

ORIGINAL ARTICLE

Seasonality in the equatorial tropics: Flower, fruit, and leaf phenology of montane trees in the highlands of Southwest Uganda

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Email: ssalifb@yahoo.co.uk**Associate Editor:** Jennifer Powers**Handling Editor:** Irene Mendoza**Abstract**

Phenology influences many forest functions and can inform forest conservation and management, yet representative phenological data for most common tropical forest tree species remain sparse or absent. Between June 2011 and December 2013, we investigated flowering, fruiting, and leafing patterns in the Bwindi Impenetrable National Park, a montane forest located near the equator in Uganda, drawing on 16,410 observations of 530 trees of 54 species located between 2066 and 2527 m in elevation. The park's climate is equatorial with two wet and dry seasons each year. Flowering and fruiting were strongly seasonal while patterns in leafing were less pronounced. Flower occurrence peaked at the beginning of the short dry season followed by a pronounced trough during the beginning and the middle of the short wet season. Fruit occurrence had a pronounced peak during high rainfall months in March through April with most fruits ripening during drier months in May through July. Fruit scarcity was observed for a 4-month period spanning September to December and most flushing of leaves noted at the end of the wet season in November and December. Our binomial generalized linear mixed models indicated that flowering and fruiting were negatively associated with temperature and that leafing activity was positively associated with rainfall and temperature. These findings are consistent with the insolation- and water-limitation hypotheses suggesting that the seasonally varying availability of resources such as light, water, and nutrients determines these phenological patterns. Ideally, prolonged, multi-year community-level studies would be supported so as to better characterize the influence of climate and of climate variability.

KEYWORDS

afromontane, flowering, fruiting, leaf flush, leaf senescence, phenophase synchrony, tropical montane forest

1 | INTRODUCTION

Tree phenology examines the timing of recurrent biological events and processes in a tree's life-cycle. Knowledge of tree phenology

offers improved understanding of diverse aspects of forest ecology and functioning. Specific examples include food availability (e.g., fruits for frugivores), interactions among species (e.g., competition and understorey shade), and stand properties such as albedo and

evapotranspiration (e.g., leaf properties; see Abernethy et al., 2018; Adamescu et al., 2018; Adole et al., 2016; Chapman et al., 2018; Morissette et al., 2009; Polansky & Boesch, 2013). Among tropical studies, most have focused on spatiotemporal trends in the fruiting phenology of selected species valued as food by specific wildlife (e.g., Doran-Sheehy et al., 2009; Potts et al., 2020; Walther et al., 2018; Watts et al., 2012). In the case of African montane forests, most emphasize the availability of foods for selected primates (e.g., Basabose, 2002; Matthews et al., 2019; Stanford & Nkurunungi, 2003). Such a focus is not surprising given that much of the research interest in these regions has been determined by the presence of charismatic frugivores (e.g., the great apes, *Gorilla* spp, *Pan* spp, and *Pongo* spp; see Marshall et al., 2016). One outcome of this focus is that broader, community level, and phenological patterns are less often described (but see Sun et al., 1996). In particular, though there have been various systematic and scattered observations of specific processes for specific species (Adamescu et al., 2018; Adole et al., 2016; Babweteera et al., 2018), few studies have described the phenology of the broader tree community within the montane forests of the Albertine Rift which sustain an unmatched animal species diversity on the African continent, most of which are endemic and globally threatened (Brooks et al., 2001; Plumptre et al., 2007). These African montane forests hold unique value in terms of biodiversity and carbon (Cuni-Sanchez et al., 2021), and serve as natural laboratories for examining the relationship between phenological observations and climate (e.g., see Mainali et al., 2015).

Evidence shows that phenological events generally follow consistent seasonal patterns. Such patterns influence species interactions and related ecosystem processes. For instance, observations in tropical forests show that availability of fruits and other ephemeral resources influence animal abundance and behaviors (Babweteera et al., 2018; Butt et al., 2015; Huang et al., 2012). The abundance of frugivores, critical for the dispersal of many plant species, generally increases when fruiting is abundant (e.g., Gross-Camp, Masozera, & Kaplin, 2009; Poulsen et al., 2021). Studies in temperate biomes have shown that insect pollinators time their emergence to correspond with local flowering seasons with a general tendency for insects at higher elevations to emerge later than those at lower elevations (Bartomeus et al., 2011; Forrest, 2016; Forrest & Thomson, 2011). Further, we know from studies in temperate and Neotropical locations that the presence of herbivorous insects, and consequently the presence of insectivorous birds and mammals, varies with the availability of young leaves (Barbehenn & Constabel, 2011; Barlow et al., 2007; Lamarre et al., 2014).

Changes in phenology are typically attributed to various climatic trends and events. For example, in Barro Colorado Island, Panama, variation in flowering in many tree species has been linked to changes in solar irradiance (Wright, 2018) while in a rainforest of southeastern Madagascar, fruit availability is linked with seasonal variation in rainfall, with increased rain in the dry season affecting fruiting more strongly than increased rain in the rainy season (Dunham et al., 2018). Variation in fruit production and phenology in Kibale National Park

in Uganda has been linked most clearly to changing irradiance and the occurrence of El Niño (Chapman et al., 2018). Leaf fall and leaf flush have also been found to vary with rainfall and temperature in a South American cerrado woodland (Camargo et al., 2018).

There are analytical and inferential challenges in trying to distinguish among the various cues and influences given that many are often related, and may act in concert within a single species while acting differently among the taxa that comprise the wider community. Conditions and responses may also involve significant lag-times, for example, masting tree species need to accumulate sufficient energy reserves over the preceding years for appropriate cues to initiate the onset of flowering and fruiting (Detto et al., 2018; Pearse et al., 2016). Such relationships cannot be unambiguously detected in non-experimental field data over short periods, though it is possible to examine whether the patterns conform to different expectations. Whether we can understand them or not it is important to observe and explore phenology patterns and clarify their potential implications (Abernethy et al., 2018; Butt et al., 2015; Morellato et al., 2016). The need is particularly urgent at higher elevations where climate change is predicted to have more severe impacts than at lower elevations and may disrupt the synchrony between plants and their pollinators and dispersers (Bucher et al., 2018; Menzel et al., 2020; Suzuki, 1998).

To monitor flowering, fruiting, and leafing, we set up a study along 18 transects in the Bwindi Impenetrable National Park ("Bwindi") in Uganda. Specific objectives were to (1) describe the flowering, fruiting, and leafing patterns of common tree species in a montane forest located near the equator, (2) examine how the duration and synchrony of the phenophases vary with fruit size, sexual system, and seed dispersal mode of the trees, and (3) determine whether and how flowering, fruiting, and leafing events relate to patterns and variation in rainfall and temperature. This study examines multiple phenophases using a dataset comprising common and comparatively representative tree species within a tropical montane forest of considerable conservation importance (Hamilton et al., 2000; Plumptre et al., 2021). Given the equatorial setting with little seasonal variation in daylight and temperature, we were uncertain on what environmental cues would provide reliable proximate or evolutionary cues for trees in these forests. Thus, we did not develop formal hypotheses on the cues, but we anticipated that new leaves, flower buds, and pollination would favor less clouded and drier conditions while fruits would develop in anticipation of rains and the dispersal of seeds into moist soils.

2 | METHODS

2.1 | Study area

This study was conducted from June 2011 to December 2013 in the Bwindi Impenetrable National Park ("Bwindi") in Uganda (0°53'–1°08' S, 29°35'–29°50' E). The 321 km² montane forest spans 1160 to 2607 m a.s.l. and has been a National Park since 1991

and a UNESCO World Heritage site since 1994 (Howard, 1991; IUCN, 1994). Bwindi comprises a range of vegetation types which, along with old-growth rain forest, include areas of disturbed forest and regrowth, with areas dominated by bamboo *Sinarundinaria alpina* (K. Schum.) C.S. Chao & Renvoize, tree heathers *Erica benguelensis* (Welw. ex Engl.) E.G.H.Oliv. and bracken *Pteridium aquilinum* (L.) Kuhn (Butynski, 1984; Ssali, Moe & Sheil, 2017). The climate is equatorial with rainfall peaks in both March to May and September to November. The period from December to February is typically dry (range 1.1–5.6 mm of rain per day), while June to August is the most severe dry season (range 0.8–4.7 mm of rain per day) (Kasangaki et al., 2012). Mean daily rainfall ranges between 1.4 and 8.5 mm in the March to May wet season and between 4.2 and 7.8 mm in the September to November wet season (Kasangaki et al., 2012). Mean maximum and minimum temperatures vary relatively little throughout the year, ranging between 22.1 and 25.2°C and between 14.1 and 16.8°C per month, respectively (Figure 1).

