

Long-term trends in fruit production in a tropical forest at Ngogo, Kibale National Park, Uganda

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Abstract

Fruit production in tropical forests varies considerably in space and time, with important implications for frugivorous consumers. Characterizing temporal variation in forest productivity is thus critical for understanding adaptations of tropical forest frugivores, yet long-term phenology data from the tropics, in particular from African forests, are still scarce. Similarly, as the abiotic factors driving phenology in the tropics are predicted to change with a warming climate, studies documenting the relationship between climatic variables and fruit production are increasingly important. Here, we present data from 19 years of monitoring the phenology of 20 tree species at Ngogo in Kibale National Park, Uganda. Our aims were to characterize short- and long-term trends in productivity and to understand the abiotic factors driving temporal variability in fruit production. Short-term (month-to-month) variability in fruiting was relatively low at Ngogo, and overall fruit production increased significantly through the first half of the study. Among the abiotic variables, we expected to influence phenology patterns (including rainfall, solar irradiance, and average temperature), only average temperature was a significant predictor of monthly fruit production. We discuss these findings as they relate to the resource base of the frugivorous vertebrate community inhabiting Ngogo.

KEYWORDS

abiotic factors, frugivores, fruit production, temporal variation

1 | INTRODUCTION

Phenology of tropical moist forest plant communities varies considerably in space and time (Levey, 1988; van Schaik, Terborgh, & Wright, 1993; Sun *et al.* 1996; Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Chapman *et al.*, 2005; van Schaik & Pfannes, 2005). Local variation in abiotic factors such as irradiance (Wright & van Schaik, 1994), temperature (Tutin & Fernandez, 1993), soil conditions (Clark, Clark, & Read, 1998), and rainfall (Lieberman, 1982) combines with variation in biotic factors such as the density and activity of pollinators and seed dispersers

(Wheelwright, 1985; Wheelwright & Orians, 1982) to produce local patterns in the timing of reproductive events and leaf flushing (Chapman, Valenta, Bonnell, Brown, & Chapman, 2018; Chapman *et al.*, 1999). These localized patterns can profoundly influence the behavior, abundance, and population dynamics of primary consumers. For instance, migrations of bearded pig (*Sus barbatus*) populations across tens to hundreds of kilometers in Borneo closely track the pulsed seed production of mast-fruiting Dipterocarpaceae (Curran & Leighton, 2000), and gray mouse lemurs (*Microcebus murinus*) show pronounced variations in reproductive rates across a latitudinal gradient of primary productivity and in response to temporal

fluctuations of resource availability (Lahann, Schmid, & Ganzhorn, 2006). Previous studies have demonstrated that animals relying heavily on fruit resources often must respond behaviorally to temporal fluctuations in fruit availability (e.g., chimpanzees [*Pan troglodytes*]: Anderson, Nordheim, Boesch, & Moermond, 2002, Mitani, Watts, & Lwanga, 2002, Potts, Baken, Levang, & Watts, 2016), and that variation in fruit availability can impact animal reproduction (Anderson, Nordheim, & Boesch, 2006; Emery Thompson, 2013) and population density (Potts, Chapman, & Lwanga, 2009; Watts, Potts, Lwanga, & Mitani, 2012b).

Although the effects of temporal fluctuations in fruit availability on behavior and physiology are well-established for tropical frugivores (e.g., primates: Peres, 1994, Tutin, Ham, White, & Harrison, 1997, Knott, 1998, Brugiére, Gautier, Mougazi, & Gautier-Hion, 2002, Mitani *et al.* 2002, Worman & Chapman, 2005, Janmaat, Polansky, Ban, & Boesch, 2014, Marshall, Beaudrot, & Wittmer, 2014), the abiotic drivers of these fluctuations (e.g., rainfall, temperature, irradiance) are highly variable across sites (Sauther, 1998; Tutin & Fernandez, 1993; Chapman *et al.*, 1999; Chapman *et al.*, 2018; Stevenson, 2004; Mendoza, Peres, & Morellato, 2017, Dunham, Razafindratsima, Rakotonirina, & Wright, 2018). For instance, while rainfall correlates closely with fruit availability in certain tropical environments (e.g., Madagascar: Dunham *et al.*, 2018; Sauther, 1998), this is not universally the case (Mitani & Watts 2001, Polansky & Boesch, 2013).

Additionally, tropical forests can show annual, subannual, and suprannual periodicities in fruit production, but the exact nature and magnitude of these periodicities, as well as their intra- and interspecific variability, are not always well documented (though see Adamescu *et al.* [2018] for comparative analyses from several sites in equatorial Africa). Nemani *et al.* (2003) documented a long-term, multi-decade trend of increasing productivity in tropical forests on a global scale, but how widely such long-term upward trends characterize individual forests or sites is less well-established.

With certain notable exceptions (e.g., Kibale National Park, Uganda: Chapman *et al.*, 2005; Chapman *et al.*, 2018; Taï National Park, Côte d'Ivoire: Polansky & Boesch, 2013; Lopé National Park, Gabon: Bush *et al.*, 2017), few studies from tropical moist forests in equatorial Africa have sufficient time depth to address these issues adequately (Abernethy, Bush, Forget, Mendoza, & Morellato, 2018). For example, in a recent meta-analysis of reproductive cycles in African tropical forest trees, sufficient data were available from only 17 sites, and only eight of these sites yielded time series of a decade or longer (Adamescu *et al.* 2018). This is unfortunate, as recent climate models (e.g., Niang *et al.*, 2014) predict substantial increases in average temperatures (Niang *et al.*, 2014) and solar irradiance (Cai *et al.*, 2014) in the forested equatorial belt of Africa during the next century, as well as long-term declines in tropical forest productivity over multi-decadal scales (e.g., Wieder, Cleveland, Kolby Smith, & Todd-Brown, 2015, Lyra *et al.*, 2017; though these multi-decadal effects are likely to be geographically heterogeneous, Rifai, Li, & Malhi, 2019). As these modeling efforts make clear, understanding trends in fruiting phenology, as well as

the functional relationships between phenology and the climatic forces that influence it, is necessary to generate informed predictions regarding the responses of tropical forest frugivores to climate change.

