Article:

Adamescu, Gabriela Simina, Plumptre, Andrew J., Abernethy, Katharine A. et al. (36 more authors) (2018) Annual cycles are the most common reproductive strategy in African tropical tree communities. Biotropica. pp. 418-430. ISSN 0006-3606

https://doi.org/10.1111/btp.12561

BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

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

Journal:	*Biotropica*
Manuscript ID	BITR-17-100.R3
Manuscript Type:	Paper
Date Submitted by the Author:	24-Mar-2018
Complete List of Authors:	Adamescu, Gabriela; University of York, Department of Biology Plumptre, Andrew; WCS, Albertine Rift; Abernethy, Katharine; University of Stirling, School of Natural Sciences; CENAREST, Institut de Recherche en Ecologie Tropicale Polansky, Leo; Max-Planck-Institut fur evolutionare Anthropologie, Department of Primatology Bush, Emma; University of Stirling, Biological and Environmental Sciences Chapman, Colin; McGill University, Anthropology/School of Environment Shoo, Luke; The University of Queensland, School of Biological Sciences Fayolle, Adeline; Gembloux Agro-Bio Tech / ULg, Unit of Forest and Nature Management Janmaat, Karline; Max-Planck-Institut fur evolutionare Anthropologie, Department of Primatology Robbins, Martha; Max Planck Institute of Evolutionary Anthropology, Primatology Ndangalasi, Henry; University of Dar es Salaam, Botany Cordeiro, Norbert; Roosevelt University, Biology Aud 520; The Field Museum, Departments of Zoology & Botany Glibly, Ian; Arizona State University School of Human Evolution and Social Change Wittig, Roman; Max-Planck-Institut fur evolutionare Anthropologie Breuer, Thomas; Wildlife Conservation Society - Congo Program, Mbeli Bai Study; Max Planck Institute for Evolutionary Anthropology, Primatology Ndoundou Hockemba, Mireille; Wildlife Conservation Society - Congo Program, Mbeli Bai Study; Sanz, Crickette; Washington University in St Louis, Anthropology Morgan, David; Lester E. Fisher Center for the Study and Conservation of Apes Pusey, Anne; Duke University, Department of Evolutionary Anthropology Mugerwa, Badru ; University of Dar es Salaam Gilagiza , Baraka ; Gombe Stream Research Centre Tutin, Caroline; University of Stirling, Biological and Environmental Sciences Ewango, Corneille; Wildlife Conservation Society Sheil, Douglas; Center for International Forestry Research, Dimoto, Edmond; Agence Nationale des Parcs Nationaux (ANPN) Baya, Fidèle; Agence Nationale des Parcs Nationaux (ANPN) Flort, Bujo; Wildlife Conservation Society Ssali, Fredrick; University of Dar es Salaam, Department of Botany

Dikangadissi, Jean-Thoussaint ; Agence Nationale des Parcs Nationaux (ANPN)
Jeffery, Kathryn; University of Stirling, Biological and Environmental Sciences; Institut de Recherche en Écologie Tropicale, CENAREST; Agence Nationale des Parcs Nationaux (ANPN)
Valenta, Kim; University of Toronto, Anthropology
White, Lee; Agence Nationale des Parcs Nationaux (ANPN); University of Stirling, Biological and Environmental Sciences; Institut de Recherche en Écologie Tropicale, CENAREST
Masozera, Michel; Wildlife Conservation Society
Wilson, Michael; University of Minnesota, Department of Ecology, Evolution and Behavior
Bitariho, Robert; University of Dar es Salaam
Ndolo Ebika, Sydney ; Initiative des Champignons et des Plantes du Congo (ICPC)
Gourlet-Fleury, Sylvie; CIRAD, FORESTRY
Mulindahabi , Felix; Wildlife Conservation Society
Beale, Colin; University of York, Department of Biology

Keywords: Phenology, Annual cycles, Seasonality, Flowers, Fruits, Tropical forest, Africa

BIOTROPICA

THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

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

Authors: Gabriela S. Adamescu[1], Andrew J. Plumptre[2,3], Katharine A. Abernethy[4,5], Leo Polansky[6], Emma R. Bush[4], Colin A. Chapman[7], Luke P. Shoo[8], Adeline Fayolle[9], Karline R. L. Janmaat[6], Martha M. Robbins[6], Henry J. Ndangalasi[24], Norbert J. Cordeiro[10], Ian C. Gilby[11], Roman M. Wittig[6, 12], Thomas Breuer[2, 13], Mireille Breuer-Ndoundou Hockemba[13], Crickette M. Sanz[14, 15], David B. Morgan[16], Anne E. Pusey[17], Badru Mugerwa[25], Baraka Gilagiza[18], Caroline Tutin[4], Corneille E.N. Ewango[2], Douglas Sheil[25], Edmond Dimoto[19], Fidèle Baya[20], Flort Bujo[2], Fredrick Ssali[25], Jean-Thoussaint Dikangadissi[19], Kathryn Jeffery[4,19], Kim Valenta[7], Lee White[4,5,19], Michel Masozera[2], Michael L. Wilson[21], Robert Bitariho[25], Sydney T. Ndolo Ebika[22], Sylvie Gourlet-Fleury[23], Felix Mulindahabi[2] and Colin M. Beale[1]

1. Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK
2. Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA
3. Conservation Science Group, Department of Zoology, Cambridge University, Pembroke Rd, Cambridge, United Kingdom
4. Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK

5. Institut de Recherche en Ecologie Tropicale, CENAREST, BP 842, Libreville, Gabon
6. Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Deutscher Platz 6, 04103, Leipzig, Germany
7. Department of Anthropology and McGill School of Environment, McGill University, Montreal, Quebec, Canada, and Wildlife Conservation Society, Bronx, NY, U.S.A.
8. School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia
9. TERRA Teaching and Research Center, Gembloux Agro-Bio Tech, Liège University, Passage des Déportés 2, 5030 Gembloux, Belgium

10. Roosevelt University, Dept. of Biology, 430 Michigan Ave, Chicago, IL 60605, U.S.A. & Science and Education, The Field Museum, 1400 S. Lake Shore Dr., Chicago, IL 60605, U.S.A.
11. School of Human Evolution and Social Change, Arizona State University
12. Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, BP 1303, Abidjan 01, Ivory Coast
13. Mbeli Bai Study, Wildlife Conservation Society – Congo Program, 151 Avenue Charles de Gaulle, 14537 Brazzaville, Republic of Congo
14. Washington University in St. Louis, Department of Anthropology, 1 Brookings Drive, Saint Louis, MO 63130, U.S.A.
15. Congo Program, Wildlife Conservation Society, 151 Avenue de Gaulle, Brazzaville, Republic of Congo
16. Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, 2001 North Clark Street, Chicago, IL 60614, U.S.A.