2.2 | Study setup

We established 106 plots each comprising five trees (>8 cm diameter at 1.3 m or DBH and known to be mature, reproductive trees) spread over 18 transects located to cover and represent a range of elevations, topographic positions, and vegetation types (see also Ssali, Moe & Sheil, 2019). Plot locations were predetermined on maps in advance and located for on the ground using a GPS. These locations were selected to be at least 50 m from any paths or trails while also

being relatively accessible. Elevation ranged from 2066 to 2527 m a.s.l. Each transect had six plots with two each located in the lower-, mid-, and upper-slope positions except for two transects: one with eight plots located in gentler terrain and another with only two plots located in the heather forest. The location, height, and diameter of each tree were recorded, and the stem marked to aid relocation.

A total of 530 trees were monitored each month for two and a half years, starting in June 2011 and ending in December 2013. Our team observed each tree at monthly intervals using binoculars and recorded comparable estimated counts of flowers, fruits, and leaves (Table S4). The presence and quantity per tree of flower buds, open flowers, fallen flowers, unripe fruits, ripe fruits, rotten or dry fruits, fallen fruits, new leaves, old leaves, damaged leaves, senescent leaves, and fallen leaves were recorded by assigning a score between zero and four. The score of 0 represents absence of a phenophase, 1 represents an abundance of 1–10, 2 represents an abundance of 10–100, 3 represents an abundance of 100–1000, and 4 represents an abundance greater than 1000 counts of a given phenophase. Similar scores have previously been used in the quantification of fruit production in two afro-montane forests in KwaZulu-Natal in South Africa (Wirminghaus et al., 2007). Categories of flowers, fruits, and leaves of some species were deemed “difficult to distinguish” and subsequently dropped from the data collection protocol (see Table S2 for a more complete description). For instance, damaged leaves were not scored for *E. benguelensis*. We replaced trees that died ($n=8$) with nearby trees of the same species.

2.3 | Data analysis

Categorical abundance measures of each phenological variable for each individual tree were converted into activity indices, that is, absence–presence data (absent if zero, present if greater than zero), and used to calculate the proportion of each of the 54 study species observed bearing flowers, fruits, and leaves in each calendar month. The absence–presence data were also used to test for seasonality and the role of rainfall and temperature on the occurrence of phenological events.

To test for seasonality in the occurrence of flowering, fruiting, and leafing events, we applied circular statistics and Rayleigh tests using a script developed by Bush et al. (2017) and the R package “circular” (Agostinelli & Lund, 2011). The Rayleigh test provides a robust and straightforward way to evaluate whether phenological activity is uniformly distributed through the year (Landler et al., 2018; Morellato, Alberti, & Hudson, 2010) and is commonly applied in phenological research (see, e.g., Adamescu et al., 2018; Chang-Yang et al., 2013; Morellato, Camargo, et al., 2010). To simplify analyses, we removed trees which never flowered or fruited during the study period and to ensure robust summaries included only species with 10 or more individuals which survived through the period (this also applied to dioecious species as we were unable to determine the sexes in advance). To perform Rayleigh tests, we converted calendar months to angles with 30° intervals and thus

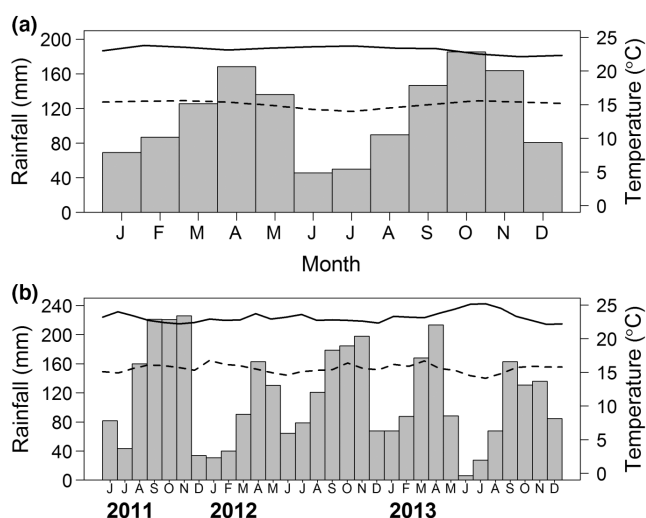


FIGURE 1 Estimated mean monthly values of total rainfall (bars), minimum temperature (broken lines) and maximum temperature (solid lines) at Ruhija, Bwindi Impenetrable National Park, for (a) the period January 1983 through December 2013 and (b) the study period starting in June 2011 and ending in December 2013. Data were downloaded from Columbia University's online IRI/LDEO Climate Library (<http://iridl.ldeo.columbia.edu>) as the data recorded manually or by the automated weather station at Ruhija could not be used because of too many missing records across several calendar months of our study.

assigned January 15°, February 45°, March 75°, and December 345° (see Morellato, Camargo, et al., 2010). The mean angle (μ) and vector length (r) were then calculated. The mean angle (μ) is the period around which a given phenophase occurred for most individuals. The null hypothesis tested was that phenology lacked seasonality. High values of r indicated a high degree of seasonality while p -values $<.05$ indicated significant seasonality (Morellato, Camargo, et al., 2010).

We further determined the duration and synchrony of flowering, fruiting, and leafing phenophases and evaluated differences in phenological patterns between dioecious and non-dioecious species and between zoochorous and non-zoochorous species. Phenophase duration was estimated for a given species by averaging the time in months between the first and the last month the phenophase of interest was seen. Synchrony between conspecific individuals was calculated following Augspurger (1983):

$$X_i = \left(\frac{1}{n-1} \right) \left(\frac{1}{f_i} \right) \sum_{j=1}^n e_{j \neq i}$$

where X_i denotes the index of synchrony X for an individual i , e_j number of months that individuals i and j overlapped in a given phenophase, f_i the total number of months individual i exhibited the given phenophase and n the number of individuals in the sample. Overall synchrony of each phenophase was obtained by averaging the synchronies of all individuals in the sample. This index ranges from 0 (no overlap) to 1 (total overlap). A phenophase was considered to indicate high synchrony if its index value was greater than 0.5, low synchrony if its index value ranged from 0.25 to 0.5 and asynchrony if its index value was less than 0.25. We used Mann–Whitney tests to detect if the duration and synchrony of phenophases vary by fruit size, sexual system (here dioecious vs. non-dioecious species), and seed dispersal mode. A given species was assigned to a sexual system, fruit size, and dispersal mode following Katende et al. (1995), Lovett et al. (2006) and other authorities on African forest trees (Table 3).

Given the non-experimental nature of the data and the relatively short period of observation, we consider our study largely descriptive and recognize that the use of these data to explore causal hypotheses is limited. Nonetheless, exploring these relationships and their meaning has value given the paucity of current knowledge about the phenology of these high elevation equatorial forests. Thus, we examined how phenological patterns related to climatic conditions, using binomial generalized linear mixed models (GLMMs) with presence or absence of an event with an abundance score >0 and presence or absence of an event with an abundance score >2 as response variables and each climatic variable as a fixed effect. Total rainfall, average maximum temperature, and average minimum temperature calculated over a 2-month period encompassing the concurrent and previous calendar months (data from Columbia University's online IRI/LDEO Climate Library) were used in each model. We included year, species, and plot identity as random factors with plot identity nested within site. We used the *glmer* function in the lme4 package (Bates et al., 2015) to fit

the GLMMs and checked for model adequacy by plotting residuals versus fitted values to verify homogeneity and residuals versus each explanatory variable to check independence following Crawley (2013) and Zuur and Hilbe (2013). All analyses used R (R Core Team, 2020).

3 | RESULTS

We recorded a total of 16,410 phenological observations from 530 trees comprising 54 species from 39 families (Figure 2; Table S2). The number of trees per species ranged from 1 to 42. A total of 36 tree species had fewer than 10 individuals which survived through the study period, and this left us with 18 species (five dioecious and 13 non-dioecious, and 14 zoochorous and four non-zoochorous) for our analyses ranging from 10 to 42 stems (henceforth "common species"). Over the 31 months of observation, these 18 common species exhibited more pronounced peaks and troughs in flower and fruit occurrence compared to the occurrence of new leaves, old leaves, damaged leaves, and fallen leaves (Figure 3; Figures S6–S11).

3.1 | Flowering patterns

Over the course of the study, flower buds were observed on 493 (93.0%) individual trees, open flowers on 452 (85.3%) trees while fallen flowers were found beneath 418 (78.9%) tree canopies. Flower buds exhibited a seasonal pattern (Rayleigh test; $p < .001$; $n = 2647$ flowering events for 373 trees), with a peak at the onset of the dry season in December and a trough at the onset and in the middle of the wet season in March and April (Figures 1 and 4; Figure S1). Seventeen of our 18 common tree species exhibited significant unimodal patterns in the occurrence of flower buds with peaks during the dry season in June and July ($p < .05$; Table 1; Figure S1). Open flowers also exhibited strong seasonality ($p < .001$): anthesis peaked at the onset of the dry season in December and had a distinct trough in the middle and at the end of the rainy season in April and May (Figure 4). With the exception of *Strombosia scheffleri* Engl. ($n = 26$) which revealed a bimodal pattern, our common species exhibited significant unimodal patterns in anthesis and had marked peaks in the middle of the long dry season in July ($p < .05$; Table 1; Figure S2). Fallen flowers, although their occurrence appeared to reach the peak at the onset of the dry season in December (Figure 4), their seasonality overall did not reach significance ($p = .074$). Nonetheless, 17 out of 18 common species exhibited significant seasonality in this phenophase (Table 1; Figure S3).

