wind	1	NA	NA	1
Balthasaria schliebenii	Nyungwe	Theaceae	Melchiora	0	0	auto	1	NA	NA	NA
Beilschmiedia rwandensis	Nyungwe	Lauraceae	Beilschmiedia	0	0	zoo	NA	1	NA	NA
Bersama abyssinica	Nyungwe	Meliantaceae	Bersama	0	0	zoo	1	1	NA	NA
Blighia welwitschii	Okapi Edozo	Sapindaceae	Blighia	1	0	zoo	1	NA	NA	NA
Blighia welwitschii	Okapi Edozo	Sapindaceae	Blighia	1	0	zoo	1	NA	NA	NA

Bobgunnia fistuloides	Lope	Fabaceae	Bobgunnia	0	0	zoo	1	NA	NA	NA
Bridelia brideliifolia	Nyungwe	Euphorbiaceae	Bridelia	0	0	zoo	NA	1	NA	NA
Calpocalyx aubrevillei	Tai	Fabaceae	Calpocalyx	0	0	Ball	1	NA	NA	NA
Calpocalyx brevibracteatus	Tai	Fabaceae	Calpocalyx	0	0	Ball	1	NA	NA	NA
Canarium schweinfurthii	Lope	Burseraceae	Canarium	0	0	zoo	NA	1	NA	NA
Carapa grandiflora	Nyungwe	Meliaceae	Carapa	0	0	zoo	NA	1	NA	NA
Casearia runssorica	Nyungwe	Flacourtiaceae	Casearia	0	0	zoo	NA	1	NA	NA
Cassia mannii	Okapi Edo	Fabaceae	Cassia	0	0	auto	1	NA	NA	NA
Cassipourea ruwenzoriensis	Nyungwe	Rhizophoraceae	Cassipourea	0	0	zoo	1	NA	NA	NA
Celtis adolfi-fridericii	Goualougo	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Celtis africana	Amani	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Celtis durandii	Kibale	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Celtis durandii	Kibale	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Celtis mildbraedii	Okapi Lenda	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Celtis tessmannii	Lope	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
Cephalosphaera usambarensis	Amani	Myristicaceae	Cephalosphaera	0	0	zoo	NA	1	NA	NA
Chaetacme aristata	Kibale	Ulmaceae	Chaetachme	1	0	zoo	NA	1	NA	NA
Chionanthus africanus	Nyungwe	Oleaceae	Chionanthus	0	0	zoo	NA	1	NA	NA
Chrysophyllum africanum	Mbaiki	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
Chrysophyllum boukokoense	Mbaiki	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
Chrysophyllum gorungosanum	Nyungwe	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
Chrysophyllum rwandense	Nyungwe	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
Chrysophyllum	Tai	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA

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7		subnudum									
8	Chrysophyllus africanum	Lope	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
9	Cissus dinklagei	Lope	Vitaceae	Cissus	0	1	zoo	NA	1	NA	NA
10	Cleistanthus pierlotti	Okapi Edo	Euphorbiaceae	Cleistanthus	0	0	auto	1	NA	NA	NA
11	Cola lateritia	Okapi Lenda	Sterculiaceae	Cola	0	0	zoo	1	NA	NA	NA
12	Cola lizae	Lope	Sterculiaceae	Cola	0	0	zoo	1	NA	NA	NA
13	Comiphyton gabonense	Okapi Edo	Anisophyllaceae	Comiphyton	0	1	zoo	NA	1	NA	NA
14	Coula edulis	Tai	Olacaceae	Coula	0	0	zoo	NA	1	NA	NA
15	Croton haumanianus	Okapi Edo	Euphorbiaceae	Croton	0	0	zoo	NA	1	NA	NA
16	Croton macrostachyus	Bwindi	Euphorbiaceae	Croton	0	0	zoo	1	NA	NA	NA
17	Cynometra alexandri	Okapi Edo	Fabaceae	Cynometra	0	0	auto	1	NA	NA	NA
18	Cynometra alexandri	Okapi Edo	Fabaceae	Cynometra	0	0	auto	1	NA	NA	NA
19	Dacryodes buettneri	Lope	Burseraceae	Dacryodes	1	0	zoo	1	NA	NA	NA
20	Dacryodes klaineana	Tai	Burseraceae	Dacryodes	1	0	zoo	1	NA	NA	NA
21	Daniellia thurifera	Tai	Fabaceae	Daniellia	0	0	auto	1	NA	NA	NA
22	Detarium macrocarpum	Mbeli	Fabaceae	Detarium	0	0	zoo	NA	1	NA	NA
23	Dialium aubrevillei	Tai	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
24	Dialium corbisieri	Okapi Edo	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
25	Dialium lopense	Lope	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
26	Dialium pentandrum	Okapi Edo	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
27	Dictyophleba lucida	Gombe	Apocynaceae	Dictyophleba	0	0	zoo	NA	1	NA	NA
28	Diospyros dendo	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
29	Diospyros ivoriensis	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
30	Diospyros polystemon	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
31	Diospyros sanza-minika	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
32	Diospyros soubreana	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
33	Diospyros zenkeri	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
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Diplorhynchus condylocarpon	Gombe	Apocynaceae	Diplorhynchus	0	0	zoo	1	NA	NA	NA
Dombeya goetzenii	Nyungwe	Sterculiaceae	Dombeya	0	0	auto	1	NA	NA	NA
Dombeya mukou	Kibale	Sterculiaceae	Dombeya	0	0	auto	1	NA	NA	NA
Drypetes gerrardii	Bwindi	Euphorbiaceae	Drypetes	1	0	zoo	NA	1	NA	NA
Duboscia macrocarpa	Mbeli	Tiliaceae	Duboscia	1	0	zoo	1	NA	NA	NA
Duboscia macrocarpa	Mbeli	Tiliaceae	Duboscia	1	0	zoo	1	NA	NA	NA
Duguetia staudtii	Tai	Annonaceae	Duguetia	1	0	zoo	1	NA	NA	NA
Duguetia staudtii	Tai	Annonaceae	Duguetia	1	0	zoo	1	NA	NA	NA
Elaeis guineensis	Gombe	Arecaceae	Elaeis	0	0	zoo	NA	1	1	NA
Entandrophragma angolense	Tai	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	NA
Entandrophragma cylindricum	Mbaiki	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	1
Entandrophragma excelsum	Nyungwe	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	1
Erythrophleum suaveolens	Okapi Lenda	Fabaceae	Erythrophleum	0	0	auto	1	NA	NA	NA
Erythrophleum suaveolens	Okapi Lenda	Fabaceae	Erythrophleum	0	0	auto	1	NA	NA	NA
Erythroxylum mannii	Tai	Erythroxylaceae	Erythroxylum	0	0	zoo	NA	1	NA	NA
Eucalyptus	Kibale	Myrtaceae	Eucalyptus	0	0	NA	NA	NA	NA	NA
Ficalhoa laurifolia	Nyungwe	Theaceae	Ficalhoa	0	0	auto	1	NA	NA	NA
Ficus lutea	Okapi Edo	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
Ficus oreodryadum	Nyungwe	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
Ficus sansibarica	Tai	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
Funtumia latifolia	Kibale	Apocynaceae	Funtumia	0	0	wind	1	NA	NA	1
Galiniera coffeoides	Nyungwe	Rubiaceae	Galiniera	0	0	zoo	NA	1	NA	NA
Ganophyllum giganteum	Lope	Sapindaceae	Ganophyllum	1	0	zoo	NA	1	NA	NA