17. Department of Evolutionary Anthropology, Duke University
18. Gombe Stream Research Centre, Tanzania
19. Agence Nationale des Parcs Nationaux (ANPN), B.P. 20379, Libreville, Gabon
20. Ministère des Eaux, Forêts, Chasse et Pêche, BP 3314 Bangui, Central African Republic
21. Departments of 1) Anthropology and 2) Ecology, Evolution & Behavior, University of Minnesota
22. Initiative des Champignons et des Plantes du Congo (ICPC), B.P. 2300, Brazzaville, Republic of Congo
23. UPR Bsef, CIRAD, Montpellier, France
24. Department of Botany, University of Dar es Salaam, P.O. Box 35060, Dar es Salaam, Tanzania
25. Institute of Tropical Forest Conservation (ITFC), PO BOX 44, Kabale, Uganda
26. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences.

Corresponding author: Gabriela S. Adamescu, adamescusimina@gmail.com

Received _____; revision accepted _____.

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

Word count: 5096

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

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

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

METHODS

DATA COLLECTION — We assembled data from 12 long-term research sites across East, Central and West Africa (Fig. 1), including montane, submontane, semi-deciduous, evergreen and swamp forests (Table 1). With the exception of M'baïki, which was in a conservation area within a logging concession, all forest sites were located within protected areas. Site elevation and total protected area around the study trees varied between 80 to 3000 m and from 35 km^2 to approximately 13,000 km^2, respectively. Each site experiences two main seasons, dry and wet, each present once or twice a year, depending on the site location. Average minimum and maximum monthly temperatures were between 12 and 30 °C, with maximum rainfall ranging between 200 mm and 700 mm per month (Table 2). Data collection of flowering and fruiting events (data for ripe fruit only are used in these analyses) at each site was done monthly and was accomplished by the investigators and trained field assistants. Each tree was visually monitored for the presence/absence of flowers or ripe fruits. In some sites the phenophase response was quantified, but as different scoring methods were used at different sites, we restricted our analyses to presence/absence. Monitored individuals were originally selected based on different research questions at each site and thus most sites represent a non-random subset of the total forest coverage and species diversity (More information on species diversity in Supplementary material A). One site (M'baïki) selected species important in the timber trade, but with the exception of Amani in Tanzania where phenological transects were randomly located, all other sites preferentially sampled species producing fleshy fruits, as original research questions focussed on resource availability for large mammals, mainly primates or elephants. Although the 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 spans depending on the time series length to give a bandwidth of 0.1. The 0.1 bandwith 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 sites. To describe the most common flowering and fruiting cycles found at each site and to compare among sites, we plotted the distribution of dominant cycles at each site using violin plots. We treated flowering and fruiting events separately and not as a dependent process. Hence, it is worth noting that not all individuals considered in the flowering analysis were shared in the fruiting analysis. For 851 trees, fruiting was more erratic than flowering and these individuals were excluded from analysis of fruiting, but retained in the flowering analysis. This also led to five species from the flowering analysis to being excluded from the fruiting analysis as less than 10 individuals showed regular fruiting.

COMMUNITY LEVEL SEASONALITY - We assessed the seasonal rainfall pattern at each site by calculating a mean monthly rainfall value (Table 3) over the maximum phenology data collection period (28 years starting in 1986 and finishing in 2014) using rainfall data from the Climate Hazards Group InfraRed Precipitation with Station dataset (CHIRPS) (Funk *et al*. 2015: http://chg.geog.ucsb.edu/data/chirps/). This dataset combines ground-based monitoring with satellite derived rainfall data starting in 1986 and finishing in 2014. For the two sites (Lopé and Mbeli) for which rainfall data were available locally the empirically observed monthly time-series data were poorly matched in the CHIRPS dataset. However, seasonal patterns (average monthly rainfall across all years) were strongly correlated ($r > 0.9$ observed at Lopé and Mbeli sites) (data not shown). To standardise across sites, we defined the dry season as any months where rainfall was less than 60 mm (after van Schaik *et al*. 1993). We assessed canopy level flowering and fruiting status for trees at each site, by calculating at each site the proportion of trees in the phenology sample flowering and fruiting within each month and year. To test for 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 Edoro, Goualougo, Mbeli, Lopé and Taï. Elsewhere annual cycles were not most common, with M’Baïki 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 Edoro 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 3, 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 Taï, 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'Baïki, Lope, Goualougo, Okapi Lenda and Okapi Edoro 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 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 are 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 &

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.

ACKNOWLEDGEMENTS

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

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

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

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

Science Foundation, and Fonds Québécois de la Recherche sur la Nature et les Technologies. Fieldwork: Richard Wrangham.

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

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

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

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

DATA AVAILABILITY STATEMENT

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

LITERATURE CITED

ABERNETHY, K., F. MAISELS AND L. J. T. WHITE. 2016. Environmental Issues in Central Africa. Annu. Rev. Environ. Resour. 41: 1-33.

AGOSTINELLI C. AND U. LUND. 2011. R package ’circular’: Circular statistics (version 0.4-3). URL https://rforge.r-project. org/projects/circular.

ANDERSON, D. P., E. V. NORDHEIM, T. C. MOERMOND, Z. B. GONE BI, AND C. BOESCH. 2005. Factors Influencing Tree Phenology in Taï National Park, Côte d’Ivoire. Biotropica 37: 631–640.

ARINO, O., P. BICHERO, F. ACHA, J. LATHAM, R.WITT AND J. L. WEBER. 2009. Globcover: the most detailed portrait of Earth. ESA Bulletin 136, European Space Agency.

BAWA, K. S., H. KANG AND M. H. GRAYUM. 2003. Relationships among time, frequency, and duration of flowering in tropical rain forest trees. Am. J. Bot. 90: 877–887.

BORCHERT, R. 1983. Phenology and control of flowering in tropical trees. Biotropica 15: 81–89.

BROWN, C. J., M. I. O’CONNOR, E. S. POLOCZANSKA, D. S. SCHOEMAN, L. B. BUCKLEY, M. T. BURROWS, C. M. DUARTE, B. S. HALPERN, J. M. PANDOLFI, C. PARMESAN AND A. J. RICHARDSON. 2016. Ecological and methodological drivers of species’ distribution and phenology responses to climate change. Glob. Change Biol. 22: 1548–1560.

BULLOCK, S. H. AND J. A. SOLIS-MAGALLANES. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22: 22–35.

BUSH, E. R., K. A. ABERNETHY, K. JEFFERY, C.E. G. TUTIN, L. J. T. WHITE, E. DIMOTO, J.-T. DIKANGADISSI, A. S. JUMP AND N. BUNNEFELD. 2017. Fourier analysis to detect phenological cycles using long-term tropical field data and simulations. Methods Ecol. Evol. 8: 530-540

BUTT, N., L. SEABROOK, M. MARON, B. S. LAW, T. P. DAWSON, J. SYKTUS AND C. A. MCALPINE. 2015. Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. Glob. Change Biol. 21: 3267–3277.