3.2 | Fruiting patterns

Ripe and unripe fruits were observed in 357 (67.4%) and 431 (81.3%) tree canopies, respectively, while rotten or dry fruits and fallen fruits were observed in and under 346 (65.3%) and 382 (72.1%)

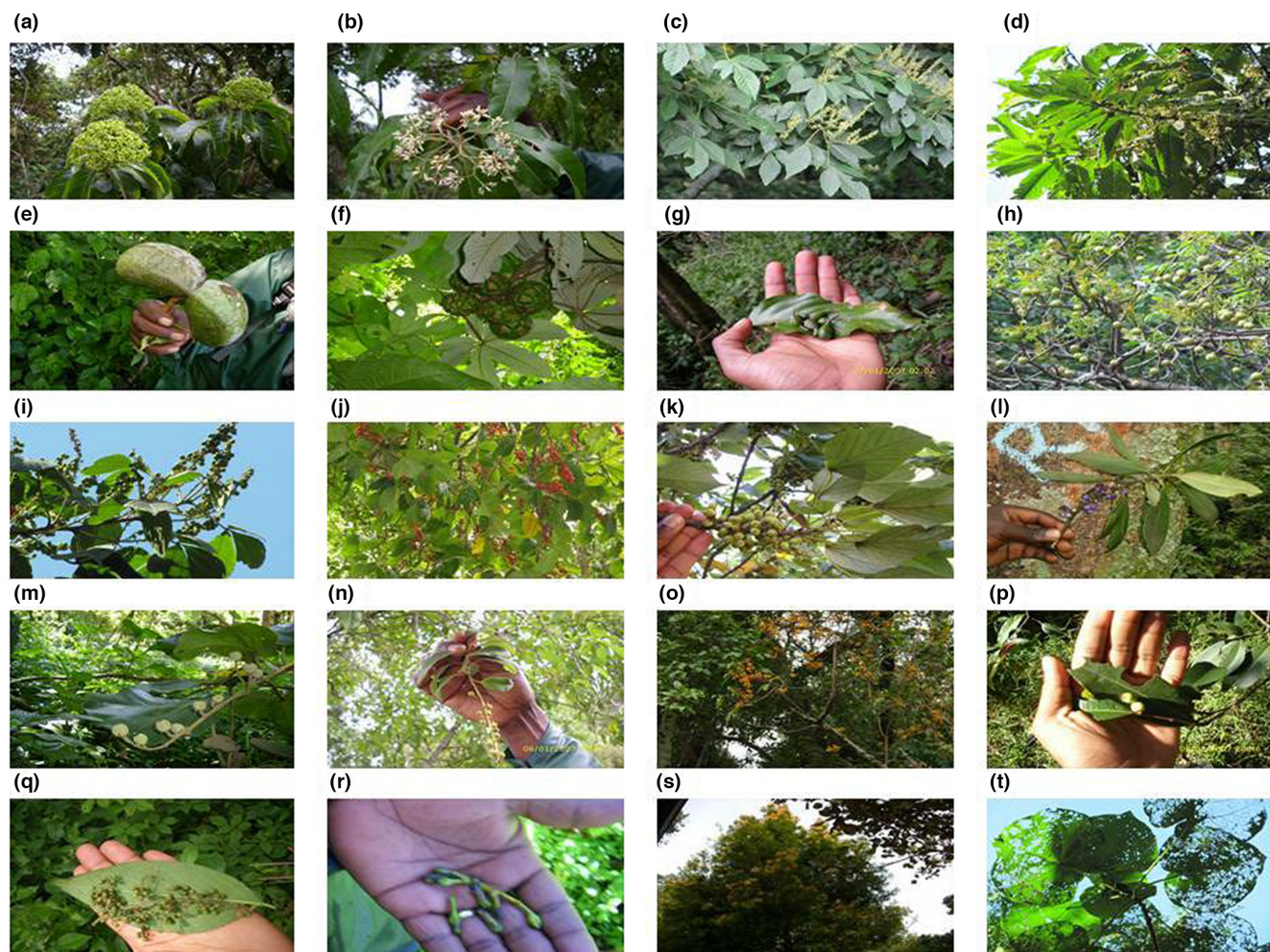


FIGURE 2 Selected images of flowers, fruits and leaves of the study species: (a) *Nuxia congesta* (flower buds), (b) *N. congesta* (open flowers), (c) *Allophylus abyssinicus* (open flowers), (d) *Galiniera saxifraga* (open flowers), (e) *Tabernaemontana pachysiphon* (fallen fruit), (f) *Myrianthus holstii* (unripe fruits), (g) *Strombosia scheffleri* (fallen fruits), (h) *Ekebergia capensis* (unripe fruits), (i) *Allophylus abyssinicus* (unripe fruits), (j) *Allophylus abyssinicus* (ripe fruits), (k) *Macaranga capensis* (unripe fruits), (l) *Rapanea melanophloeos* (ripe fruits), (m) *Neoboutonia macrocalyx* (unripe fruits), (n) *Agauria salicifolia* (unripe fruits), (o) *Pittosporum viridiflorum* (ripe fruits), (p) *Syzygium guineense* (unripe fruits), (q) *Maesa lanceolata* (fallen fruits), (r) *Tabernaemontana pachysiphon* (fallen flowers), (s) *Podocarpus latifolius* (new leaves), and (t) *Neoboutonia macrocalyx* (damaged leaves).

canopies. Unripe fruits exhibited a clearly seasonal pattern (Rayleigh test; $p < .001$; $n = 2459$ fruiting events for 355 trees) peaking in the wet season, primarily in March and April (Figure 4). Most common species (14 out of 18 species) showed significant seasonality in the occurrence of unripe fruits with peaks between January and April ($p < .05$; Table 2; Figure S4). Ripe fruits were also seasonal ($p < .001$) and peaked in May through July with scarcity (i.e., fruit availability $< 10\%$) through the entire September–November wet season and the start of the December–February dry season (Table 2; Figure 4). All but two common species, that is, *Syzygium guineense* (Willd.) DC. ($n = 16$) and *Xymalos monospora* (Harv.) Baill. ($n = 16$), showed significant seasonality in the occurrence of ripe fruits with most peaks observed during the dry season in July ($p < .05$; Table 2; Figure S5). The occurrence of rotten or dry fruits was also seasonal and peaked at the onset and in the middle of the wet season in March and April ($p < .001$). Fourteen of 18 common species exhibited significant

seasonality in this phenophase ($p < .05$; Table 2; Figure S6). Fallen fruits were also seasonal ($p < .001$): peaking at the onset and in the middle of the wet season in March and April (Figure 4). Thirteen of our 18 common species exhibited seasonality in this phenophase with six peaking during the March–May wet season ($p < .05$; Table 2; Figure S7).

3.3 | Leafing patterns

On average, we observed 10 (1.9%) leafless trees at any time during our study. New leaves were continuously produced by 289 (54.5%) trees while old leaves, damaged leaves, senescent leaves, and fallen leaves occurred in or under 478 (90.2%), 458 (86.4%), 49 (9.2%), and 373 (93%) tree canopies, respectively. Leaf flushing exhibited significant seasonality (Rayleigh test; $p = .003$;