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7	Garcinia huillensis	Gombe	Clusiaceae	Garcinia	0	0	zoo	NA	1	NA	NA
8	Gilbertiodendron										
9	dewevrei	Okapi Lenda	Fabaceae	Gilbertiodendron	0	0	auto	1	NA	NA	NA
10	Gilbertiodendron										
11	splendidum	Tai	Fabaceae	Gilbertiodendron	0	0	auto	1	NA	NA	NA
12	Greenwayodendron										
13	suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	NA	NA	NA
14	Greenwayodendron										
15	suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	NA	NA	NA
16	Grewia oligoneura	Mbeli	Tiliaceae	Grewia	0	0	zoo	NA	1	NA	NA
17	Hallea stipulosa	Okapi Edo	Rubiaceae	Hallea	0	0	auto	1	NA	NA	NA
18	Harungana										
19	madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
20	Harungana										
21	madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
22	Harungana montana	Nyungwe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
23	Heisteria parvifolia	Lope	Olacaceae	Heisteria	0	0	zoo	NA	1	NA	NA
24	Heritiera utilis	Tai	Sterculiaceae	Tarrietia	1	0	wind	NA	NA	NA	1
25	Ilex mitis	Nyungwe	Aquifoliaceae	Ilex	1	0	zoo	NA	1	NA	NA
26	Irvingia excelsa	Mbeli	Irvingiaceae	Irvingia	0	0	zoo	NA	1	NA	NA
27	Irvingia gabonensis	Lope	Irvingiaceae	Irvingia	0	0	zoo	NA	NA	NA	NA
28	Irvingia grandifolia	Lope	Irvingiaceae	Irvingia	0	0	zoo	NA	NA	NA	NA
29	Irvingia wombolu	Okapi Edo	Irvingiaceae	Irvingia	0	0	zoo	NA	1	NA	NA
30	Ixora burundensis	Nyungwe	Rubiaceae	Ixora	0	0	zoo	NA	1	NA	NA
31	Julbernardia seretii	Okapi Edo	Fabaceae	Julbernardia	0	0	auto	1	NA	NA	NA
32	Klainedoxa gabonensis	Lope	Irvingiaceae	Klainedoxa	0	0	zoo	NA	1	NA	NA
33	Macaranga capensis	Amani	Euphorbiaceae	Macaranga	1	0	zoo	1	NA	NA	NA
34	Macaranga										
35	kilimandscharica	Nyungwe	Euphorbiaceae	Macaranga	1	0	zoo	1	NA	NA	NA
36	Macaranga	Okapi Edo	Euphorbiaceae	Macaranga	1	0	auto	1	NA	NA	NA
37											
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schweinfurthii										
Maesa lanceolata	Nyungwe	Myrsinaceae	Maesa	0	0	zoo	NA	1	NA	NA
Maesopsis eminii	Amani	Rhamnaceae	Maesopsis	0	0	zoo	NA	1	NA	NA
Maesopsis eminii	Amani	Rhamnaceae	Maesopsis	0	0	zoo	NA	1	NA	NA
Magnistipula butayei	Nyungwe	Chrysobalanaceae	Magnistipula	0	0	zoo	1	NA	NA	NA
Magnistipula butayei	Nyungwe	Chrysobalanaceae	Magnistipula	0	0	zoo	1	NA	NA	NA
Manilkara zenkeri	Okapi Edo	Sapotaceae	Manilkara	0	0	zoo	NA	1	NA	NA
Maranthes goetzeniana	Amani	Chrysobalanaceae	Maranthes	0	0	zoo	NA	1	NA	NA
Margaritaria discoidea	Okapi Lenda	Euphorbiaceae	Margaritaria	1	0	zoo	NA	1	NA	NA
Massularia acuminata	Lope	Rubiaceae	Massularia	0	0	zoo	NA	1	NA	NA
Maytenus acuminata	Nyungwe	Celastraceae	Gymnosporia	0	0	zoo	1	NA	NA	NA
Memecylon lateriflorum	Tai	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Memecylon polyanthemos	Tai	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Memecylon walikalense	Nyungwe	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Mesogyne insignis	Amani	Moraceae	Mesogyne	0	0	zoo	NA	1	NA	NA
Milicia excelsa	Lope	Moraceae	Milicia	0	0	zoo	NA	1	NA	NA
Milletia dura	Kibale	Fabaceae	Millettia	0	0	auto	1	NA	NA	NA
Milletia dura	Kibale	Fabaceae	Millettia	0	0	auto	1	NA	NA	NA
Monanthotaxis congoensis	Lope	Annonaceae	Monanthotaxis	0	0	zoo	NA	1	NA	NA
Monanthotaxis poggei	Gombe	Annonaceae	Monanthotaxis	0	0	zoo	NA	1	NA	NA
Musanga cecropioides	Okapi Lenda	Moraceae	Musanga	0	0	zoo	NA	1	NA	NA
Myrianthus arboreus	Lope	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Myrianthus holstii	Amani	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Myrianthus holstii	Amani	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Nauclea diderrichii	Okapi Edo	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA

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7	Nauclea xanthoxylon	Tai	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA
8	Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
9	Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
10	Newtonia buchananii	Nyungwe	Mimosaceae	Newtonia	0	0	wind	1	NA	NA	NA
11	Ochna afzelii	Nyungwe	Ochnaceae	Ochna	0	0	zoo	NA	1	NA	NA
12	Ocotea usambarensis	Nyungwe	Lauraceae	Ocotea	0	0	zoo	NA	1	NA	NA
13	Odyendea zimmermannii	Amani	Simaroubaceae	Quassia	0	0	zoo	NA	1	NA	NA
14	Olea capensis	Bwindi	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
15	Olea welwitschii	Kibale	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
16	Olinia rochetiana	Nyungwe	Oliniaceae	Olinia	0	0	zoo	NA	1	NA	NA
17	Ongokea gore	Lope	Olacaceae	Ongokea	0	0	zoo	NA	1	NA	NA
18	Panda oleosa	Lope	Pandaceae	Panda	0	0	zoo	NA	1	NA	NA
19	Parinari capensis	Gombe	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
20	Parinari excelsa	Okapi Edo	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
21	Parkia bicolor	Lope	Fabaceae	Parkia	0	0	zoo	1	NA	NA	NA
22	Pentaclethra macrophylla	Lope	Fabaceae	Pentaclethra	0	0	auto	1	NA	NA	NA
23	Pentadesma butyracea	Tai	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
24	Pentadesma reyndersii	Nyungwe	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
25	Podocarpus latifolius	Nyungwe	Podocarpaceae	Podocarpus	0	0	zoo	NA	1	NA	NA
26	Polyathia suaveolens	Amani	Annonaceae	Polyathia	0	0	zoo	NA	1	NA	NA
27	Polyscias fulva	Nyungwe	Araliaceae	Polyscias	0	0	zoo	NA	1	NA	NA
28	Porterandia cladantha	Lope	Rubiaceae	Aoranth	0	0	zoo	NA	1	NA	NA
29	Pouteria altissima	Mbaiki	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
30	Pouteria aningeri	Tai	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
31	Prunus africana	Nyungwe	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
32	Prunus africanum	Kibale	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
33	Pseudospondias	Lope	Anacardiaceae	Pseudospondias	1	0	zoo	NA	1	NA	NA
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microcarpa										
Pseudospondias										
microcarpa	Lope	Anacardiaceae	Pseudospondias	1	0	zoo	NA	1	NA	NA
Psidium guineense	Lope	Myrtaceae	Psidium	0	0	zoo	NA	1	NA	NA
Psychotria mahonii	Nyungwe	Rubiaceae	Psychotria	0	0	zoo	NA	1	NA	NA
Psychotria vogeliana	Lope	Rubiaceae	Psychotria	0	0	zoo	NA	1	NA	NA
Pterocarpus soyauxii	Lope	Fabaceae	Pterocarpus	0	0	wind	1	NA	NA	NA
Pterocarpus tinctorius	Gombe	Fabaceae	Pterocarpus	0	0	wind	1	NA	NA	NA
Pycnanthus angolensis	Tai	Myristicaceae	Pycnanthus	0	0	zoo	NA	1	NA	NA
Pycnanthus angolensis	Tai	Myristicaceae	Pycnanthus	0	0	zoo	NA	1	NA	NA
Rapanea melanophloeos	Nyungwe	Myrsinaceae	Rapanea	0	0	zoo	NA	1	NA	NA
Rawsonia lucida	Amani	Flacourtiaceae	Rawsonia	0	0	zoo	NA	1	NA	NA
Ricinodendron heudelotii	Okapi Lenda	Euphorbiaceae	Ricinodendron	0	0	zoo	NA	1	NA	NA
Ricinodendron heudelotii	Okapi Lenda	Euphorbiaceae	Ricinodendron	0	0	zoo	NA	1	NA	NA
Rytiginia kigeziensis	Nyungwe	Rubiaceae	Rytigynia	0	0	zoo	NA	1	NA	NA
Saba comorensis	Gombe	Apocynaceae	Saba	0	1	zoo	NA	1	NA	NA
Sacoglottis gabonensis	Tai	Humiraceae	Sacoglottis	0	0	zoo	NA	1	NA	NA
Santiria trimera	Lope	Burseraceae	Santiria	0	0	zoo	NA	1	NA	NA
Sarcocephalus pobeguinii	Okapi Lenda	Rubiaceae	Sarcocephalus	0	0	zoo	NA	1	NA	NA
Schefflera goetzenii	Nyungwe	Araliaceae	Schefflera	0	0	zoo	NA	1	NA	NA
Scottelia klaineana	Tai	Flacourtiaceae	Scottellia	0	0	zoo	NA	1	NA	NA
Scytopetalum tieghemii	Tai	Scytopetalaceae	Scytopetalum	0	0	zoo	NA	1	NA	NA
Sorindeia										
madagascariensis	Amani	Anacardiaceae	Sorindeia	0	0	zoo	NA	1	NA	NA
Staudtia kamerunensis										
var. gabonensis	Lope	Myristicaceae	Staudtia	0	0	zoo	NA	1	NA	NA
Sterculia oblonga	Tai	Sterculiaceae	Eribroma	0	0	zoo	1	NA	NA	NA