CHAMBERS, L.E., R. ALTWEG, C. BARBRAUD, P. BARNARD, L.J. BEAUMONT, R.J.M. CRAWFORD, J.M. DURANT, L. HUGHES, M. R. KEATLEY, M. LOW, P. MORELLATO, E. S. POLOCZANSKA, V. RUOPOLLO, R.E.T. VANSTREELS, E.J. WOEHLER, A.C. WOLFAARDT, B. HÉRAULT. 2013. Phenological Changes in the Southern Hemisphere. PloSOne 8: e75514.

CHAPMAN, C. A., L. J. CHAPMAN, A. E. ZANNE, J. R. POULSEN, AND C. J. CLARK. 2005. A 12-Year Phenological Record of Fruiting: Implications for Frugivore Populations and Indicators of Climate Change. *In* J. L. Dew and J. P. Boubli (Eds.) *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 75–92. Springer Netherlands, Dordrecht.

CHAPMAN, C. A., K. VALENTA, T.M. BONNELL, K. BROWN, L.J. CHAPMAN. 2018. Solar radiation and ENSO predict fruiting phenology patterns in a 16-Year record from Kibale National Park, Uganda. Biotropica, this issue.

CHAPMAN, C. A., R. W. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD AND A. E. ZANNE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. J. Trop. Ecol. 15: 189–211.

CLELAND, E. E., I. CHUINE, A. MENZEL, H. A. MOONEY, AND M. D. SCHWARTZ. 2007. Shifting plant phenology in response to global change. Trends Ecol. Evol. 22: 357–365.

CORLETT, R. T. AND J. V. LAFRANKIE. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. Clim. Change 39: 439–453.

DUNHAM, A., O.H. RAZAFINDRATSIMA, P. RAKOTONIRINA AND P.C. WRIGHT. 2018. ENSO and Rainfall Variability Impact Fruiting Phenology in a Madagascar Rainforest. Biotropica, this issue.

FUNK, C., P. PETERSON, M. LANDSFELD, D. PEDREROS, J. VERDIN, S. SHUKLA, G. HUSAK, J. ROWLAND, L. HARRISON AND A. HOELL. 2015. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. Sci. Data 2: 150066.

GENTRY, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica 6: 64–68.

HUDSON, I. L. AND M. R. KEATLEY. 2010. *Phenological Research: methods for environmental and climate change analysis*. Springer, The Netherlands.

JANMAAT, K. R., C. BOESCH, R. BYRNE, C. A. CHAPMAN, G. BI, B. ZORO, J. S. HEAD, M. M. ROBBINS, R. W. WRANGHAM AND L. POLANSKY. 2016. Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit. Am. J. Primatol.78 : 626-645.

MAIDMENT, R. I., R. P. ALLAN AND E. BLACK. 2015. Recent observed and simulated changes in precipitation over Africa. Geophys. Res. Lett. 42: 8155–8164.

MCEWAN, R. W., AND B. C. MCCARTHY. 2005. Phenology: An integrative environmental science. BioOne.

MEDWAY, L. 1972. Phenology of a tropical rain forest in Malaya. Biol. J. Linn. Soc. 4: 117–146.

MENDOZA, I., C. A. PERES AND L. P. C. MORELLATO. 2017. Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. Glob. Planet. Change 148: 227–241.

MORELLATO, L. P. C., L. F. ALBERTI AND I. L. HUDSON. 2010. Applications of circular statistics in plant phenology: a case studies approach. *In* Hudson, I. L. and M. R. Keatley (Eds). *Phenological research: methods for environmental and climate change analysis*. pp. 339–359. Springer, The Netherlands.

MORELLATO, L.P.C., CAMARGO, M.G.G. AND GRESSLER, E., 2013. A review of plant phenology in South and Central America. *In* Schwartz, M.D. (Ed.), *Phenology: An Integrative Environmental Science*, pp. 91–113. Springer, The Netherlands.

NATIONAL WEATHER SERVICE (2010) Inter-tropical convergence zone. Jet Stream. Available at: http://www.srh.noaa.gov/jetstream/tropics/itcz.htm [Accessed July 29, 2017].

NEWSTROM, L. E., G. W. FRANKIE, AND H. G. BAKER. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica 26: 141–159.

OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. J. Biogeogr. 3: 231–236.

PARMESAN, C. AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37.

PAU, S., E. M. WOLKOVICH, B. I. COOK, C. J. NYTCH, J. REGETZ, J. K. ZIMMERMAN AND S. J. WRIGHT. 2013. Clouds and temperature drive dynamic changes in tropical flower production. Nat. Clim Change 3: 838–842.

PLATT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology. Annu. Rev. Ecol. Syst. 6: 189–210.

PLUMPTRE, A. J. 2012. Changes in Tree Phenology across Africa : A comparison across 17 sites. Technical Report or the Wildlife Conservation Society, New York.

599 POLANSKY, L., AND C. BOESCH. 2013. Long-term changes in fruit phenology in a West African lowland tropical rain forest are not explained by rainfall. Biotropica 45: 434–440.

601 SAKAI, S. 2001. Phenological diversity in tropical forests. Popul. Ecol. 43: 77–86.

602 SAKAI, S., K. MOMOSE, T. YUMOTO, T. NAGAMITSU, H. NAGAMASU, A. A. HAMID, AND T. NAKASHIZUKA. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest,Sarawak, Malaysia. Am. J. Bot. 86: 1414–1436.

606 SLIK, F., J. FRANKLIN, V. ARROYO-RODRÍGUES, R. FIELD, S. AGUILAR, N. AGUIRRE, J. AHUMADA, S-I. AIBA, L. F. ALVES, K. ANITHA, ET AL. 2018. Phylogenetic Classification of the world's tropical forests. Proc. Nat. Acad. Sci. USA. 115: 1837-1842

609 SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Am. Nat. 104: 25–35.

611 STAGGEMEIER, V.G., J. A. F.,DINIZ-FILHO, V. B. ZIPPARRO, E. GRESSLER, E. R. DE CASTRO, F. MAGAZINE, I. R. DA COSTA, E. LUCAS, L. P. C. MORELLATO. 2015. Clade-specific responses regulate phenological patterns in Neotropical Myrtaceae. Perspect. Plant Ecol. 17: 476–490.

615 STEPHENSON, A. G. 1981. Flower and Fruit Abortion: Proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12: 253–279.

617 SUN, C., B. A. KAPLIN, K. A. KRISTENSEN, V. MUNYALIGOGA, J. MVUKIYUMWAMI, K. K. KAJONDO, AND T. C. MOERMOND. 1996. Tree phenology in a tropical montane forest in Rwanda. Biotropica 28: 668–681.

620 TAKENOSHITA, Y., C. ANDO AND J. YAMAGIWA. 2008. Fruit phenology of the great ape habitat in the Moukalaba-Doudou National Park, Gabon. Afr. Study. Monogr. Suppl. 39 : 23-39.