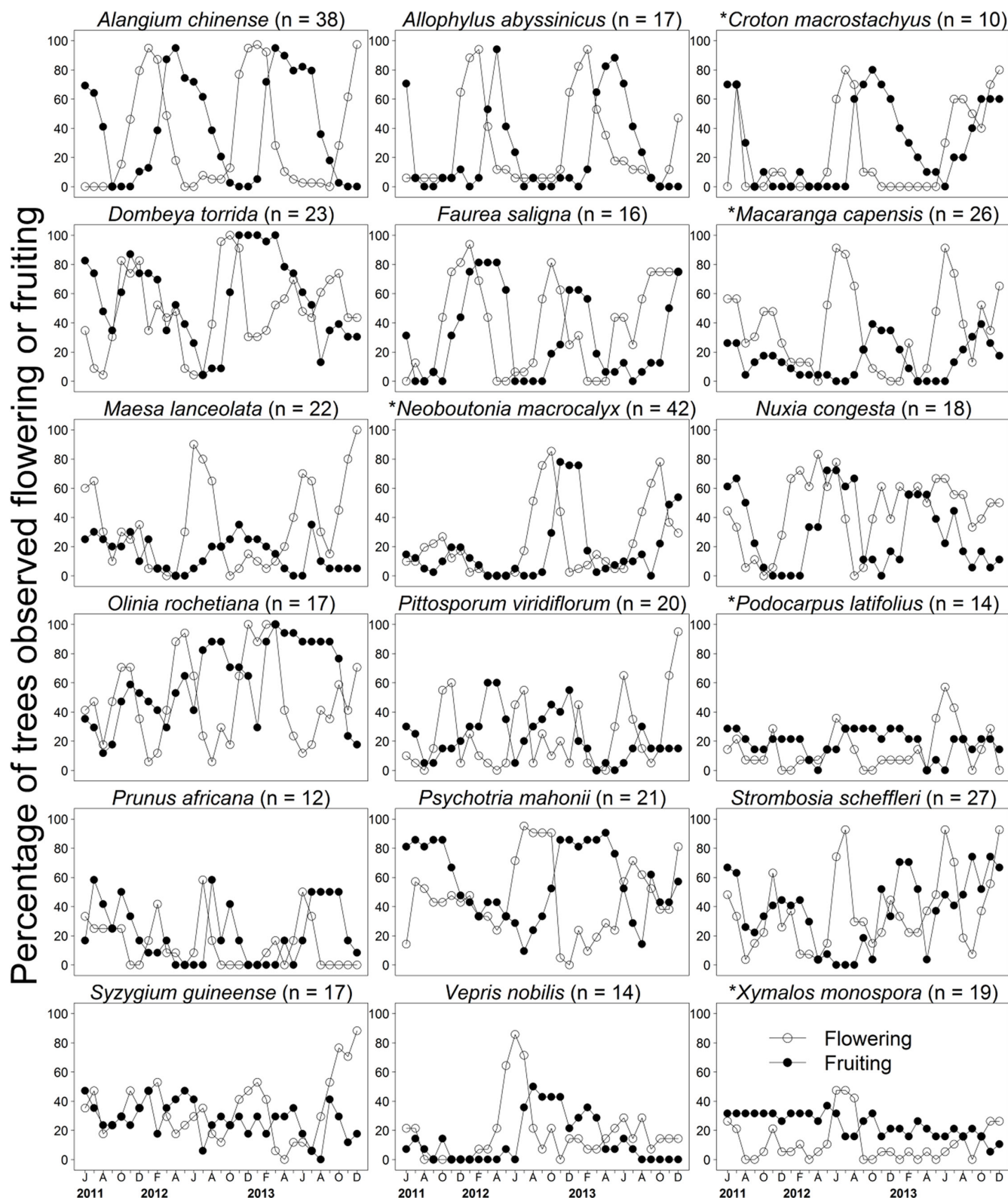


FIGURE 3 Monthly variation in the percentage of common trees observed flowering or fruiting. The species denoted with asterisks are considered dioecious.

$n=8055$ leafing events for 373 trees), peaking in the rainy season in November and December (Figure 4). Species with significant seasonality in leaf flushing were *Alangium chinense* (Lour.) Harms ($n=38$, $p<.001$), *Allophylus abyssinicus* (Hochst.) Radlk. ($n=17$,

$p=.009$), and *X. monospora* ($n=16$, $p=.043$; Table S3; Figure S8). Senescent leaves peaked during the long dry season in August ($p<.001$, Figure 4). Marked seasonality in leaf senescence was exhibited by *A. chinense* ($p<.001$) and *A. abyssinicus* ($p=.009$;

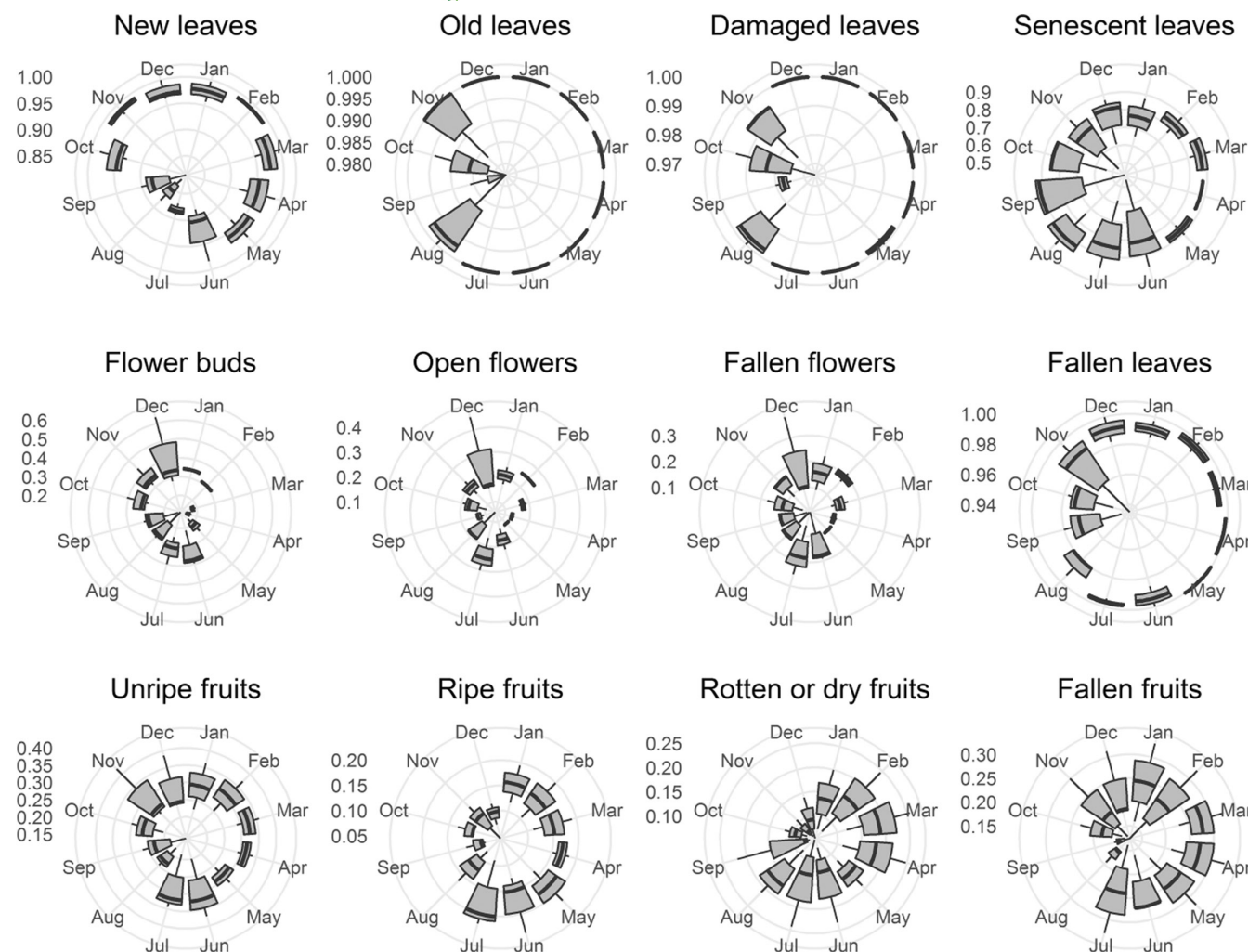


FIGURE 4 Boxplots showing the proportion of individual trees ($n=489$) that bore flowers, fruits and leaves in each month from June 2011 to December 2013. Only the tree species with ≥ 10 stems that survived until the last census ($n=18$ species) were considered.

Figure S12). Old, damaged, and fallen leaves lacked clear seasonality ($p > .05$ for all three) although declines were apparent during the commencement and in the middle of the wet season in September and October (Figure 4).

3.4 | Duration of phenophases

Flowering duration of our 18 common species ranged between 1.7 and 5.8 months per year and decreased significantly as fruit size of the species increased (Kendall's rank correlation, $\tau = -0.1$, $n=357$, $p = .007$, see Table 3). Zoochorous species bore flowers for a shorter period than non-zoochorous species (mean ± 1 SE: 3.6 ± 0.12 vs. 5.1 ± 0.29 months per year; Mann-Whitney test, $W=6020.5$, $p < .001$) while dioecious species bore flowers for a shorter period than non-dioecious species (2.9 ± 0.2 vs. 4.3 ± 0.13 months per year; $W=8250.5$, $p < .001$). Fruiting duration (i.e., duration of the period during which ripe or unripe fruits were seen) ranged between 1.6 and 7.2 months per year but did not vary significantly with fruit size ($\tau = 0.03$, $n=357$, $p = .496$). Zoochorous species remained in

fruit for a shorter period than non-zoochorous species (3.6 ± 0.17 vs. 4.8 ± 0.3 months per year; $W=6919$, $p = .001$) while dioecious species fruited for a shorter period than non-dioecious species (2.5 ± 0.29 vs. 4.2 ± 0.17 months per year; $W=7863$, $p < .001$). The duration of new leaf occurrence ranged between 8.4 and 12 months per year. Dioecious species exhibited a slightly longer period of new leaf occurrence than non-dioecious species (11.6 ± 0.08 vs. 11.1 ± 0.09 months per year; $W=15,952$, $p < .001$) but the leafing period of zoochorous species did not differ significantly from that of non-zoochorous species (11.2 ± 0.08 vs. 11.4 ± 0.1 months per year; $W=9549$, $p = .930$; Table 3).