The Ngogo research site, in Kibale National Park, Uganda, supports large populations of frugivorous species (most notably primates; Lwanga, Struhsaker, Struhsaker, Butynski, & Mitani, 2011; Mitani, Struhsaker, & Lwanga, 2000) and is the site of long-term research on an unusually large community of chimpanzees (Watts, 2012). Previous research at Ngogo provided preliminary evidence of relatively low temporal fluctuation in resource availability (Potts, Baken, Ortmann, Watts, & Wrangham, 2015; Potts *et al.*, 2009; Watts *et al.*, 2012b). However, Potts *et al.* (2009) did not explicitly quantify temporal fluctuations in fruit availability. Also, while Watts *et al.* (2012b) provided summary statistics on variation within and among months in fruit production—both overall and for figs and non-fig fruit separately—and illustrated this variation graphically, its main focus was the diet of chimpanzees. The authors did not provide detailed statistical analysis of fruiting phenology or its relationship to abiotic variables. Meanwhile, Chapman *et al.* (2018) presented data on variation in fruit production and analyzed the relationships between fruit abundance and abiotic factors (rainfall, temperature, irradiance, and El Niño events) at Kanyawara, a second site in Kibale located 10 km to the northwest of Ngogo. Kanyawara and Ngogo differ in altitude, temperature regimes, and annual rainfall (Struhsaker, 1997), and tree species composition differs between the sites in ways that are important for the feeding ecology of frugivores (Butynski 1990, Potts *et al.*, 2009; Watts, Potts, Lwanga, & Mitani, 2012a).

Watts *et al.* (2012b) reported 144 months of phenology data on species of importance in the diet of frugivores at Ngogo. In this paper, we utilize phenology data from an additional 95 months (making the total sample 239 continuous months) to characterize the overall spatiotemporal abundance of fruit resources in greater detail and with more time depth than previously possible, to quantify both short- and long-term trends in fruit availability, and to determine which abiotic factors most likely drive fruit production.

2 | METHODS

2.1 | Study site

Kibale National Park (795 km²) is located in southwestern Uganda, directly east of the Rwenzori Mountains, and is classified as a moist evergreen or semi-deciduous forest transitional between lowland and montane forest (Struhsaker, 1997). The forest at Ngogo is a mosaic of various successional stages, including large tracts of old-growth stands adjacent to early- to mid-stage colonizing forests, swamp forests, and anthropogenic grasslands (Lwanga, Butynski, & Struhsaker, 2000, Potts, 2008). *Chrysophyllum albidum*, *Celtis* spp., *Pterygota mildbraedii*, and *Piptadeniastrum africanum* are co-dominant in the central area of

the park, where Ngogo is located (Chapman & Lambert, 2000). Plant species diversity at Ngogo is moderately high compared with similar sites in the Congo Basin, but considerably lower than tropical lowland evergreen forests (Potts & Lwanga, 2014).

2.2 | Monitoring of tree reproductive phenology and abiotic variables

To assess temporal fluctuations in the availability of fruits important in the diet of chimpanzees, we analyzed long-term data obtained from a permanent phenology sample established in 1998. Because the bulk of research at the site has focused on the behavior and ecology of chimpanzees and other primates, this sample focuses on 20 species important in the diets of the frugivorous primates at Ngogo (e.g., the plant species included in this analysis make up > 75% of time spent feeding by Ngogo chimpanzees; Potts, Watts, & Wrangham, 2011; Watts et al., 2012a). We took advantage of a trail grid used to facilitate follows of chimpanzees to identify approximately 20 individuals of each species ($N = 717$ stems total on the phenology trail, of which the 400 belonging to the species of interest were used here). All 400 trees were checked once monthly by three highly trained field assistants. One assistant did so throughout the entire study, another from 1998 to 2011, and the third from 2011 to the end of the study period. For each tree or hemi-epiphytic fig on the phenology trail, the observers noted the presence or absence of fruits in the canopy. If an individual tree died, it was replaced by one of the same species and similar size. Our measure of habitat-wide fruit availability is the proportion of stems on the phenology trail bearing ripe fruit per month; this measure is similar to that used by Chapman et al. (2018). Data presented here come from 19 years of monitoring between January 1998 and December 2017.

We collected daily records of maximum and minimum temperatures and rainfall during the study period. Observations were made each morning at our camp (located in a small clearing adjacent to the forest), with total rainfall over the preceding 24 hr measured to the nearest 0.1 mm and temperatures measured to $\pm 0.1^\circ\text{C}$. Because we did not have the capacity to collect ground-level solar radiation data in our camp, we obtained monthly mean irradiance (W/m^2) values derived from satellite data from the Helio-Clim3 Database of Daily Solar Irradiance v4 (maintained by MINES ParisTech-Armines; <http://www.soda-is.com>).