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7	Strombosia pustulata	Tai	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA	
8	Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA	
9	Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA	
10	Strombosiopsis tetrandra	Okapi Edo	Olacaceae	Strombosiopsis	0	0	zoo	NA	1	NA	NA	
11	Symphonia globulifera	Nyungwe	Clusiaceae	Symphonia	0	0	zoo	NA	1	NA	NA	
12	Synsepalum afzelii	Tai	Sapotaceae	Synsepalum	0	0	zoo	NA	1	NA	NA	
13	Syzygium cordatum	Bwindi	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA	
14	Syzygium guineense	Nyungwe	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA	
15	Tabernaemontana penduliflora	Mbeli	Apocynaceae	Tabernaemontana	0	0	zoo	NA	1	NA	NA	
16	Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA	
17	Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA	
18	Thomandersia laurifolia	Mbeli	Acanthaceae	Thomandersia	0	0	auto	1	NA	NA	NA	
19	Trichoscypha acuminata	Mbeli	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA	
20	Trichoscypha arborea	Tai	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA	
21	Triplochiton scleroxylon	Mbaiki	Malvaceae	Triplochiton	0	0	wind	NA	NA	NA	1	
22	Uapaca corbisieri	Tai	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA	
23	Uapaca guineensis	Okapi Edo	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA	
24	Uvariastrum pierreanum	Lope	Annonaceae	Uvariastrum	0	0	zoo	NA	1	NA	NA	
25	Vitex doniana	Mbeli	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA	
26	Vitex fischeri	Gombe	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA	
27	Xylia evansii	Tai	Fabaceae	Xylia	0	0	auto	1	NA	NA	NA	
28	Xylophia aethiopica	Lope	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA	
29	Xylophia hypolampra	Lope	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA	
30	Xylophia quintasii	Tai	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA	
31	Zanha golungensis	Tai	Sapindaceae	Zanha	1	0	zoo	NA	1	NA	NA	
32	Zanthoxylum gillettii	Okapi Lenda	Rutaceae	Zanthoxylum	1	0	zoo	NA	1	NA	NA	
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- NA = not applicable
- 1 = applicable
- 0 = absent