3.5 | Synchrony of phenophases

Of the 18 common species, six exhibited high synchrony (i.e., index of synchrony > 0.5) in flowering times, seven indicated high synchrony in fruiting times while all 18 exhibited high synchrony in leafing times (Table 3). Four species, that is, *A. chinense* ($n=38$), *Faurea saligna* ($n=15$), *Olinia rochetiana* Juss. ($n=17$), and *Psychotria mahonii*

TABLE 1 Results of circular statistical analysis for the occurrence of seasonality in the flowering phenology of species with 10 or more individuals in 31 monthly phenological censuses.

Species	N trees	Flower buds			Open flowers			Fallen flowers		
		Mean angle (μ)	Vector length (r)	p	Mean angle (μ)	Vector length (r)	p	Mean angle (μ)	Vector length (r)	p
<i>Alangium chinense</i> (Lour.) Harms	38	7°	0.699	<.001	30°	0.783	<.001	30°	0.771	<.001
<i>Allophylus abyssinicus</i> (Hochst.) Radlk.	17	34°	0.638	<.001	60°	0.668	<.001	58°	0.748	<.001
<i>Croton macrostachyus</i> Hochst. ex Delile	9	235°	0.532	<.001	231°	0.530	<.001	229°	0.488	<.001
<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	23	291°	0.169	<.001	298°	0.167	.007	301°	0.125	.146
<i>Faurea saligna</i> Harv.	15	295°	0.456	<.001	334°	0.528	<.001	304°	0.428	<.001
<i>Macaranga capensis</i> (Baill.) Sim	23	190°	0.389	<.001	216°	0.497	<.001	204°	0.533	<.001
<i>Maesa lanceolata</i> Forssk.	20	212°	0.306	<.001	205°	0.439	<.001	200°	0.440	<.001
<i>Neoboutonia macrocalyx</i> Pax	39	267°	0.681	<.001	271°	0.681	<.001	275°	0.780	<.001
<i>Nuxia congesta</i> R.Br. ex Fresen.	18	70°	0.156	.008	112°	0.477	<.001	124°	0.436	<.001
<i>Olinia rochetiana</i> Juss.	17	352°	0.247	<.001	55°	0.268	<.001	60°	0.301	<.001
<i>Pittosporum viridiflorum</i> Sims	20	268°	0.203	.014	342°	0.321	.003	352°	0.342	.016
<i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb.	13	158°	0.366	.013	196°	0.652	<.001	183°	0.523	<.001
<i>Prunus africana</i> (Hook.f.) Kalkman	10	147°	0.433	.002	176°	0.684	<.001	186°	0.618	<.001
<i>Psychotria mahonii</i> C.H. Wright	21	227°	0.291	<.001	219°	0.344	<.001	237°	0.445	<.001
<i>Strombosia scheffleri</i> Engl.	26	214°	0.099	.103	240°	0.128	.113	215°	0.207	.007
<i>Syzygium guineense</i> (Willd.) DC.	16	331°	0.404	<.001	0°	0.280	.002	345°	0.327	.002
<i>Vepris nobilis</i> (Delile) Mziray	14	170°	0.436	<.001	173°	0.672	<.001	162°	0.623	<.001
<i>Xymalos monospora</i> (Harv.) Baill.	16	212°	0.390	<.001	202°	0.455	.006	210°	0.483	.021
Large-fruited species (fruit >10 mm long)	129	259°	0.289	<.001	256°	0.298	<.001	251°	0.331	.074
Small-fruited species (fruit ≤10 mm long)	226	331°	0.115	<.001	33°	0.137	<.001	44°	0.128	<.001
Dioecious species	100	238°	0.426	<.001	247°	0.522	<.001	243°	0.506	.074
Non-dioecious species	255	335°	0.142	<.001	30°	0.138	<.001	36°	0.121	<.001
Zoochorous species	290	297°	0.128	<.001	346°	0.063	.008	348°	0.049	.089
Non-zoochorous species	65	290°	0.152	<.001	320°	0.091	.028	263°	0.090	.093
All species (n = 2913 flowering events)	355	295°	0.134	<.001	338°	0.069	<.001	322°	0.044	.074

Note: Only the tree species with ≥10 stems that survived until the last census and had flowered or fruited at least once during the study period were considered. $p < .05$ are indicated in bold and show significant seasonality.

TABLE 2 Results of circular statistical analysis for the occurrence of seasonality in the fruiting phenology of species with 10 or more individuals in 31 monthly phenological censuses.

Species	N trees	Ripe fruits		Unripe fruits		Rotten or dry fruits		Fallen fruits	
		Vector length (r)	p	Vector length (r)	p	Vector length (r)	p	Vector length (r)	p
<i>Alangium chinense</i> (Lour.) Harms	38	0.719	<.001	0.542	<.001	0.724	<.001	0.600	<.001
<i>Allophylus abyssinicus</i> (Hochst.) Radlk.	17	0.812	<.001	0.717	<.001	0.623	<.001	0.738	<.001
<i>Croton macrostachyus</i> Hochst. ex Delile	9	0.547	<.001	0.644	<.001	0.419	<.001	0.607	<.001
<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	23	0.348	<.001	0.224	<.001	0.201	<.001	0.328	<.001
<i>Faurea saligna</i> Harv.	15	0.588	<.001	0.678	<.001	0.375	.001	0.631	<.001
<i>Macaranga capensis</i> (Baill.) Sim	23	0.687	<.001	0.626	<.001	0.668	<.001	0.645	<.001
<i>Maesa lanceolata</i> Forssk.	20	0.529	.002	0.303	.004	0.408	.048	0.298	.023
<i>Neoboutonia macrocalyx</i> Pax	39	0.868	<.001	0.675	<.001	0.525	<.001	0.727	<.001
<i>Nuxia congesta</i> R.Br. ex Fresen.	18	0.365	.007	0.429	<.001	0.141	.093	0.412	<.001
<i>Olinia rochetiana</i> Juss.	17	0.394	<.001	0.166	.001	0.515	<.001	0.231	<.001
<i>Pittosporum viridiflorum</i> Sims	20	0.343	.004	0.163	.066	0.138	.346	0.229	.257
<i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb.	13	0.673	<.001	0.266	.015	–	–	0.176	.137
<i>Prunus africana</i> (Hook.f.) Kalkman	10	0.781	<.001	0.570	<.001	0.546	.009	0.582	<.001
<i>Psychotria mahonii</i> C.H. Wright	21	0.507	<.001	0.201	<.001	0.321	<.001	0.254	<.001
<i>Strombosia scheffleri</i> Engl.	26	0.555	<.001	0.293	<.001	0.394	<.001	0.350	<.001
<i>Syzygium guineense</i> (Willd.) DC.	16	0.182	.163	0.094	.410	0.222	.108	0.082	.691
<i>Vepris nobilis</i> (Delile) Mziray	14	0.423	.021	0.213	.099	0.216	.302	0.266	.067
<i>Xymalos monospora</i> (Harv.) Baill.	16	0.173	.927	0.101	.366	0.553	<.001	0.138	.529
Large-fruited species (fruit >10mm long)	129	0.326	<.001	0.300	<.001	0.345	<.001	0.337	<.001
Small-fruited species (fruit ≤10mm long)	226	0.227	<.001	0.137	<.001	0.133	<.001	0.192	<.001
Dioecious species	100	0.607	<.001	0.439	<.001	0.437	<.001	0.484	<.001
Non-dioecious species	255	0.213	<.001	0.116	<.001	0.150	<.001	0.171	<.001
Zoochorous species	290	0.187	<.001	0.048	.010	0.145	<.001	0.066	.002
Non-zoochorous species	65	0.311	<.001	0.174	<.001	0.142	<.001	0.259	<.001
All species (n = 2714 fruiting events)	355	0.159	<.001	0.064	<.001	0.121	<.001	0.101	<.001

Note: Only the tree species with ≥10 stems that survived until the last census and had flowered or fruited at least once during the study period were considered. Significant values ($p < .05$) are highlighted in bold.

($n = 21$) showed high synchrony in flowering and fruiting. None of the relationships between phenophase synchrony and tree species traits were significant (i.e., with fruit size, sexual system or seed dispersal mode).

3.6 | Relationship with rainfall and temperature

Total monthly rainfall ranged from 6.0 to 226.0mm (average $\pm$ SD = 115.3 ± 65.7) and exhibited strong seasonality with peaks between March and May and September and November and troughs from December to February and June to August during the 31 months of our study (Figure 1b). Mean monthly maximum temperature was 23.2°C (SD = 0.8°C, range = 22.1–25.2°C) while mean monthly minimum temperature was 15.6°C (SD = 0.6°C,

range = 14.1–16.8°C). Total monthly rainfall was negatively correlated with mean monthly maximum temperature ($r = -0.28$, $n = 31$, $p = .030$) and positively correlated with mean monthly minimum temperature ($r = 0.31$, $n = 31$, $p = .015$), while mean monthly maximum temperature and mean monthly minimum temperature values were negatively correlated ($r = -0.34$, $n = 31$, $p = .007$; Figure 1). When we examined phenological events against conditions in the period encompassing the previous and concurrent calendar months, we found that flowering was negatively associated with maximum temperature (GLMM tests, $p < .001$) while fruiting was positively associated with minimum temperature ($p < .001$; Table 4; Figure 5 and Figure S12). We also found that leaf flushing was positively associated with total rainfall, negatively associated with maximum temperature and positively associated with minimum temperature ($p < .001$ in all cases, see Table 4, Figure 5 and Figure S12).