2.3 | Data analysis

We used an information-theoretic approach (Burnham & Anderson, 2002) to build candidate generalized additive models (GAM) explaining variation in the proportion of stems bearing fruit in a given month as a function of main effects and interactions between predictor variables. Predictors included monthly

average rainfall, temperature, and irradiance. Because previous exploration of this dataset suggested that fruit production had increased since initiation of the study, although perhaps not linearly, we included a nonlinear smooth term “date” in our set of GAMs to detect any such trend statistically and to dampen short-term (month-to-month) fluctuations that might have obscured it (Polansky & Robbins, 2013). Because numerous studies have demonstrated regular seasonality in ripe fruit availability in tropical forests (e.g., van Schaik et al., 1993; Terborgh, 1983), we included “month” as an unspecified nonlinear smooth predictor, which allowed us to examine short-term (monthly) periodicity in fruit production. Smooth terms are generally constructed using penalized splines, in which a penalty λ is imposed on the second derivative of the function, thereby promoting “smoothness” (Wood, 2006). We used the pyGAM library (Servén & Brummitt, 2018) in the Python programming environment to create penalized basis splines (or b-splines) for the long-term smooth function and cubic splines for the short-term smooth function. We modeled climatic variables as linear terms in all models in which they appeared (see below for details of model construction). To determine appropriate λ penalization values for the smooth terms in each model, we first fit a full model (including all smooth and linear terms, plus additional parameters described below), then used the resulting smoothing penalties as λ values for reduced models.

Besides the linearly modeled covariates and the smooth terms, we included two additional components in each model: (a) a first-order autoregressive (AR1) term in each model to account for the temporal autocorrelation inherent in this monthly dataset (autocorrelation analyses, showing a sharp drop off and increase in width of confidence intervals beyond a lag of one month, are available upon request); (b) a term to remove the potential influence of repeated measures of the same trees on the phenology trail each month. Because our primary objective was to characterize forest community-wide patterns of fruit production (a “population level” estimate), as opposed to fruiting patterns at the individual tree or species level (“individual level” estimates), we could not account for repeated sampling by specifying plant species or tree ID as random effects factors, as would be appropriate in a generalized additive mixed model (GAMM) framework (Bolker et al., 2009). Nor could we easily utilize a marginal-type modeling approach (e.g., a generalized estimating equation [GEE]; Hubbard et al. 2010), because such models, at least as they are currently implemented in available programming packages, do not deal well with fitting penalized b-splines and other non-parametric functions (though some work has recently been done in this area, e.g., Stoklosa & Warton 2018). Instead, we approached the problem of repeated measures by a two-step procedure. First, we produced separate models for each plant species describing month-to-month variability in percent stems bearing fruit as a function of time (specifying a smooth function for time using penalized regression splines as above). We then included the following term, for each month of the study i , to reduce the bias imposed by the random slopes and

intercepts associated with the individual plant species repeatedly sampled over the course of the study:

$$\rho_i = \sum_{s=1}^n d_{s,i}$$

where \mathbf{d} is the vector containing all n plant species' deviance residuals d_s .

Because the response variable (proportion of stems bearing fruit) consisted of non-negative numbers on a continuous scale, we assigned the data to a gamma distribution and specified an inverse link function for all models. Although a beta distributed error structure might have been more appropriate because our data were bounded by 0 and 1, beta errors are not readily implemented in standard GLM packages, including the PyGAM package. Because a visual examination of the kernel density estimate (KDE) function of the response variable indicated that the data conformed reasonably well to a gamma distribution, we concluded that specifying this in subsequent models was acceptable. Each model took the form:

$$g(E[y_i]) = \beta_0 + \beta_1 y_{i-1} + \rho_i + s(\text{date}_i) + s(\text{month}_i) + \mathbf{X}_i \boldsymbol{\beta}$$

where the expected value of y in month i is a function of $\mathbf{X}_i \boldsymbol{\beta}$ (the matrix of linearly modeled covariates and their associated parameter estimates), the nonlinear smooth functions, the AR1 component ($\beta_1 y_{i-1}$), the term representing the influence of repeated measures of the same phenology species (ρ_i), and the intercept (g represents the link function). The only change we made among candidate models was in the composition of $\mathbf{X}_i \boldsymbol{\beta}$. All other components were included in each model because (a) we needed to account for repeated measures and autocorrelation in each case, and (b) one of the primary motivations of the study was to investigate the long- and short-term patterns of change in fruit production, so we thought it important to retain $s(\text{date})$ and $s(\text{month})$ in each model. We generated a full model set including all possible combinations of linear predictors.

To make inferences about the relative ability of each model to explain variability in the percentage of stems fruiting while avoiding overfitting by incorporating excess predictors, we took an approach similar to that of Anderson, Burnham, and Thompson, (2000). For each model, we assigned a score based on Akaike's Information Criterion modified to account for small sample size (AIC_c). We then computed Akaike weights (w_i) for each model which, when combined with the log-likelihood and data on parameter number contained in the AIC_c score, provided a means of approximating the likelihood $L(m_i | \mathbf{X}_p, s_i(d), s_i(m))$ of the i th model given linear and smooth predictors (Anderson et al. 2000). We used these criteria to assess the value of including each of the various linear predictors in a given model, as well as the strength of the short- and long-term smooth functions as predictors. We then conducted a model averaging procedure on all the smooth function terms and linear predictors. The averaged predicted value of

smooth parameter s was determined by summing the value of its estimated partial dependence at each value of the response for each model in the model set, weighted by each model's Akaike weight ($\hat{s} = \sum \hat{s}_i \omega_i$). We also report the percentage of null deviance explained by each model.