Tutin, C. E. G. and M. Fernandez. 1993. Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. J. Trop. Ecol. 9: 241-248

Van Schaik, C. P., J. W. Terborgh and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu. Rev. Ecol. Syst. 24: 353–377.

Visser, M. E. and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proc. R. Soc. B Biol. Sci. 272: 2561.

Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. B. Hubbell and R. B. Foster. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. J. Trop. Ecol. 21: 307-315

Zhou, L., Y. Tian, R. B. Myneni, P. Ciais, S. Saatchi, Y. Y. Liu, S. Piao, H. Chen, E. F. Vermote, C. Song, and T. Hwang. 2014. Widespread decline of Congo rainforest greenness in the past decade. Nature 509: 86–9.

635

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

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=13.2)
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)
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)

Sources: **Amani Nature Reserve**, Tanzania – Henry Ndangalasi and Norbert Cordeiro; **Gombe Stream National Park** , Tanzania – Ian Gilby, Anne Pusey, Michael Wilson and Baraka Gilagiza; **Nyungwe National Park**, Rwanda – Felix Mulindahabi; **Bwindi Impenetrable National Park**, Uganda – Badru Mugerwa, Frederick Ssali, Douglas Sheil and Martha Robbins**; Kibale National Park**, Uganda – Colin Chapman, **Okapi Wildlife Reserve**; Democratic Republic of Congo – Flory Bujo, Corneille Ewango and Terese Hart; Lopé **Reserve**, Gabon – Kate Abernethy, Emma Bush, Edmond Dimoto, Jean-Thoussaint Dikangadissi, Kath Jeffery, Caroline Tutin and Lee White; **Mbeli Bai**; Nouabalé-Ndoki National Park, Republic of Congo– Mireille Breuer-Ndoundou Hockemba and Thomas Breuer; **M'Baïki**, Central African Republic – Adeline Fayolle, **Taï National Park**; Ivory Coast – Christophe Boesch, Leo Polansky; **Goualougo**, Republic, Republic of Congo– Sydney Ndolo, Dave Morgan, and Crickette Sanz.

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

	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'Baïki	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 Edoro	61	850	30	439	27	111	24	140	29	188
M'Baïki	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'Baïki	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 Edoro	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'Baïki	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'Baïki	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

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 Edoro. 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 ([illegible]no *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 Edoro = 30, M'ba[illegible] = 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 Edoro = 439, M'Baïki = 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'[illegible]ki = 6,

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

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

FIGURES

FIGURE 1.

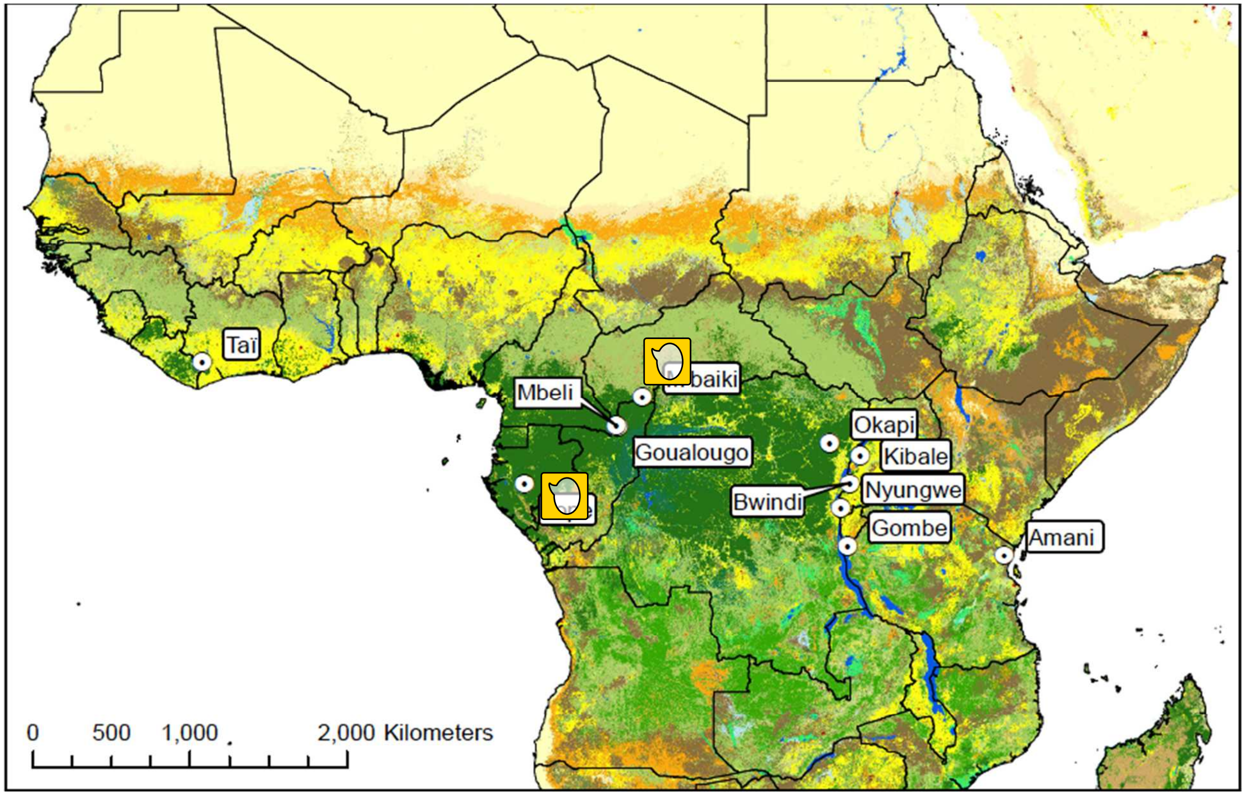


FIGURE 2.