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Responses to Editor's comments

We thank the editor and reviewers for their particularly thorough reviews and suggestions for improving the manuscript. We have attempted to address all these issues and believe the manuscript is considerably improved as a consequence. To conveniently document the changes we have made in response to specific comments, we summarise the key comments, changes we have made and an example of the line numbers where we have made changes relevant to this in the table below – though we note that the manuscript has been extensively redrafted so changes are present throughout. We hope you will agree that our changes have improved the manuscript and look forward to hearing from you in due course.

First of all, the writing still needs to be polished. I have done my best for signalling a few grammar errors or typos, but I guess that authors would need to use a professional linguistic editorial service.

The manuscript has been checked by at least 3 UK faculty staff with native English. We believe the English now to be error-free and apologise if there are any remaining typos.

Second, I would still recommend some rewriting of the discussion section. Try to avoid repetition of ideas regarding the common annual patterns (e.g. L308-311, 330-331, L331-333, L347-348, L409-410 say virtually the same) or the lack of quality weather data in Africa (repeated in L344-346 and 421-422). By contrast, some deeper discussion of differences among sites would be interesting and this is still lacking (despite the interesting pattern from west to east), with more site-specific description (Referee #3 signalled this too in the previous review).

We have added a few sentences to discuss the lack of clear geographic patterning in fruiting season (wet vs dry) or seasonality or aseasonality in flowering or fruiting, and to clarify that the west to east patterning in cycle profile remains only a weak effect. We feel that further discussion of patterning across sites may be an over-interpretation of our data thus far, but we have made recommendations for addressing this need.

Lines 308-311 state “Using Fourier based analysis we effectively estimated flowering patterns for 5446 individual trees of 196 species and fruiting patterns for 4595 trees of 191 species across 12 and 11 sites, respectively, both at the site level and among tropical forests spanning from western to eastern Africa.

We think this is necessary information to recall our main dataset for the reader.

Lines 331-333 were repetitive of lines 330-331 and have been removed.

Lines 347-348 considered the likelihood of cycles being driven by an annual environmental cue, which is a different subject from the original statement of results.

However, our broader revisions to the discussion mean that these lines have been deleted.

Lines 409-410 do repeat the major conclusion, but we believe this is standard practice within a conclusions section.

Lines 421-422 are a recommendation for future data collection to address the lacunae mentioned in lines 344-346 and thus do not really repeat the earlier statement.

We have revised the whole discussion section and reduced repetition throughout.

Third, there is a major misunderstanding regarding the interpretation of the Rayleigh test: when the distribution is uniform or multimodal, you cannot technically say that there is any kind of seasonality, as the test is not correctly applied in those cases.

Therefore, sentence in L385-387 is not correct, as Kibale had a uniform flowering seasonality. When the distribution is bimodal, you can apply the Rayleigh test dividing the circle and calculating two angular means. I would also include in the circular graphs an arrow with the value of the r vector, signalling the seasonality intensity (only for unimodal distributions).

I removed the mean angles as they are likely to be meaningless and did not correspond well to the data.

Fourth, I thank authors for including the supplementary material with a final list of selected species per site (and their most important traits such as dispersal mode, etc). However, the table heading of the table is missing, and it is not cited in the text. The other supplementary information including intra-specific variation of cycles within species should be edited (titles, x axis including years, etc) before publication but I guess that might be finally removed, as it is even not cited in the text.