TABLE 3 Flowering, fruiting, and leafing duration and synchrony of the 18 tree species with 10 or more individuals that survived until the last census.

Species	N obs.	Fruit size (mm)	Sexual system	Dispersal type	Flowering			Fruiting			Leafing		
					Duration	Synchrony	Duration	Synchrony	Duration	Synchrony	Duration	Synchrony	
<i>Alangium chinense</i> (Lour.) Harms	38	10	Hermaphrodite	Zoochorous	4.0	0.64	4.8	0.64	9.1	0.86			
<i>Allophylus abyssinicus</i> (Hochst.) Radlk.	17	6	Monoecious	Zoochorous	3.3	0.10	2.8	0.56	8.4	0.71			
<i>Croton macrostachyus</i> Hochst. ex Delile	10	15	Dioecious or Monoecious	Non-zoochorous (auto)	3.1	0.63	3.9	0.43	12.0	1.0			
<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	23	10	Hermaphrodite	Non-zoochorous (auto)	5.8	0.48	6.8	0.56	12.0	1.0			
<i>Faurea saligna</i> Harv.	16	1.1	Hermaphrodite	Non-zoochorous (wind)	4.9	0.63	3.8	0.60	11.4	0.95			
<i>Macaranga capensis</i> (Baill.) Sim	26	6	Dioecious	Zoochorous	4.3	0.46	1.8	0.33	12.0	1.0			
<i>Maesa lanceolata</i> Forssk.	22	4	Hermaphrodite or monoecious	Zoochorous	4.1	0.41	1.8	0.16	12.0	1.0			
<i>Neoboutonia macrocalyx</i> Pax	42	13	Dioecious	Zoochorous	2.9	0.35	2.3	0.33	12.0	1.0			
<i>Nuxia congesta</i> R.Br. ex Fresen.	18	10	Hermaphrodite	Non-zoochorous (wind)	5.3	0.59	3.6	0.42	10.5	0.94			
<i>Olinia rochetiana</i> Juss.	17	10	Hermaphrodite	Zoochorous	5.8	0.64	7.2	0.76	11.7	0.98			
<i>Pittosporum viridiflorum</i> Sims	20	8	Hermaphrodite	Zoochorous	2.8	0.27	2.7	0.35	12.0	1.0			
<i>Podocarpus latifolius</i> (Thunb.) R.Br. ex Mirb.	14	12	Dioecious	Zoochorous	1.8	0.17	2.4	0.16	9.9	0.91			
<i>Prunus africana</i> (Hook.f.) Kalkman	12	11	Hermaphrodite	Zoochorous	1.9	0.29	3.1	0.27	11.6	0.96			
<i>Psychotria mahonii</i> C.H. Wright	21	6	Hermaphrodite	Zoochorous	5.5	0.51	6.8	0.52	12.0	1.0			
<i>Strombosia scheffleri</i> Engl.	27	23	Hermaphrodite	Zoochorous	4.4	0.49	4.5	0.54	11.9	1.0			
<i>Syzygium guineense</i> (Willd.) DC.	17	18	Hermaphrodite	Zoochorous	4.4	0.42	3.5	0.28	12.0	0.99			
<i>Vepris nobilis</i> (Delile) Mziray	14	8	Hermaphrodite or monoecious	Zoochorous	2.1	0.18	1.6	0.34	11.3	0.95			
<i>Xymalos monospora</i> (Harv.) Baill.	19	19	Dioecious	Zoochorous	1.7	0.19	3.4	0.19	11.5	0.95			

Note: Sexual system, fruit size, and dispersal type were assigned following Chapman et al. (1999), Gross-Camp, Mulindahabi, and Kaplin (2009), Katende et al. (1995), Lovett et al. (2006), Plants for A Future (www.pfaf.org), Protabase (www.prota.org), and CJB African plant Databases. A phenophase was considered to present high synchrony if its synchrony value exceeded 0.5, low synchrony if its synchrony value ranged between 0.25 and 0.5 and asynchrony if its synchrony value was less than 0.25.

TABLE 4 Effect of local climatic conditions on the occurrence of flowering, fruiting, and leaf flushing of common species based on binomial GLMMs.

	Occurrence of any event (score > 0)			Occurrence of events of high intensity (score > 2)		
	χ^2	df	p	χ^2	df	p
Flowering						
Total rainfall	2.7	1	.100	5.1	1	.024
Average maximum temperature	82.1	1	<.001	53.1	1	<.001
Average minimum temperature	3.5	1	.061	1.1	1	.292
Fruiting						
Total rainfall	1.2	1	.272	0.2	1	.667
Average maximum temperature	0.03	1	.858	1.2	1	.264
Average minimum temperature	14.6	1	<.001	6.1	1	.014
Leaf flush						
Total rainfall	44.2	1	<.001	75.0	1	<.001
Average maximum temperature	249.2	1	<.001	433.3	1	<.001
Average minimum temperature	245.4	1	<.001	172.2	1	<.001

Note: Total rainfall, average maximum temperature, and average minimum temperature were calculated over a 2-month period encompassing the concurrent and previous calendar months.

4 | DISCUSSION

Our study described patterns of flowering, fruiting, and leafing, and assessed their variation and relation to environmental conditions among a group of relatively common forest trees in an equatorial mountain forest sampled to provide a representative overview of the tree community. Flowering and fruiting exhibited more marked seasonal differences than did leafing. As we had anticipated, flowering peaked at the onset of the dry season in December while most fruiting (i.e., unripe fruits) occurred during high rainfall months in March through April though ripe fruit availability maximized during drier months in May through July, not when the soil was moist as we had expected, but several weeks in advance of the return of the rain in August. Flushing of leaves peaked in the rainy season in November and December. Climatic conditions showed strong associations with flowering, fruiting, and leafing. Among our most striking results are the marked differences in flowering and fruiting between zoochorous and non-zoochorous species. These findings highlight the importance of phenological datasets that attempt to represent the entire tree community in a more comprehensive manner. While we cannot robustly infer causation from these two and a half years of observational data, the patterns observed are consistent with the seasonally varying availability of resources such as light, water, and nutrients playing an important role.

4.1 | Flowering and fruiting seasonality

The observed peak in flower occurrence at the onset of the short dry season is consistent with other studies in East Africa (Chapman et al., 1999; Kebede & Isotalo, 2016; Sun et al., 1996) and supports the insolation-limitation hypothesis, which predicts that plants will flower during the period of maximum insolation unless limited by

water stress (van Schaik & Terborgh, 1993). Flowering in the dry season may favor pollination success given that flowers are readily visible at this time and that flowers and pollinators may avoid damage from rainstorms (Faria & Araújo, 2010; Lawson & Rands, 2019). It may also favor ripe fruits and seeds being available for dispersal in the rainy season when conditions favor establishment (Funch et al., 2002; Garwood, 1983; Stevenson et al., 2008). However, such marked seasonal fluctuation will impact resources for flower visitors and consequently have broader effects on the forest community. Our data reveal that a number of tree species including *Dombeya torrida*, *Nuxia congesta*, *P. mahonii*, and *S. guineense* also produce some flowers outside the peak and may thus support pollinators dependent on sustained access to floral resources (Figure 3). Unfortunately, we know little about the abundance and diversity of visitors to flowers of these tree species and their wider ecological roles, but a recent study conducted in Bwindi showed that dormice *Graphiurus murinus*, nectar bats *Megaloglossus woermanni* and sun birds (family Nectariniidae) frequently visit flowers of the African wild banana *Ensete ventricosum* (Ssali & Sheil, 2019). Some flower-visiting animals pollinate plant species, but some extract nectar and/or pollen without aiding pollination (Corlett, 2004; Nsor, 2015; Vizentin-Bugoni et al., 2018). Further studies are needed to clarify these relationships and dependencies.