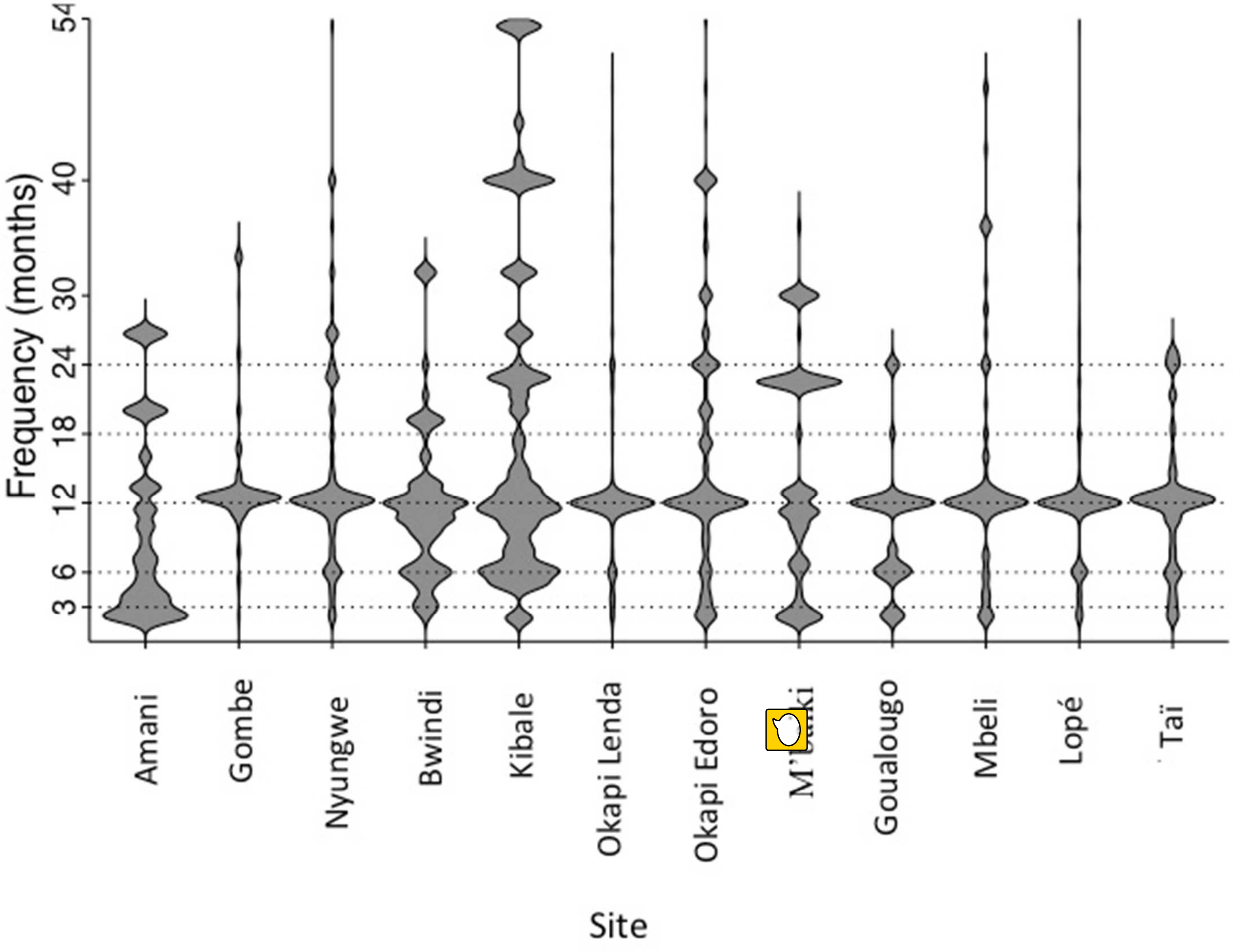

Frequency (months)
54
40
30
24
18
12
6
3
Amani
Gombe
Nyungwe
Bwindi
Kibale
Okapi Lenda
Okapi Edoro
M’ ki
Goualougo
Mbeli
Lopé
Taï
Site

FIGURE 3.

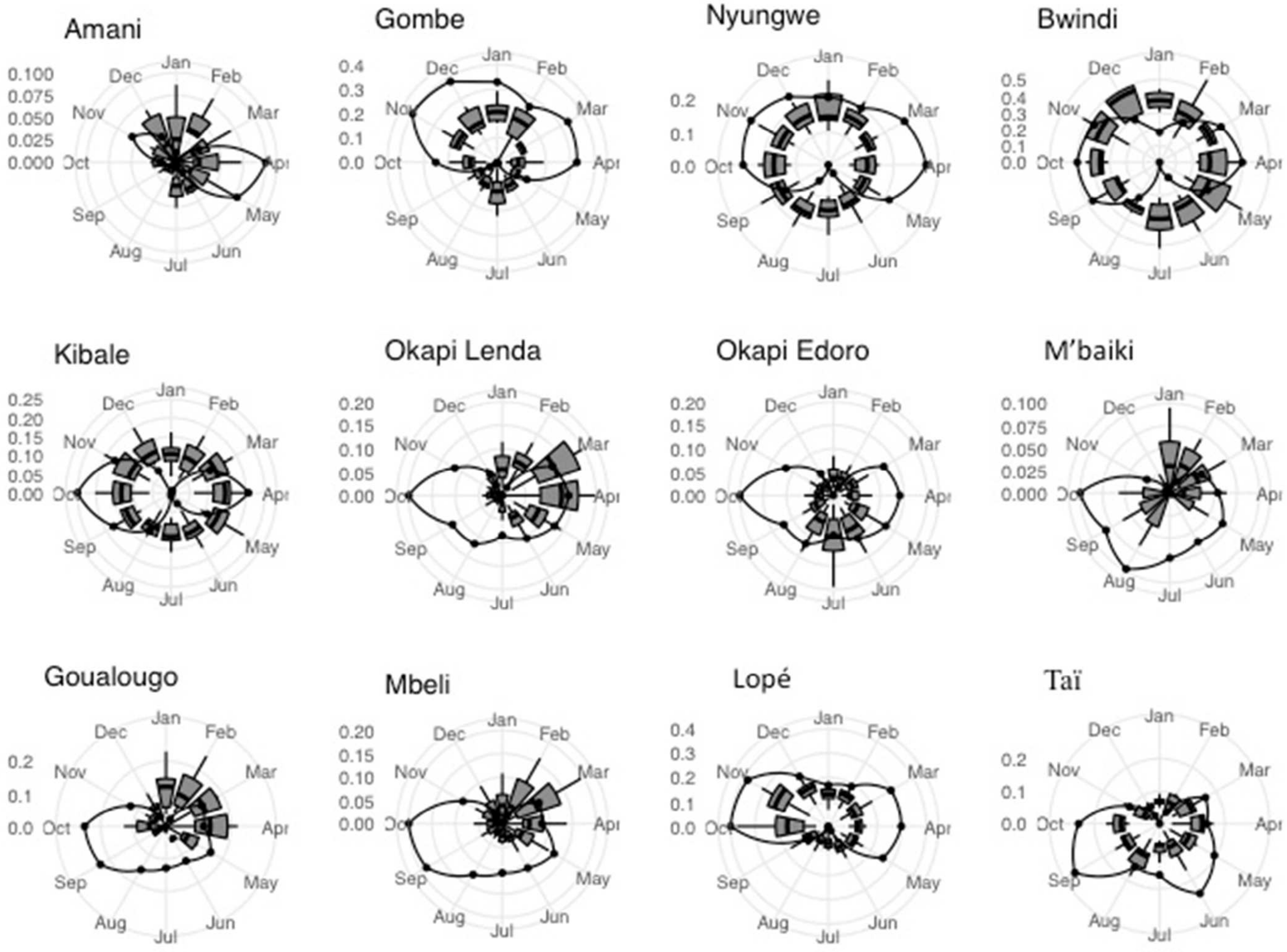

Amani
Gombe
Nyungwe
Bwindi
Kibale
Okapi Lenda
Okapi Edoro
M'baiki
Goualougo
Mbeli
Lopé
Taï
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
0.100
0.075
0.050
0.025
0.000
0.4
0.3
0.2
0.1
0.0
0.5
0.25
0.20
0.15
0.10
0.05
0.00

FIGURE 4.