I have made the suggested correction and cited in text.

In addition to all these points, the format of Biotropica is not followed at many parts of the paper (use of small caps for the first sentence and reference list, for instance, table titles in capitals, subheadings in small caps, etc), so the manuscript needs to be revised following these guidelines. Very importantly, the entire list of references needs major review, as numerous small mistakes are present, such as lacking journal and pages, etc.

The formatting has been corrected throughout.

As I signalled before, the data share statement needs to include the DOI of the WCS portal website. Sites with embargo need to be noted in detail, and also, the length of

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the embargo and the contact email for discussing the potential access to information.
Editors of Biotropica will give you more assistance regarding this.
[We have modified the statement and eagerly await into from Biotropica’s editors.](#)

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Minor comments:

L72. Include “the” before “most common”.

Done

L76. Put “cycle” in plural.

This suggestion is not grammatically correct in English; it should stay as ‘cycle’. However, the lines 75-79 have been revised in response the next comment and the point is now differently phrased.

L76-77. I find this sentence too vague: which sites had continuous flowering and fruiting?

We believe that the Introduction should build the general picture. As we have not introduced the reader to our site names, it would be confusing to talk about them in detail in the Introduction. We have revised to include general geographical patterns.

L85-86. Remove “Introduction”. Put the first line in Small Caps.

Done. But the guidelines state the first phrase (not entire line) needs to be in small caps.

L87. I believe that this sentence needs to be in singular (“phenology... is essential”).

Corrected

L168. All subheadings need to be in small caps.

Done

L170. Here and in other parts of the text, you need to be consistent with the spelling of the site M’Baiki (I believe that this might be the correct spelling). Please, consistently write the name of the site in L183, 275, 476, 477, L681, L691, Tables 1-5, Figs. 1-5.

Done

L174-176. Cite Table 3 here (although I believe that it should be condensed with Table 1). In case that you maintain the two tables as separated, you need to inverse numbers for actual Tables 2 and 3.

We have maintained the two tables separately, as a merged table seemed too large and confusing. We have checked the Table numbers in their text citations and legends. Table 2 now is referred to in the correct order.

L194 & 204. There is a major confusion with the correct citation of publications of Bush et al. Please, be aware that the article published in Methods in Ecology and Evolution is from 2017, whereas the article in Biotropica is from 2018! The same reference is repeated in the final list, in addition.

Checked and corrected throughout

L219. Remove “of”.

Done

L231. Replace by “time between flowering or fruiting events)

Done

L242. Put the entire name of the dataset (Climate Hazards Group InfraRed Precipitation with Station data) first time of use and the corresponding acronym (CHIRPS) in parenthesis later. I already signalled that the acronym is bad written.

Done

L246. Replace by CHIRPS.

Done

L254. Include “to” before “identify multi-modality”.

Done

L255. Please, see my previous comments about bimodality and the Rayleigh test. In the Kibale case, the Rayleigh could be applied with previous preparation of the data; reduce the angles to one side of the circle and calculate two means (see Morellato et al. 2010 and Zar 1999).

[See our comments in the table of major responses](#)

L258. The citation of the software used for the circular analyses is lacking (and the package if you were using R).

[Citation has been added and this section revised in the light of comments on the suitability of the Rayleigh test for multi-modal situations.](#)

L267-271. I think this fits better to the method section.

[Methods have been revised accordingly and the section moved up.](#)

L277-279. Were those two plots in Okapi the same forest type? This is not specified in Table 1.

[Now clarified in the table – they are the same forest type.](#)

L295-296. I believe this needs to be included in the methods.

[The sentence on significance levels has been removed to Methods section.](#)

L315. Lopé is written in smaller font size.