To examine long- and short-term fruiting patterns in individual plant species, we generated separate GAM models for each of the 20 species included in our analysis. Because the focus of this species-level analysis was on temporal trends, rather than on abiotic factors possibly driving these trends, these models included only the long- and short-term smooth functions described above and did not include any linear predictors. To determine the extent to which a particular species' fruit production patterns could be reliably predicted by month, we conducted likelihood ratio tests (LRT) for each species. Each LRT compared that species' GAM with the monthly smooth term included in a model that excluded month.

We used standard univariate methods (e.g., Spearman's rank coefficient) to analyze changes in rainfall, temperature, irradiance, and monthly coefficients of variation in fruiting over time. All analyses were conducted using the Python 3.7 programming language.

3 | RESULTS

3.1 | Rainfall, temperature, and irradiance patterns

Annual rainfall varied from 1,002.50 mm to 1709.90 mm ($X = 1,427.02$, $SD = 147.06$; Figure S1), with annual peaks tending to occur March-May and Sept-Nov. Average daily temperature was 20.6°C ($SD = 0.82^\circ\text{C}$, range = 19.0–23.5°C). Secular decreases in both average temperature (Spearman $r = -.272$, $p < .001$) and irradiance (Spearman $r = -.557$, $p < .001$) occurred. In contrast, monthly rainfall values increased slightly, but not significantly (Spearman $r = .087$, $df = 201$, $p > .15$). Monthly rainfall was negatively and significantly correlated with average temperature ($r = -.483$, $p < .001$) and with irradiance ($r = -.341$, $p < .001$), whereas monthly temperature and irradiance values were positively correlated ($r = .550$, $p < .001$; Figure 1).

3.2 | Overall fruit production and temporal variability

An average of 8.7% of all trees had ripe fruit each month ($SD = 4.1\%$). The number of trees that bore fruit each month varied considerably, from a low of 0.7% in August 1998 to a high of 20.3% in October 2011. Fruit production tended to peak June-November and to be lowest December-May (Figure 2). However, variability among years was substantial, and there were no significant pairwise differences in productivity between months (all Tukey HSD post hoc pairwise comparisons $p > .05$). The monthly proportion of stems bearing fruit showed a clear secular increase until early

FIGURE 1 Histograms (on diagonals) of univariate frequency distributions and bivariate correlation plots (in panels below diagonal) for each of the measured abiotic predictor variables (rainfall in mm, average temp in °C, and irradiance in W/sq m)

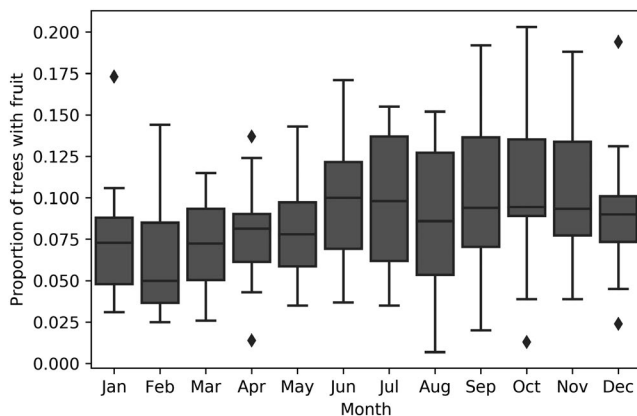
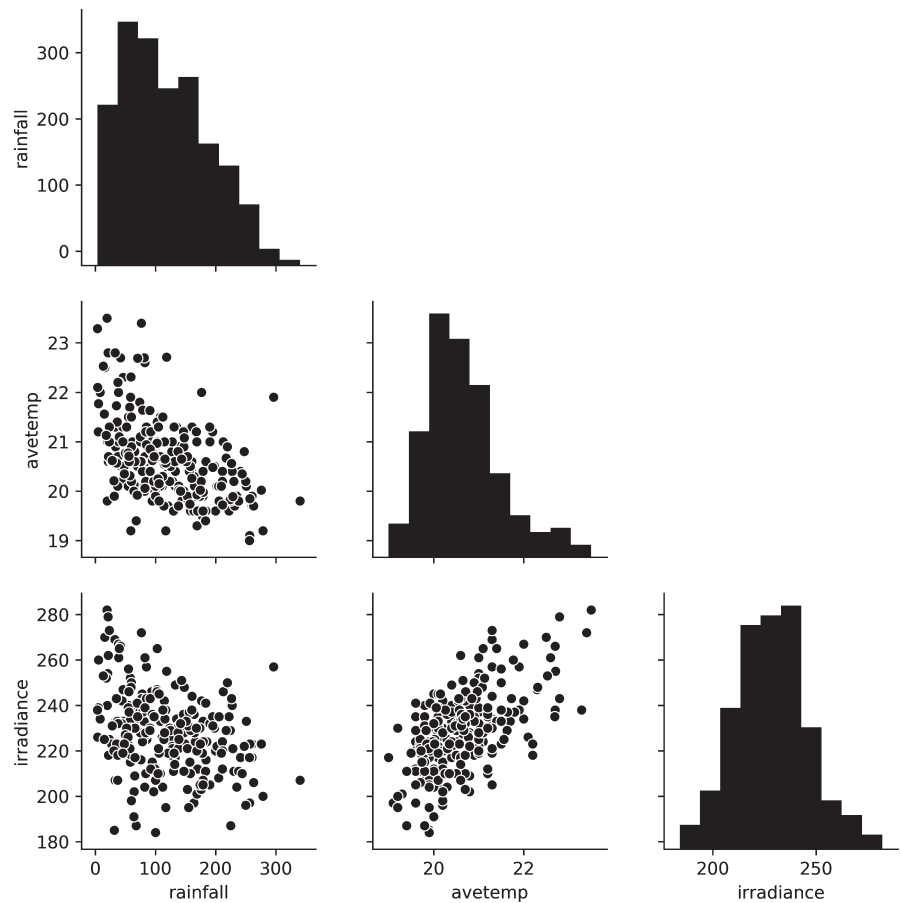


FIGURE 2 Boxplot of monthly proportion of trees bearing fruit. Each box ranges from 25th to 75th percentiles, with medians indicated by black lines within boxes. Whiskers on each extreme of each plot represent values within 1.5× the interquartile range

2008, when monthly productivity leveled off, followed by a slight decline (Figure 3).