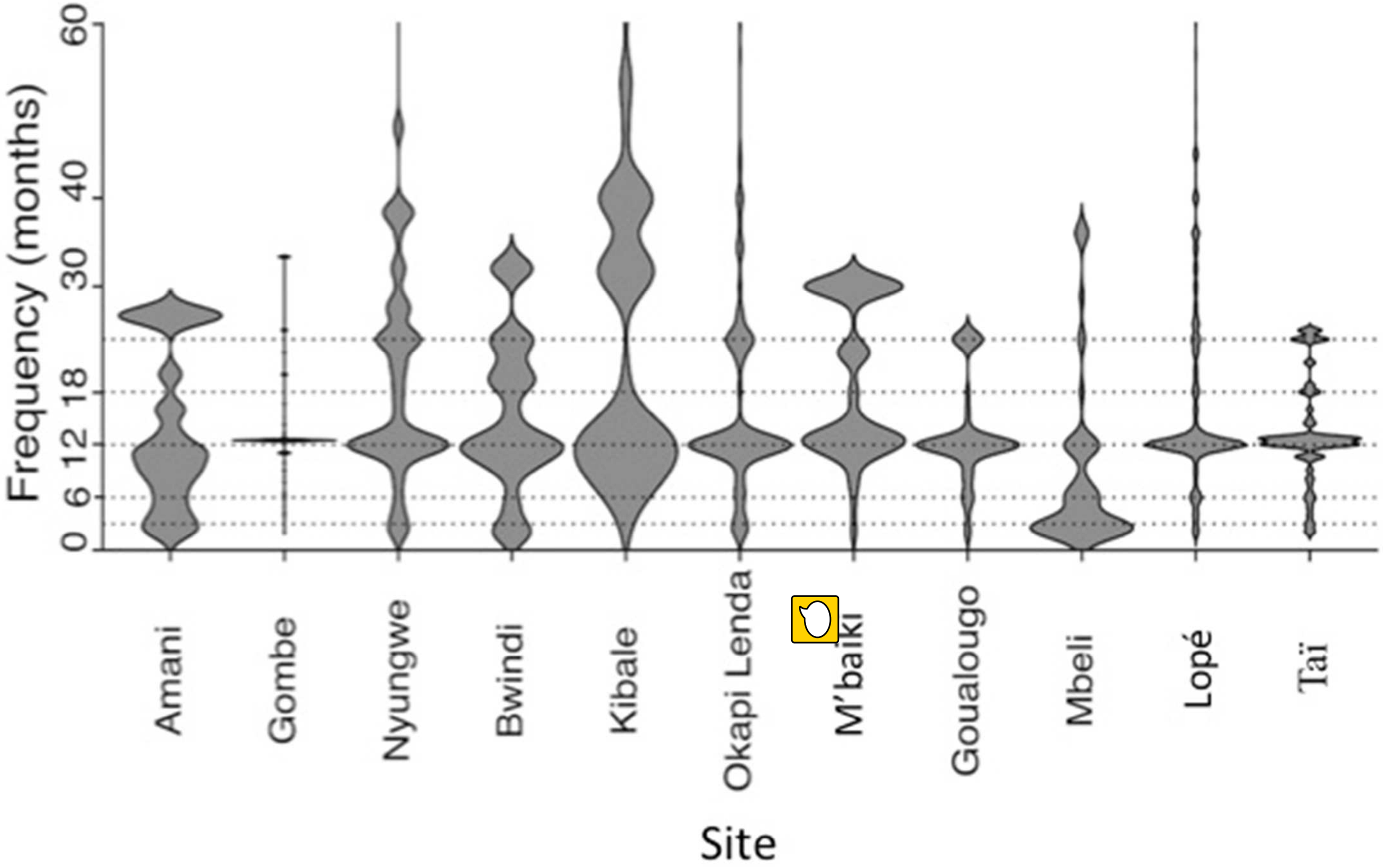
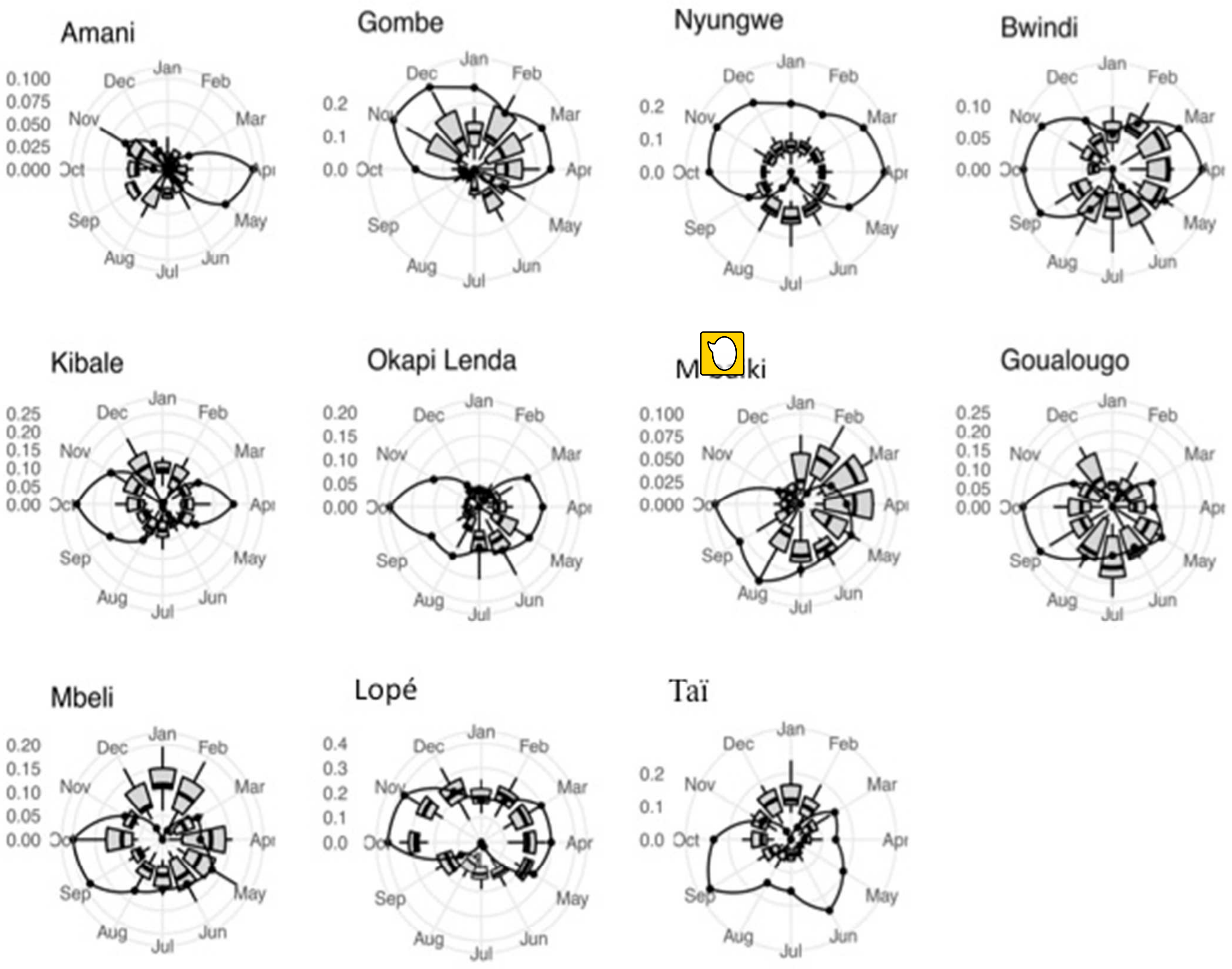