Corrected

L320. The authors say here and in other parts of the text (L349-350, 434-435) that sub-annual cycles are the most frequent in South America. I have said in my previous two reviews that I disagree with this statement; it is true that Newstrom et al. (1994) state that subannual life cycles abound for La Selva and supra-annual patterns dominate in Lambir (Sakai 2001), but other Neotropical examples show frequent annual and supra-annual patterns. For instance, Nouragues in French Guiana shows predominantly annual and supra-annual patterns (Norden et al. 2007, Mendoza et al. this issue), and there is evidence of annual variation of fruiting on Barro Colorado Island, where 54% of species showed CV larger than 1 (indicating masting) (Wright et al. 2005). I sincerely believe that life cycles of tropical plants are not well evaluated (even less using Fourier analyses) and would acknowledge some discussion on it (and the inclusion of these references).

We agree that the main conclusion from the body of literature available is that the question is as yet under studied. We have included an improved discussion of this point and used the literature suggested. The 54% of species (a small majority) showing masting – a supra-annual strategy- at BCI is in contrast to the predominance of annual cycles in African forests in general although more similar to our eastern sites, which is interesting.

L323. And also, evolutionary pressures for flowering and fruiting are different. Acknowledged – we have included a comment on this and a reference to the recent paper showing diverse evolutionary origins of African forests (Slik et al, 2018).

L373-375. The close of the parenthesis is lacking here. In addition, you should include any reference of the statement that wind dispersed seeds fruit during dry season, whereas fleshy fruits tend to appear during the rainy season.

Done

L178, 231 & 385. Remove space after and before the “/”.

Corrected – we have written out the words in other cases where we had used the /

L401. Put in Italics “et al.” here and elsewhere in the text.

Corrected throughout

L446. Substitute for “vary”.

This line has been revised and this word is no longer used.

Acknowledgements: They are exceptionally long, could be condensed and/or summarized? Put always first the complete name of the Institution and the abbreviation in parenthesis later (is written the opposite for M’Baïki site).

We do not feel it is appropriate to suppress acknowledgements that should be made. As this is an exceptionally long, multi-site comparison of empirical data, there are a lot of people, institutions and funders involved.

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Reference list: It needs massive review. First, the guidelines of Biotropica are not followed regarding small caps. The following errors have been detected:
Arino et al. 2009. The title, journal and pages are lacking.
[Corrected](#)

Bush et al. 2016 and 2017 is the same article!
[2016 deleted](#)

Hudson & Keatley was published in 2010.
[Corrected](#)

Medway 1972. I guess that is “Malaysia” and not “Malaya”.
[No, Malaya was the name in use at the time](#)

Morellato et al. 2010. Editors of the book are lacking.
[Added](#)

National Weather Service 2010. Remove the “a” of “Nationala”.
[Done](#)

Plumtre et al. 2012. Editorial and city are lacking.
[Added](#)

Polansky & Boesch 2013. Repeated the same reference at the end.
[Removed repeat](#)

Takenoshita et al 2008. Journal name and pages are lacking.
[Corrected](#)

Tutin & Fernandez. Put year after author names. Remove the quotation marks.
[Corrected](#)

Tables 1 and 3. I suggest condensing both tables 1 and 3, as the rainfall seasonality is part of the description of each site. Taï site is lacking from Table 3.
[We have added the Taï site to Table 3, however we believe that merging these two tables will result in an overly large and confusing table, thus we have kept them separated.](#)

Table 2. I still do not understand this table. I think you should also include the actual number of species and individuals used for Fourier analyses after you applied the criteria, instead of only the original dataset (from which you subtracted a substantial part). In addition, the heading of the table needs rewriting (“al” is bad spelled).
[The original data are in Column 2. The headings are corrected](#)

Figures 4 and 5. Please, correct the spelling of all sites (Lopé, M'Baïki, Taï,...). If you do not feel able to do this with R, use any kind of image processing software.

[Site spellings corrected.](#)

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