3.3 | Factors affecting ripe fruit production

Of all our candidate models, the model containing only the smooth terms plus the intercept, AR1, and the repeated measures control

received by far the highest level of support via Akaike's weights (Table 1). Thus, this model seems to optimize the balance between a high log-likelihood of the fitted function and a small number of parameters. The only alternative model receiving strong support ($\Delta AIC_c = 1.19$) included average temperature as a predictor, though AIC weight for this model was substantially lower than that of the top-ranked model and adding the temperature covariate increased the explained deviance by just 0.47% (61.77% vs. 62.24%). Model averaging showed fruit production to be a negative function of temperature (model averaged estimate = -1.095 , 95% CI: -1.910 , -0.282 , $p = .007$). Estimates of the other two parametric features in the model set were relatively small, with wide confidence intervals that included zero (rainfall estimate = -9.4×10^{-4} , 95% CI: -0.0091 , 0.0072 ; irradiance estimate = -0.0003 , 95% CI: -0.0384 , 0.0378).

Retaining the long- and short-term trend functions in each model allowed us to assess the independent strength of these terms with regard to explaining fluctuations fruit production. The multi-model averaged inter-annual and intra-annual smooth functions reflected both the long-term increase shown in Figure 3 and the cyclic nature of the dataset (Figure 4). The inter-annual smooth curve reflects the long-term increase in the proportion of stems fruiting up to the early 2008 period, after which the function declines for the remainder of the study. The intra-annual curve shows that fruit production generally increased from February to November and declined from December to February and that

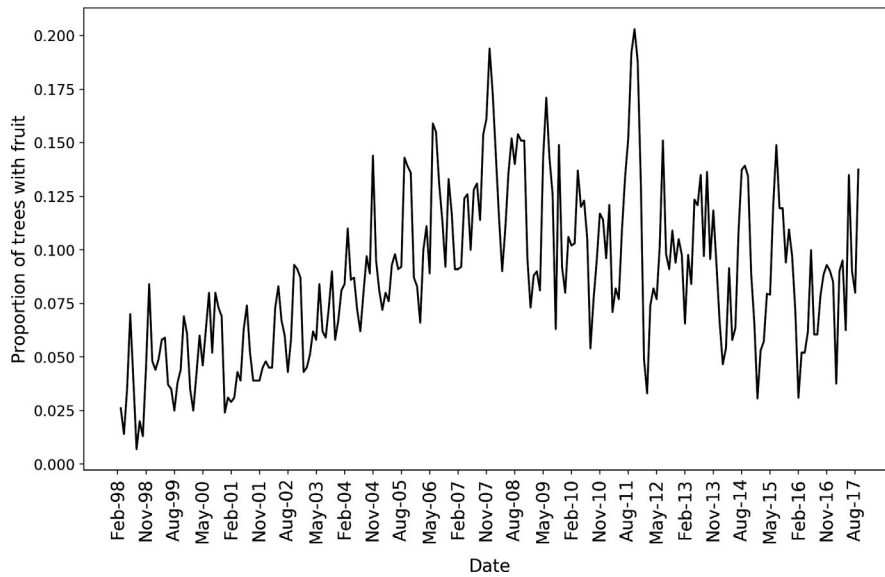


FIGURE 3 Time series of monthly proportion of trees bearing ripe fruit between Feb 1998 and Nov 2017

TABLE 1 Summary of GAM model fit results. Each model was fitted with a term to account for repeated measures and an error term, therefore “# of terms” = predictor terms + 2. “Smooth terms” refers to the intra- and inter-annual smooth functions

Parameters	Log-likelihood	No of parameters	AICc	Delta AIC	AIC weight	Null deviance explained
Smooth terms only	551.525426	5	-1082.7040	0.0000	0.412909	61.77185%
Temperature	553.002522	6	-1081.5167	1.1874	0.228046	62.24319%
Rainfall	552.211668	6	-1079.9350	2.7691	0.103409	61.98963%
Rainfall, temperature	553.967696	7	-1079.2804	3.4236	0.074546	62.54568%
Irradiance	551.794046	6	-1079.0997	3.6043	0.068106	61.85612%
Temperature, irradiance	553.726288	7	-1078.7976	3.9064	0.058558	62.46969%
Rainfall, irradiance	553.434472	7	-1078.2140	4.4901	0.043737	62.37981%
Full model	554.12148	8	-1075.3959	7.3081	0.010688	62.59480%

there were two peaks in production, the first in June–July and the second in November. However, the wide confidence intervals relative to the size of the peaks and troughs of this smooth function suggest that month alone is a poor predictor of fruit production. Of these averaged smooth functions, the inter-annual (date) function (model averaged $\chi^2 = 37.04$, $p < .0001$) was a much stronger predictor of forest community-wide fruit production than was the intra-annual (monthly) function ($\chi^2 = 2.985$, $p = .075$).