Frequency (months)
0
6
12
18
30
40
60
Amani
Gombe
Nyungwe
Bwindi
Kibale
Okapi Lenda
M'baïki
Goualougo
Mbeli
Lopé
Taï
Site

FIGURE 5.


Amani
0.100
0.075
0.050
0.025
0.000
Gombe
0.2
0.1
0.0
Nyungwe
0.2
0.1
0.0
Bwindi
0.10
0.05
0.00
Kibale
0.25
0.20
0.15
0.10
0.05
0.00
Okapi Lenda
0.20
0.15
0.10
0.05
0.00
M [illegible] ki
0.100
0.075
0.050
0.025
0.000
Goualougo
0.25
0.20
0.15
0.10
0.05
0.00
Mbeli
0.20
0.15
0.10
0.05
0.00
Lopé
0.4
0.3
0.2
0.1
0.0
Taï
0.2
0.1
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

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	Anisophyllaeceae	Anisophyllea	1	0	zoo	*NA*	1	*NA*	*NA*
Anonidium mannii	Mbeli	Annonaceae	Anonidium	0	0	zoo	*NA*	1	*NA*	*NA*
Anthonotha macrophylla	Okapi Edoro	Fabaceae	Anthonotha	0	0	auto	1	*NA*	*NA*	*NA*
Antidesma vogelianum	Lope	Euphorbiaceae	Antidesma	1	0	zoo	*NA*	1	*NA*	*NA*
Apodytes dimidiata	Okapi Edoro	Icacinaceae	Apodytes	0	0	zoo	*NA*	1	*NA*	*NA*
Apodytes dimidiata	Okapi Edoro	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	Melianthaceae	Bersama	0	0	zoo	1	1	*NA*	*NA*
Blighia welwitschii	Okapi Edoro	Sapindaceae	Blighia	1	0	zoo	1	*NA*	*NA*	*NA*
Blighia welwitschii	Okapi Edoro	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 Edoro	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

subnudum										
Chrysophyllus africanum	Lope	Sapotaceae	Chrysophyllum	0	0	zoo	*NA*	1	*NA*	*NA*
Cissus dinklagei	Lope	Vitaceae	Cissus	0	1	zoo	*NA*	1	*NA*	*NA*
Cleistanthus pierlotti	Okapi Edoro	Euphorbiaceae	Cleistanthus	0	0	auto	1	*NA*	*NA*	*NA*
Cola lateritia	Okapi Lenda	Sterculiaceae	Cola	0	0	zoo	1	*NA*	*NA*	*NA*
Cola lizae	Lope	Sterculiaceae	Cola	0	0	zoo	1	*NA*	*NA*	*NA*
Comiphyton gabonense	Okapi Edoro	Anisophyllaceae	Comiphyton	0	1	zoo	*NA*	1	*NA*	*NA*
Coula edulis	Tai	Olacaceae	Coula	0	0	zoo	*NA*	1	*NA*	*NA*
Croton haumanianus	Okapi Edoro	Euphorbiaceae	Croton	0	0	zoo	*NA*	1	*NA*	*NA*
Croton macrostachyus	Bwindi	Euphorbiaceae	Croton	0	0	zoo	1	*NA*	*NA*	*NA*
Cynometra alexandri	Okapi Edoro	Fabaceae	Cynometra	0	0	auto	1	*NA*	*NA*	*NA*
Cynometra alexandri	Okapi Edoro	Fabaceae	Cynometra	0	0	auto	1	*NA*	*NA*	*NA*
Dacryodes buettneri	Lope	Burseraceae	Dacryodes	1	0	zoo	1	*NA*	*NA*	*NA*
Dacryodes klaineana	Tai	Burseraceae	Dacryodes	1	0	zoo	1	*NA*	*NA*	*NA*
Daniellia thurifera	Tai	Fabaceae	Daniellia	0	0	auto	1	*NA*	*NA*	*NA*
Detarium macrocarpum	Mbeli	Fabaceae	Detarium	0	0	zoo	*NA*	1	*NA*	*NA*
Dialium aubrevillei	Tai	Fabaceae	Dialium	0	0	zoo	1	*NA*	*NA*	*NA*
Dialium corbisieri	Okapi Edoro	Fabaceae	Dialium	0	0	zoo	1	*NA*	*NA*	*NA*
Dialium lopense	Lope	Fabaceae	Dialium	0	0	zoo	1	*NA*	*NA*	*NA*
Dialium pentandrum	Okapi Edoro	Fabaceae	Dialium	0	0	zoo	1	*NA*	*NA*	*NA*
Dictyophleba lucida	Gombe	Apocynaceae	Dictyophleba	0	0	zoo	*NA*	1	*NA*	*NA*
Diospyros dendo	Lope	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*
Diospyros ivoriensis	Tai	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*
Diospyros polystemon	Lope	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*
Diospyros sanza-minika	Tai	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*
Diospyros soubreana	Tai	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*
Diospyros zenkeri	Lope	Ebenaceae	Diospyros	1	0	zoo	*NA*	1	*NA*	*NA*

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 Edoro	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*