Most species produced fruits during high rainfall months in March through May and September through November. This tendency was exhibited by 11 of 14 species that produce fleshy animal-dispersed fruits (Table 3; Figure S4) and has been observed elsewhere in equatorial Africa (Kagoro-Rugunda & Hashimoto, 2015; Sun et al., 1996; Tweheyo, 2007). *Podocarpus latifolius*, *Prunus africana*, and *P. mahonii* were exceptions with a high intensity of fruit production spanning low and high rainfall months. The finding is consistent with the hypothesis that many plants fruit in the rainy season to allow for dispersal, establishment and adequate growth and reduce seedling mortality

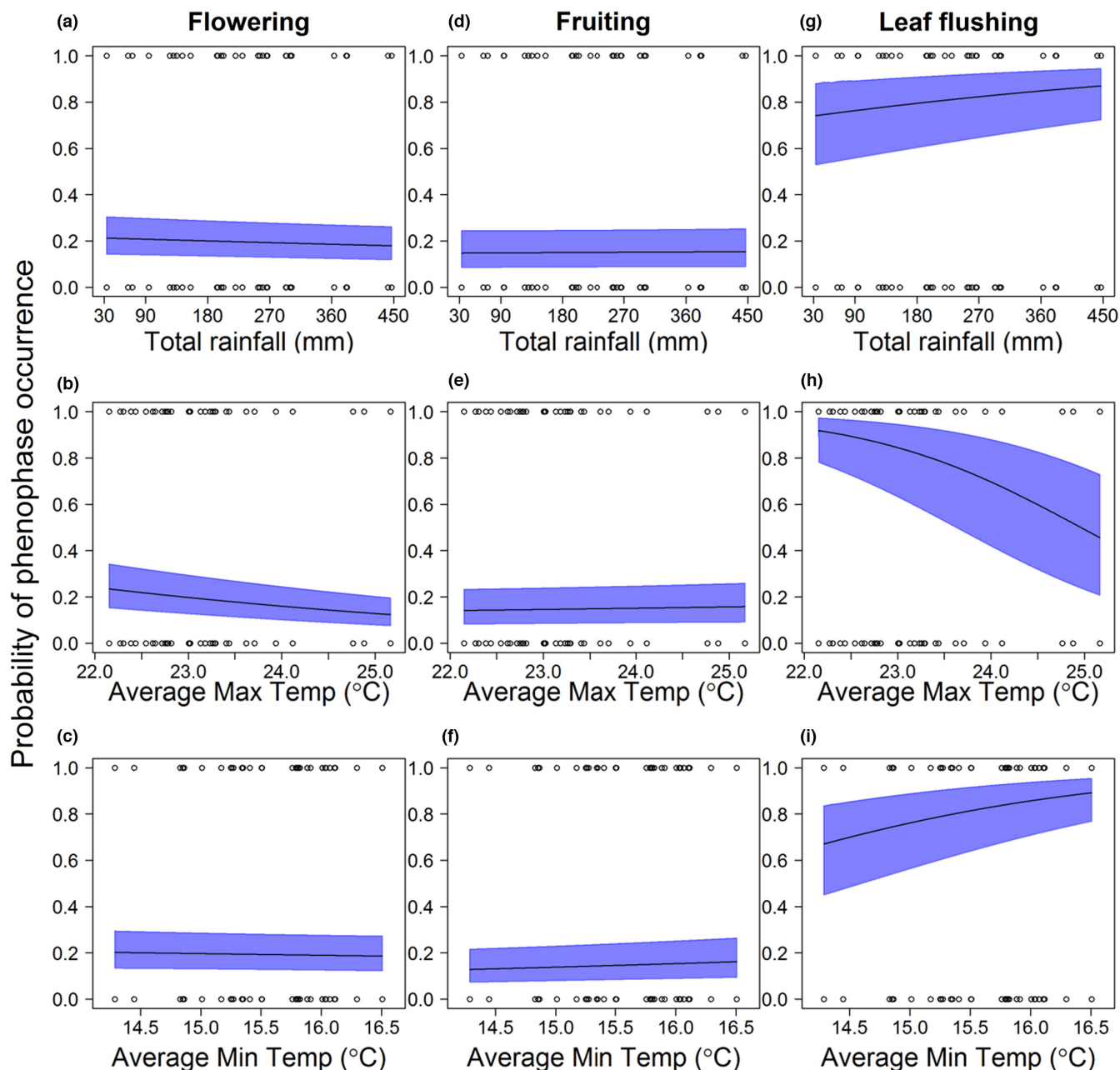


FIGURE 5 Per-stem likelihood of major flowering (a–c), fruiting (d–f) and leaf flushing (g–i) (i.e., score >2) in relation to local climatic factors in the 2-month period encompassing the concurrent and previous calendar months. Only the tree species with ≥ 10 stems that survived until the last census ($n = 18$ species) were included in the analysis. Prediction lines and 95% confidence intervals are based on coefficients of binomial GLMMs (Table 4).

during the subsequent dry season (van Schaik & Terborgh, 1993). Our observations also show that unripe fruits generally exhibit broader peaks than ripe fruits with the duration of unripe fruits lasting twice as long as that of ripe fruits (i.e., 3.4 months versus 1.6 months per year; see Figures S4 and S5). Our results further indicated that fruit fall was most pronounced during the wet season in April, coinciding with peak occurrences in immature fruit production (Figure S7). Our observations indicated that large crops of immature fruits fall during heavy rain. Future studies will be needed to clarify how weather impacts fruit production and availability.

Fruits were scarce during the entire September–November wet season and at the start of the December–February dry season. Prolonged periods of fruit scarcity have also been seen in neighboring montane forests including Nyungwe, Gishwati, and Kahuzi and are known to influence the diets and foraging range patterns of many frugivores (Basabose, 2005; Chancellor et al., 2012; Kaplin et al., 1998; Kaplin & Moermond, 1998; Matthews et al., 2019). For instance, chimpanzees sometimes switch to herbaceous pith, leaves and bark (Chancellor et al., 2012), monkeys to seeds, leaves, and insects (Lambert, 2010) while in subtropical forests in Asia palm

civets, which are not strict frugivores, are said to predate on rodents more during periods of fruit scarcity (Zhou et al., 2008). Further, chimpanzee and gorilla groups tend to fission off from others (Chapman, 1995; Seiler et al., 2017) while orangutans in equatorial Asia, pigs, and frugivorous birds migrate to more productive habitats in search of food (Buij et al., 2002; Marshall et al., 2014; Poulsen et al., 2002). Nonetheless, as seen in this study, some tree species, including *Croton macrostachyus*, *Ekebergia capensis*, *Ficus densistipulata*, *P. mahonii*, *S. scheffleri*, and *S. guineense*, continue to bear at least some fruits during periods of scarcity (Table S2; Figures S4 and S5) and thus—together with other species not included in this study (e.g., *E. ventricosum*, see Ssali & Sheil, 2019)—appear to be potential food sources for the vertebrate community during lean times. Such findings have practical implications; for instance, species that bear fruits during periods of food scarcity could be considered for use in restoration projects to attract and sustain frugivores which would promote diverse seed deposition and thus enrich and bolster forest recovery. Furthermore, we found that the occurrence of fleshy fruits tended to peak during the wet season while most peaks of non-fleshy fruits including nuts and pods like *F. saligna*, *D. torrida*, and *C. macrostachyus* were observed during the dry season (Figures S4 and S5). This suggests that more fleshy fruits are available for consumption in the wet season and nuts and pods more commonly available to be consumed in the dry season when the former are scarce (see also Plumptre, 2006).

The distinct patterns of flowering and fruiting noted for zoochorous and non-zoochorous species deserve special mention given that the phenology of non-zoochorous tree species has been neglected in the majority of phenology studies in African forests (see Adamescu et al., 2018) despite these constituting a substantial proportion of the species present (4 of 18 taxa and 65 of 355 stems in our data, or 9 of 54 taxa and 106 of 530 stems across the whole species list we initially included for Bwindi). Although there was considerable variation among observations, we found that, taken as a group, the phenology of zoochorous tree species differed from that of non-zoochorous species (Table 3; Figure 3). Thus, patterns and behaviors perceived for the selected taxa included in phenology data that focus on animal food species are unlikely to be representative of trees in general and non-zoochorous species in particular. More extended surveys that incorporate a wider range of representative taxa remain an important goal for tropical research if the necessary funds and support can be accessed and maintained.

4.2 | Leafing seasonality

Leaf flushing exhibited significant seasonality, with peak activity occurring in November and December. Such a leafing pattern may stimulate an increase in the availability of seasonal pollinators (and insects more generally) since flushing new leaves with lower tannin levels increases the availability of palatable food for insect larvae (Aide, 1993; Barbehenn & Constabel, 2011). Indeed, a recent study of leaf phenology in Bwindi found a strong link between leaf flushing,

prey availability and the food requirements of Stripe-breasted Tits *Parus fasciiventer* and inferred that increased leaf production likely stimulates a rise in caterpillar numbers (Shaw, 2017). We also found that leaf flushing declined during the long dry season (Figure 1 and Figure S8) presumably an adaptation to reduce risks from drought (Ciais et al., 2005; Doughty et al., 2015). The pattern agrees with studies that have found that persistent leaf flushing after major rains is related to improved growth potential (e.g., Eamus, 1999; Elliott et al., 2006; Manoli et al., 2018).

Our observations further indicate that 14 of 18 tree species continuously flush and produce expanded leaves (Figure S8). These trees possess adaptations that reduce water stress and may thus be less affected by dry season conditions. For example, *S. guineense* tends to grow in areas where the groundwater is near the surface while *Macaranga capensis* grows in open areas and has hairy short-lived leaves that are insulated from heat and can be readily replaced at a lower cost (Dungan et al., 2008; Katende et al., 1995; Lovett et al., 2006). Consequently, these tree species might have an advantage as they likely escape acute herbivore pressure since insect abundance tends to be lower in the dry season (Aide, 1993; Kasenene & Roininen, 1999) and could thus have a better chance of maximizing carbon gain when cloud cover is low especially during the wet season (Graham et al., 2003).