3.4 | Fruit production by individual species

Long-term trends in fruit production, as defined by an inter-annual smooth term with $p < .05$, were evident in 17 out of the 20 species included in the phenology sample (Figure 5). Among those species whose fruiting patterns exhibited the strongest inter-annual trends (those with the darkest-shaded plots in Figure 5), most were characterized by increasing trends peaking roughly halfway through the study period, followed by declining trends. This closely aligns with the community-wide trend described above. Important exceptions included *Cordia millenii*, *Pseudospondias microcarpa*, *Pterygota*

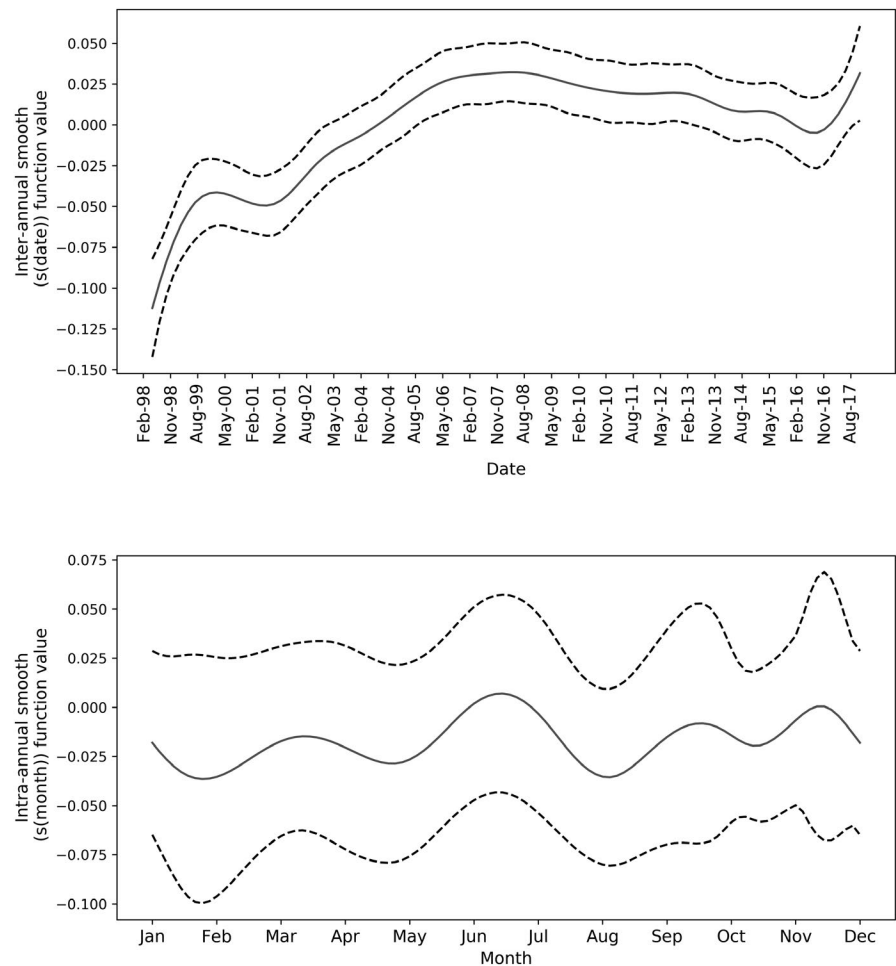
mildbraedii, and *Treculia africana*, all of which displayed generally increasing trends during the study period.

LRT tests revealed that, for 14 of the 20 important chimpanzee food species, including month as a predictor of fruit production significantly increased the likelihood function of the model (Table S1). The exceptions to this regular seasonality included 4 of the 6 fig species (all except *Ficus brachylepis* and *F. dawei*), as well as two non-fig species (*Chrysophyllum albidum* and *Zahna gologensis*).

4 | DISCUSSION

Overall fruit production steadily increased at Ngogo from 1998 until early 2008, at which point this increasing trend slowed, and fruit production has moderately declined since that time. This trend was mirrored at the species level by a majority of species included in the sample. Certain notable exceptions to this trend occurred, however. For example, the figs (*Ficus* spp.) in our sample, while generally conforming to a declining trend in the second half of the study, exhibited relatively weak inter-annual fruiting trends overall (Figure 5). This is consistent with evidence suggesting that the close fig–pollinator

FIGURE 4 Value of the inter-annual (upper figure) and intra-annual (lower figure) smooth functions. Solid lines are model averaged smooth function estimates, and dashed lines indicate the 95% credible region



coevolutionary relationship constrains reproduction and recruitment in fig species (Harrison 2005), thereby potentially moderating inter-annual fluctuations in fruit production. The fact that there was a general decline in fig productivity in the second half of the study (albeit a relatively weak one) is potentially indicative of a transitional period in the succession of the forest at Ngogo. Figs are frequently fast-growing, light-demanding pioneer species capable of exploiting large gaps in the canopy (Janzen 1979, Albrecht, Stallard, & Kalko, 2017), such as those that would have been created by humans occupying regions of Ngogo prior to Kibale being gazetted as a Crown Forest in 1932 (Struhsaker, 1997). It is therefore possible that the generally declining productivity of figs in the second half of this study is, at least in part, a reflection of the age of the individuals included in phenology sampling. For example, although large, fully mature *F. mucuso* individuals are abundant at Ngogo, seedlings and saplings of this species are extremely rare (Mitani et al., 2000; Potts & Lwanga, 2014), suggesting low recruitment of this species. If the *F. mucuso* sample in this study was dominated by particularly old individuals, perhaps the effects of senescence (c.f. Albrecht et al., 2017) were evident later in the study and contributed to the noted decline in productivity. The extent to which natural forest succession is impacting fruit production trends at Ngogo, and thereby indirectly impacting the feeding ecology of frugivores, is an important area of future inquiry.