Garcinia huillensis	Gombe	Clusiaceae	Garcinia	0	0	zoo	*NA*	1	*NA*	*NA*
Gilbertiodendron dewevrei	Okapi Lenda	Fabaceae	Gilbertiodendron	0	0	auto	1	*NA*	*NA*	*NA*
Gilbertiodendron splendidum	Tai	Fabaceae	Gilbertiodendron	0	0	auto	1	*NA*	*NA*	*NA*
Greenwayodendron suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	*NA*	*NA*	*NA*
Greenwayodendron suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	*NA*	*NA*	*NA*
Grewia oligoneura	Mbeli	Tiliaceae	Grewia	0	0	zoo	*NA*	1	*NA*	*NA*
Hallea stipulosa	Okapi Edoro	Rubiaceae	Hallea	0	0	auto	1	*NA*	*NA*	*NA*
Harungana madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	*NA*	1	*NA*	*NA*
Harungana madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	*NA*	1	*NA*	*NA*
Harungana montana	Nyungwe	Hypericaceae	Harungana	0	0	zoo	*NA*	1	*NA*	*NA*
Heisteria parvifolia	Lope	Olacaceae	Heisteria	0	0	zoo	*NA*	1	*NA*	*NA*
Heritiera utilis	Tai	Sterculiaceae	Tarrietia	1	0	wind	*NA*	*NA*	*NA*	1
Ilex mitis	Nyungwe	Aquifoliaceae	Ilex	1	0	zoo	*NA*	1	*NA*	*NA*
Irvingia excelsa	Mbeli	Irvingiaceae	Irvingia	0	0	zoo	*NA*	1	*NA*	*NA*
Irvingia gabonensis	Lope	Irvingiaceae	Irvingia	0	0	zoo	*NA*	*NA*	*NA*	*NA*
Irvingia grandifolia	Lope	Irvingiaceae	Irvingia	0	0	zoo	*NA*	*NA*	*NA*	*NA*
Irvingia wombolu	Okapi Edoro	Irvingiaceae	Irvingia	0	0	zoo	*NA*	1	*NA*	*NA*
Ixora burundensis	Nyungwe	Rubiaceae	Ixora	0	0	zoo	*NA*	1	*NA*	*NA*
Julbernardia seretii	Okapi Edoro	Fabaceae	Julbernardia	0	0	auto	1	*NA*	*NA*	*NA*
Klainedoxa gabonensis	Lope	Irvingiaceae	Klainedoxa	0	0	zoo	*NA*	1	*NA*	*NA*
Macaranga capensis	Amani	Euphorbiaceae	Macaranga	1	0	zoo	1	*NA*	*NA*	*NA*
Macaranga kilimandscharica	Nyungwe	Euphorbiaceae	Macaranga	1	0	zoo	1	*NA*	*NA*	*NA*
Macaranga	Okapi Edoro	Euphorbiaceae	Macaranga	1	0	auto	1	*NA*	*NA*	*NA*

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 Edoro	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 Edoro	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA

Nauclea xanthoxylon	Tai	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA
Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
Newtonia buchananii	Nyungwe	Mimosaceae	Newtonia	0	0	wind	1	NA	NA	NA
Ochna afzelii	Nyungwe	Ochnaceae	Ochna	0	0	zoo	NA	1	NA	NA
Ocotea usambarensis	Nyungwe	Lauraceae	Ocotea	0	0	zoo	NA	1	NA	NA
Odyendea zimmermannii	Amani	Simaroubaceae	Quassia	0	0	zoo	NA	1	NA	NA
Olea capensis	Bwindi	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
Olea welwitschii	Kibale	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
Olinia rochetiana	Nyungwe	Oliniaceae	Olinia	0	0	zoo	NA	1	NA	NA
Ongokea gore	Lope	Olacaceae	Ongokea	0	0	zoo	NA	1	NA	NA
Panda oleosa	Lope	Pandaceae	Panda	0	0	zoo	NA	1	NA	NA
Parinari capensis	Gombe	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
Parinari excelsa	Okapi Edoro	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
Parkia bicolor	Lope	Fabaceae	Parkia	0	0	zoo	1	NA	NA	NA
Pentaclethra macrophylla	Lope	Fabaceae	Pentaclethra	0	0	auto	1	NA	NA	NA
Pentadesma butyracea	Tai	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
Pentadesma reyndersii	Nyungwe	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
Podocarpus latifolius	Nyungwe	Podocarpaceae	Podocarpus	0	0	zoo	NA	1	NA	NA
Polyathia suaveolens	Amani	Annonaceae	Polyathia	0	0	zoo	NA	1	NA	NA
Polyscias fulva	Nyungwe	Araliaceae	Polyscias	0	0	zoo	NA	1	NA	NA
Porterandia cladantha	Lope	Rubiaceae	Aoranthe	0	0	zoo	NA	1	NA	NA
Pouteria altissima	Mbaiki	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
Pouteria aningeri	Tai	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
Prunus africana	Nyungwe	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
Prunus africanum	Kibale	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
Pseudospondias	Lope	Anacardiaceae	Pseudospondias	1	0	zoo	NA	1	NA	NA

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

Strombosia pustulata	Tai	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
Strombosiopsis tetrandra	Okapi Edoro	Olacaceae	Strombosiopsis	0	0	zoo	NA	1	NA	NA
Symphonia globulifera	Nyungwe	Clusiaceae	Symphonia	0	0	zoo	NA	1	NA	NA
Synsepalum afzelii	Tai	Sapotaceae	Synsepalum	0	0	zoo	NA	1	NA	NA
Syzygium cordatum	Bwindi	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA
Syzygium guineense	Nyungwe	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA
Tabernaemontana penduliflora	Mbeli	Apocynaceae	Tabernaemontana	0	0	zoo	NA	1	NA	NA
Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA
Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA
Thomandersia laurifolia	Mbeli	Acanthaceae	Thomandersia	0	0	auto	1	NA	NA	NA
Trichoscypha acuminata	Mbeli	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA
Trichoscypha arborea	Tai	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA
Triplochiton scleroxylon	Mbaiki	Malvaceae	Triplochiton	0	0	wind	NA	NA	NA	1
Uapaca corbisieri	Tai	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA
Uapaca guineensis	Okapi Edoro	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA
Uvariastrum pierreanum	Lope	Annonaceae	Uvariastrum	0	0	zoo	NA	1	NA	NA
Vitex doniana	Mbeli	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA
Vitex fischeri	Gombe	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA
Xylia evansii	Tai	Fabaceae	Xylia	0	0	auto	1	NA	NA	NA
Xylopia aethiopica	Lope	Annonaceae	Xylopia	0	0	zoo	NA	1	NA	NA
Xylopia hypolampra	Lope	Annonaceae	Xylopia	0	0	zoo	NA	1	NA	NA
Xylopia quintasii	Tai	Annonaceae	Xylopia	0	0	zoo	NA	1	NA	NA
Zanha golungensis	Tai	Sapindaceae	Zanha	1	0	zoo	NA	1	NA	NA
Zanthoxylum gilletii	Okapi Lenda	Rutaceae	Zanthoxylum	1	0	zoo	NA	1	NA	NA

- NA = not applicable
- 1 = applicable
- 0 = absent

Responses to Edito'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 pattering 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 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.

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’Baïki (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.

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 cofusing 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 your 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.