Senescent leaves peaked during the long dry season in August, although they occurred in only 49 tree canopies (9.2%), with fast-growing deciduous species *A. chinense* and *A. abyssinicus* exhibiting pronounced seasonality (Figure S11). This finding is in line with the water limitation hypothesis and indicates that water availability has a strong influence on leaf phenology (Ouédraogo et al., 2013; Sade et al., 2018; Vico et al., 2015). The long dry season in Bwindi and other forests in Eastern, but not Western, equatorial Africa also coincides with the peak in maximum temperature (Figure 1; Kasangaki et al., 2012; Munzimi et al., 2015; Philippon et al., 2014). During periods of low water availability, leaf loss can lower water demand and thus help avoid drought and the associated risks of xylem cavitation and plant desiccation (see Figure 1; see also Alberton et al., 2019; Eamus, 1999; Marchin et al., 2010). Leaf senescence has also been reported to coincide with the major flowering season and may thus favor an evolutionary strategy for some species that allows flowers to be more visible at the commencement of the wet season (Singh, 2005).

4.3 | Phenophase duration and synchrony

Our observed flowering periods of 1.7–5.8 months, fruiting periods of 1.6–7.2 months, and leafing periods of 8.4–12 months per year are similar to those reported for similar species in tropical African forests (Anderson et al., 2005; Ratovonamana et al., 2011; Sun et al., 1996). The relatively short flowering and fruiting periods indicate that reproductive structures are released or removed after ripening while the prolonged duration of new leaf occurrence indicates that soil moisture is high enough to maintain leaf function for most

of the year (Obeso, 2002; Singh, 2005; Vico et al., 2015). When performing single factor analysis, we found that flowering duration varies by fruit size, sexual system, and dispersal type, and that fruiting duration varies by sexual system and dispersal type, while variation in leafing duration was mainly due to differences between dioecious and non-dioecious species (Table 3)—factors that have rarely been examined in studies of tropical montane forest phenology. Our finding that flowering duration is negatively correlated with fruit size points to a resource allocation strategy in which trees flower quickly to allow for a more extended period of fruit maturation (Ashman & Schoen, 1997; Bolmgren & Cowan, 2008; Lord & Westoby, 2006). These trees may avoid additional investment that would be needed to maintain and replace the flowers which are damaged during a long period of exposure (Santangelo & Thompson, 2019). Our data also revealed a shorter flowering duration for dioecious species compared to non-dioecious species (Table 3). This finding potentially reflects the greater resource-demand by dioecious species, particularly by females which produce more seeds and invest more in reproduction compared to hermaphrodites (Asikainen & Mutikainen, 2003; Obeso, 2002). Furthermore, we found that zoochorous species remain in fruit for a shorter period than non-zoochorous species. This observation indicates that wind-dispersed fruits remain on a tree for several months perhaps providing the seeds a better chance of being dispersed in favorable environmental conditions, that is, low humidity and high wind intensity (Griz & Machado, 2001; van Schaik & Terborgh, 1993). Another explanation is that fruits of zoochorous species are, once they are edible, rapidly removed by frugivorous vertebrates. The observation that dioecious species show a longer period of new leaf occurrence than non-dioecious species may be linked to the tendency for females of dioecious species to produce more and larger seeds compared to hermaphrodites (Table 3; see also Asikainen & Mutikainen, 2003; Carpenter et al., 2003; Renner, 1995). As such, the extended presence of new leaves likely provides adequate resources and energy for fruit and seed development.

Out of 18 species included in our analysis, six showed marked synchrony in flowering times (Table 3). These species may benefit from synchronized flowering because of the increased number of pollinators which may lead to greater seed set and reduced predation, but may experience increased competition for pollinators (Borchert et al., 2005; Parra-Tabla & Vargas, 2007; Pires et al., 2014). These plants appear to share a common pool of pollinators comprising mainly bees and other insects attracted by flowers (Katende et al., 1995; Lovett et al., 2006). Four of these species also indicated high synchrony in fruiting. This further suggests that they compete for seed dispersal arising because of increased fruit availability (Günter et al., 2008; Poulin & Lefebvre, 1999; Wheelwright, 1985). On the contrary, the large number of less synchronous species, the majority of which are dispersed by animals (Table 3), suggests that various tree species in Bwindi supply fruit to forest animals during periods of scarcity and may benefit from these animals due to the increased probability that the seeds are dispersed away from conspecifics in periods when animals have to forage more widely to find fruit (see also Polansky & Robbins, 2013; Ssali & Sheil, 2019). Our dataset

further revealed high synchrony in leafing times for all our 18 common species (Table 3). This observation may reflect the most energy efficient moment to produce young leaves that have high photosynthetic potential (Kitajima et al., 2002; Manoli et al., 2018; Uribe & Sierra, 2021) and the tendency to satiate herbivores as a way of minimizing leaf damage (Aide, 1993; Lamarre et al., 2014; Wright, 1994).

4.4 | Environmental cues

The determinants of phenological processes at the equator have long been viewed as enigmatic (e.g., see Borchert, 1983). While the changes at the equator and throughout the tropics are small, many factors change in unison as we see in Bwindi in the negative correlation between monthly rainfall and maximum temperature and the positive correlation of rainfall with mean monthly minimum temperature. Unmeasured factors, such as cloud cover, solar radiation, soil water, and humidity likely varied in a similarly distinct but correlated manner over the same periods. Thus, we see temperature as a proxy for the season more generally rather than necessarily acting as a cue in itself. Furthermore, each tree's response is likely to combine and integrate conditions over an extended period prior to the observations with the relationships to our chosen variables (temperature or rainfall) within a given month arguably playing only a partial or indirect role. This view is consistent with the hypothesis that flower induction in tropical trees is determined primarily by internal factors and secondarily by environmental factors that affect the seasonal development of vegetative structures (Borchert, 1983; Wright, 2018). It is also recognized in various contexts around the world that many plant adaptations appear to precede rather than follow key environmental factors—for example, in many monsoon environments deciduous trees develop new leaves and start to transpire in an apparent anticipation of the rains, so despite a correlation the rains and the cues of leaf growth are distinct (Dang Hoi & Dung, 2021; Elliott et al., 2006; Nanda et al., 2015; Singh, 2005). Teasing out what is causal and what is merely correlated due to common seasonal patterns will require multiple years of data with adequate variation in and among the key variables.

4.5 | Synthesis and future directions

This study provides new insights into the phenology and associated seasonality of one of the most species-rich forests in equatorial Africa. Few previous multi-species studies have examined multiple phenophases using observations from a broadly representative subset of common tree species within a tropical montane forest (e.g., Sun et al., 1996; see Table S1). Our data highlight that all the 18 tree species exhibit marked seasonal behavior despite the equatorial location that in other biogeographic regions is sometimes referred to as “aseasonal” (e.g., Mendoza et al., 2018; Peres, 1994; Satake et al., 2019). Despite its relatively short duration, the study yielded consistent results that indicate that

phenological processes likely reflect ecological constraints and opportunities including reproduction costs, competition, greater seed set, and reduced predation. A recent study showed that a number of tropical African forests including Bwindi exhibit remarkably little seasonality in flowering and fruiting (Adamescu et al., 2018), but this reflects the specific set of species included in that study which encompassed potential “keystone species” such as figs that provide fruit for a number of species and are exceptional for their species diversity and asynchronous fruiting patterns (see Kattan & Valenzuela, 2013; Tweheyo, 2003). Studies of animal food species may vary considerably from a selection of species that better represent the tree community (Table S1). We thus advocate a cautious generalization of such patterns among food species to the forest more generally. Longer term studies are needed for a more robust assessment of community-wide phenology and its correlates in our study system.

5 | CONCLUDING REMARKS

Flowering and fruiting exhibited strong seasonality. Flowering peaked at the beginning of the short dry season while fruiting peaked at the beginning and in the middle of the short rainy season. These patterns were significantly associated with seasonal variations in temperature. Seasonality in leafing was less pronounced and appeared to correlate to rainfall and temperature. While there was considerable variation among species we noted that, taken as a group, the phenology of common zoochorous tree species differed from that of common non-zoochorous species with flowers and fruits remaining on trees for a shorter period—perhaps a reflection of florivore and frugivore activity. Thus, a wider and more representative range of species should be considered in phenology monitoring. Given that tree phenology influences many forest properties, and interspecific interactions, these findings have important implications for ensuring a broader and deeper understanding of wider ecosystem dynamics and conservation. Morellato et al. (2018) have previously advocated the need to build, maintain, and support long-term (decade or more) phenology studies across the tropics—we back this idea and highlight that the selection of species included should be broad and representative of the sites involved.

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CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interest with respect to the research, authorship, and/or publication of this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m0cfxpp7z> (Ssali & Sheil, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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