Our results resemble those from a similar analysis of long-term data from Kanyawara (Chapman et al., 2018), but notable contrasts between the two sets of results also exist. Chapman *et al.* (ibid.) also found a secular increase in overall fruit production during a time period that largely corresponded to that covered at Ngogo (1998–2013) and that confirmed results of an earlier analysis of phenology data from multiple Kibale sites, including Kanyawara (Chapman et al., 2005). As at Ngogo, variation in rainfall was not significantly associated with variation in fruit production (Chapman et al., 2018). However, there were important differences between the two studies' findings. Perhaps most notably, Chapman et al. (ibid.) found that fruit production was a positive function of solar radiation at Kanyawara. In striking contrast, irradiance was not a strong independent predictor of fruit production at Ngogo, where increasing production from 1998 to 2008 was accompanied by a steady *decrease* in irradiance, something that has been continuous since the onset of the study. In another striking contrast, fruit production was significantly associated with temperature at Ngogo, but not at Kanyawara.

These differences between two areas in the same contiguous forest that are just 10 km apart could have resulted partly from the inexact temporal overlap in data collection. Also, Chapman *et al.*'s (ibid.) species list overlapped with ours, but was not identical, and the mean number of stems per species in their sample (7.6; range 1–13) was less than half that in ours, implying that some of the difference could have

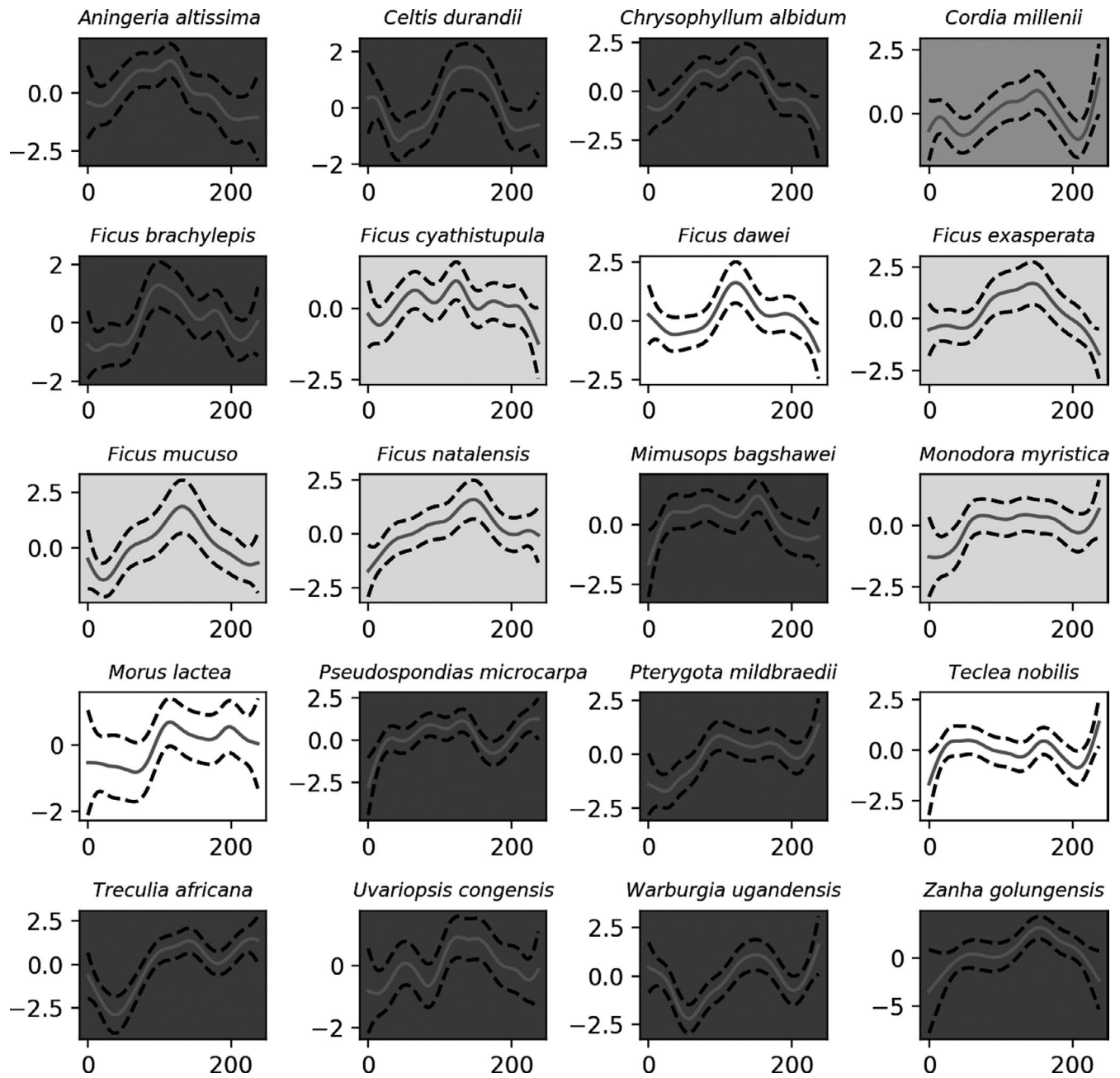


FIGURE 5 Inter-annual smooth term functions with 95% credible regions for each of the 20 most important chimpanzee food resources included on the phenology trail. Interior plot shading corresponds to the log-likelihood value of the fitted model, with darker shades indicating stronger fit (species with unshaded plots had smooth terms with p values $> .05$). Y-axes represent smooth function values, x-axes show time since onset of the study

resulted from sampling error. However, previous comparisons of shorter-term data from multiple sites in Kibale (Chapman et al., 2005, 1999) already indicated that important phenological variation can occur over short distances, and our further documentation of such variation reinforces this argument. Likewise, Kibale data highlight the importance of sampling multiple sites (*ibid.*) and urge caution with regard to taking a single site as representative of an entire habitat, especially one that, like Kibale, is characterized by gradients of altitude, rainfall, and temperature, considerable topographical variation, and wide contrasts in histories of anthropogenic disturbance (Struhsaker, 1997).

The upward trends in productivity over time documented at Ngogo from 1998 to 2008 and at Kanyawara from 1998–2013 were not unique. Polansky and Boesch (2013) found a similar long-term pattern from Taï National Park in Côte d'Ivoire. More generally, in several decades leading up to the early 2000s, there had been a trend toward increasing net primary productivity in the tropics (Nemani et al., 2003, but see Babweteera et al., 2018), due in large part to decreasing cloud cover and concomitant increases in solar radiation (Wild et al., 2005). Increased fruit production despite decreased irradiance, as found at Ngogo, is paradoxical, because increasing

irradiance reduces light limitation on plant reproduction. However, any resulting enhancement in productivity as a consequence of increased irradiance can be negated if the accompanying decrease in cloud cover results in enough reduction in rainfall (Malhi & Wright, 2004) or increase in temperature (Potter, Klooster, & Brooks, 1999). Such effects could help account for the variability in, for example, responses of tropical forests to El Niño-induced increases in irradiance. While productivity is generally high during these periods (van Schaik 1986, Curran et al., 1999, Wright and Calderón 2006, Chapman et al., 2018), extreme El Niño events can produce drought conditions (Wright, Carrasco, Calderon, & Paton, 1999) and result in increased tree mortality rates (Condit, Hubbell, & Foster, 1995).

We suggest that a similar, though less extreme, relationship holds at Ngogo. Our multivariate models indicate that the long-term increasing trend in fruit production over much of the course of the study was probably most strongly influenced by a corresponding long-term decrease in average temperature, rather than by the decrease in irradiance. The relationship with temperature supports previous findings from the Neotropics (Morellato et al., 2000) and elsewhere in the Paleotropics (Gabon: Tutin & Fernandez, 1993, Uganda: Chapman et al., 1999; though see Corlett & LaFrankie, 1998). The apparent lack of an independent relationship between fruit production and irradiance is in stark contrast to the strong importance of solar radiation for the timing of plant phenophases demonstrated in studies at multiple other sites in the humid tropics (Chapman et al., 2018; Hamann, 2004; Stevenson, 2004; White, 1994; Wright & van Schaik, 1994; Zimmerman, Wright, Calderón, Aponte Pagan, & Paton, 2007). If it is true that temperature constrains fruiting at Ngogo more than either rainfall or irradiance do, and if unusually high temperatures reduce the ability of trees to produce ripe fruit, then irradiance levels may be sufficiently high during most of the year to promote fruiting, whereas temperature increases during months of especially high irradiance may result in conditions unsuitable for reproduction. If irradiance only impacts fruiting at Ngogo in extreme cases and this impact is simultaneously mediated by increases in temperature, this would help to explain the lack of an independent relationship between irradiance and fruiting. To fully substantiate these claims, we plan to conduct a robust analysis of the role of ENSO in driving phenology patterns at Ngogo. This will furthermore allow for a more direct comparison with the results of Chapman et al. (2018), who found a strong relationship between the El Niño Southern Oscillation (ENSO) index and ripe fruit production at Kanyawara.

Unlike the long-term trend in fruit production, seasonal (monthly) trends were only moderately evident in our time series. This relative lack of regular monthly periodicity is surprising, given the extent of seasonality documented at other comparable sites (see Sakai 2001 for a review of temporal trends across sites). This is, however, consistent with previous findings at Ngogo. For example, using a different dataset, Chapman et al. (1999) found that fruiting patterns at Ngogo from 1990 to 1996 were irregular and lacked discernible peaks, especially in comparison to Kanyawara (cf. Chapman et al., 2018). More recently, Watts et al. (2012b)

found that temporal variability in fruit production was higher within than among months, and the timing of fruit production was inconsistent across years. Taken together, these findings suggest a resource base for frugivores that experiences relatively muted and unpredictable short-term fluctuations. Nevertheless, most of the individual species monitored on the phenology trail showed significantly stronger likelihood functions when month was included as a predictor variable than when it was excluded. This suggests that the few species for which this was not the case play a critical role in reducing the overall fruiting seasonality of the forest community. Besides the irregularly reproducing figs (e.g., *Ficus mucuso*), these species notably included *Chrysophyllum albidum* and *Zahna golungensis*, both of which produce fruit on a supra-annual timescale. *Chrysophyllum albidum*, in particular, produces little to no fruit in most months, but every few years (in an unpredictable manner) produces extremely large crops of fruit synchronously among individuals (Potts et al., 2009; Watts et al., 2012a).

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gf1vhhmk8> (Potts, Watts, Langergraber, and Mitani 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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